The Ecology of the Viburnum Whitefly, *Aleurotrachelus jelinekii* (Frauenf.).

by

Patricia Mary Reader B.Sc.

A thesis submitted for the Degree of Doctor of Philosophy of the University of London.

Department of Zoology and Applied Entomology

Imperial College at Silwood Park

Ascot

Berkshire

April 1981



ABSTRACT

A long term study on the Viburnum whitefly, Aleurotrachelus jelinekii (Frauenf.) was begun in 1962. This is an introduced species to Britain, originally from the Mediterranean, with southern England representing the northern edge of its range. Previously, (Southwood & Reader, 1976), it had been shown that the major controlling factors for the population on the bushes at Silwood Park were adult mortality and factors affecting fecundity. Consequently this thesis focuses on the adult stage and examines, in the first place, the effects of such factors as host plant, density and temperature, on the fecundity of the insect, all of which have some influence on the number of eggs produced. The extent of migration is then discussed, with the conclusion that this is not likely to be a major cause of population dilution. Indeed, tests show that this whitefly will not pursue the prolonged flights expected in a migrating insect. The impact of various predators on the whitefly populations was also examined and only one, Conwentzia psociformis, responded numerically to changes in population densities mainly because it is multivoltine; all the other predator species had one generation a year. Finally, the relationship between the host plant and the insect was assessed. Food quality was expressed in amino acid levels found in the leaves both within and between seasons, and it was concluded that a relationship between total levels and egg numbers per leaf could be established. The increased ratio of favourable to unfavourable amino acids in new leaves was linked to the brief egg laying period.

The thesis ends with a comparison of all these components indicating their relative importance and contribution to the population dynamics of this whitefly.

TABLE OF CONTENTS

	PAGE
ABSTRACT	2
CHAPTER 1 INTRODUCTION	11
CHAPTER 2 FECUNDITY	19
2.1 Introduction	19
2.2 Larval conditions	19
2.2.1 Introduction	19
2.2.2 Methods and Results	20
1. Length of larval development	21
a. Aleurotrachelus	21
b. Trialeurodes	23
2. Density during development	25
3. Temperature during development	25
4. Weight of female at emergence	31
2.3 Adult conditions	32
2.3.1 Host Plant	32
1. Effect of leaf age on fecundity	34
2. Seasonal variations in fecundity	35
3. Effect of host plant	36
2.3.2 Density	41
1. Aleurotrachelus	41
2. Trialeurodes	49
2.3.3 Climate	54
Methods and Results	54
2.4 Discussion	57
CHAPTER 3 DISPERSAL	67
3.1 Introduction	67
3.2 Methods	69
3.2.1 Field experiments	69

PAGE

3.2.2 Experimental assessments --- --- 70

3.3 Results --- --- 74

3.3.1 Field experiments --- --- 74

1. Daily totals on sticky traps and trap plants. --- --- 74

2. Climatic effects on the total numbers caught. --- --- 77

3. Dispersal with distance --- --- 77

4. Numbers caught at different heights --- --- 92

5. Sex ratio --- --- 92

6. The influence of population size and density. --- --- 100

3.3.2 The experimental assessment of flight and landing characteristics. --- --- 103

1. Effect of age on flight activity --- --- 103

2. Flight and landing in a flight chamber --- --- 104

a. The duration of flight. --- --- 104

b. The length of individual flights --- --- 107

c. Landing site preference --- --- 110

3.3.3 Dissections --- --- 111

3.4 Discussion --- --- 111

CHAPTER 4 PREDATORS --- --- 117

4.1 Introduction --- --- 117

4.2 Methods and Results --- --- 120

4.2.1 Spiders --- --- 120

4.2.2 Other Predators --- --- 127

4.3 Discussion --- --- 138

PAGE

CHAPTER 5 THE NITROGEN LEVEL IN THE HOST PLANT --- --- 142

5.1 Introduction --- --- 142

5.2 Methods --- --- 142

5.3 Results --- --- 144

5.3.1 Total Amino Acid levels --- --- 144

5.3.2 Individual Amino Acid levels --- --- 152

5.3.3 Seasonal Variation in Amino Acid levels --- --- 152

5.4 Discussion --- --- 161

CHAPTER 6 ADULT POPULATION DYNAMICS

6.1 Introduction --- --- 169

6.2 Methods --- --- 169

6.3 Analysis of natality --- --- 172

CHAPTER 7 GENERAL DISCUSSION --- --- 188

SUMMARY --- --- 196

ACKNOWLEDGEMENTS --- --- 198

REFERENCES --- --- 199

APPENDICES --- --- 217

LIST OF FIGURES

		PAGE
FIGURE 1.1	The study sites at Silwood Park --- ---	13
FIGURE 1.2	Leaves from bushes A and B showing differences in scale of larval populations --- ---	16
FIGURE 2.1	Design of clip cages --- ---	22
FIGURE 2.2	Effect of length of development on the fecundity of *Aleurotrachelus* --- ---	24
FIGURE 2.3	Effect of length of development on the fecundity of *Trialeurodes* --- ---	26
FIGURE 2.4	Effect of larval density on the fecundity of *Trialeurodes* --- ---	28
FIGURE 2.5	Effect of temperature on the fecundity of *Trialeurodes* --- ---	30
FIGURE 2.6	Seasonal variations in fecundity of *Aleurotrachelus*--	38
FIGURE 2.7	Effect of host plant on fecundity of *Aleurotrachelus* --- ---	40
FIGURE 2.8	Effect of density on fecundity of *Aleurotrachelus* --- ---	44
FIGURE 2.9	Relationship between available space for female and eggs laid. --- ---	46
FIGURE 2.10	Relationship between the total eggs per female and the total number laid --- ---	48
FIGURE 2.11	Effect of density on fecundity of *Trialeurodes* on tomatoes --- ---	51
FIGURE 2.12	Effect of density on fecundity of *Trialeurodes* on beans --- ---	51
FIGURE 2.13	Effect of increased space of fecundity of *Trialeurodes* --- ---	53

PAGE

FIGURE 2.14	Daily total of eggs laid by Trialeurodes	--- ---	56
FIGURE 2.15	Effect of temperature on the fecundity of Aleurotrachelus	--- ---	59
FIGURE 2.16	Effect of June temperature on the fecundity of Aleurotrachelus in the field	--- ---	61
FIGURE 3.1	Position of sticky traps round Bush A	--- ---	72
FIGURE 3.2	Daily totals of whitefly caught on the first annulus of traps 1972-1974	--- ---	76
		--- ---	76
FIGURE 3.3	Daily totals reaching the nearest trap plant	--- ---	79
FIGURE 3.4	Numbers of adults caught on each annulus of sticky traps	--- ---	81
FIGURE 3.5	Fit of Hawkes' and Paris' equations to the data from the sticky traps	--- ---	87
FIGURE 3.6	Fit of Hawkes' and Paris' equations from the data from the trap plants	--- ---	90
FIGURE 3.7	Fit of Paris'& Hawkes' models to the mean catches	---	94
FIGURE 3.8	Numbers caught at different heights	--- ---	96
FIGURE 3.9	Relationship between the number of males caught on the sticky traps and adult numbers	--- ---	99
FIGURE 3.10	Percentage of the population caught on each annuli of sticky traps	--- ---	102
FIGURE 3.11	Effect of age on take off by Aleurotrachelus	--- ---	105
FIGURE 3.12	Relationship between length of flight and age of female	--- ---	109
FIGURE 3.13	Decline in aerial density with distance	--- ---	114
FIGURE 4.1	Phenology of Aleurotrachelus and its associated species	--- ---	119
FIGURE 4.2	Number of spiders compared with whitefly density-	---	122

PAGE

FIGURE 4.3 Relationship between number of whitefly trapped and spider numbers. --- --- 124

FIGURE 4.4 Number of whitefly trapped per spider --- --- 126

FIGURE 4.5 Number of whitefly trapped per spider compared with adult density --- --- 129

FIGURE 4.6 Percentage trapped compared with population density --- --- 131

FIGURE 4.7 Relationship between whitefly density and predator species richness --- --- 133

FIGURE 4.8 Seasonal fluctuations in numbers of predator species --- --- 135

FIGURE 4.9 Relationship between total numbers of individual predators and population density --- --- 137

FIGURE 4.10 Relationship between number of coniopterygids and whitefly density --- --- 140

FIGURE 5.1 Seasonal variations in total amino acid levels --- --- 147

FIGURE 5.2 Comparison between number of eggs laid per leaf and amino acid levels --- --- 150

FIGURE 5.3 Individual amino acid levels --- --- 153

FIGURE 5.4 Seasonal variations in amino acid levels --- --- 156

FIGURE 5.5 Seasonal variations in the percentage of individual amino acids --- --- 158

FIGURE 5.6 Seasonal differences in amino acid quality --- --- 163

FIGURE 6.1 Functional response of mirids to Aleurotrachelus --- 174

FIGURE 6.2 k_o and its component values. --- --- 179

FIGURE 6.3 k_o and the corresponding values for quality density and temperature --- --- 184

LIST OF TABLES

		PAGE
TABLE 2.1	Weights of whitefly from Bushes A and B --- ---	31
TABLE 2.2	Numbers of eggs laid on old and young leaves --- ---	34
TABLE 2.3	Numbers of eggs laid on 1 year and older leaves-- ---	34
TABLE 2.4	Survival of 1st and 2nd instar --- ---	35
TABLE 2.5	Significance of host plant on fecundity --- ---	41
TABLE 3.1	Six models for density with distance --- ---	82
TABLE 3.2	Total numbers caught of ten sticky traps during 1968-1976 --- ---	82
TABLE 3.3	Total numbers caught on the trap plants --- ---	83
TABLE 3.4	Fit of the six equations to the data from the sticky traps --- ---	84
TABLE 3.5	Fit of the six equations to the data from the trap plants --- ---	85
TABLE 3.6	Departure from a 50 : 50 sex ratio of adults caught on the sticky traps --- ---	92
TABLE 3.7	Sex ratio of adults from the inner and outer annuli of sticky traps --- ---	97
TABLE 3.8	Sex ratio of adults from the trap plants --- ---	100
TABLE 3.9	Comparison between numbers caught on outer and inner annuli --- ---	103
TABLE 3.10	Population density and percentage of the population caught on trap plants --- ---	103
TABLE 3.11	Flight development time --- ---	104
TABLE 3.12	Flight willingness of 1 day old Aleurotrachelus -- ---	106
TABLE 3.13	Flight willingness of whitefly of different ages-- ---	106
TABLE 3.14	Frequency of individual flights of females --- ---	107
TABLE 3.15	Landing site preference --- ---	110

PAGE

TABLE 3.16	Effects of host plant on landing site preference-- ---	110
TABLE 5.1	Amino acids identified during analysis --- ---	145
TABLE 5.2	Amino acid amounts found in old leaves --- ---	151
TABLE 5.3	Index of amino acid quality --- ---	161
TABLE 6.1	Estimate of adult numbers --- ---	175
TABLE 6.2	k - values for egg loss --- ---	176
TABLE 6.3	Percentage egg loss --- ---	181
TABLE 6.4	Values of k_u --- ---	182
TABLE 6.5	Correlation coefficients of values plotted against k_u --- ---	186
TABLE 7.1	Larval survival on the three bushes --- ---	189

CHAPTER 1 - INTRODUCTION

Long term studies on particular populations have proved very rewarding and are essential for the understanding of animal population dynamics. There are several examples of such studies on insects, the work of Morris (1963) on the spruce budworm, Varley and Gradwell (1968) and Varley Gradwell and Hassell (1973) on the winter moth, Klomp (1968) on the pine looper, Bupalus piniarius and Baltensweiler (1968) on the grey larch Tortrix. All of these have required regular sampling which has allowed life tables to be built up over many years and from which the importance of the processes involved can be first recognised and then categorised (Richards and Southwood 1968). This can lead to the observation of long term patterns in fluctuations of animal numbers e.g. the cycles found in Zeiraphera griseana (Baltensweiler 1968); to the identification of key factors which are responsible for changes in population numbers, (Southwood 1975a);and to the recognition of any density dependent processes.

Of the examples which show interrelationships between host plants and herbivore numbers, some indicate that synchrony between the host and insect is a major mortality factor. Varley and Gradwell (1960, 1968) working on the winter moth at Wytham Wood in England, and Embree (1965) on the same insect in Nova Scotia, emphasized the importance of timing between egg hatch and bud burst if the larvae are to be able to enter the bud and thus find food.

In addition to the availability of food, its quality is also important, McNeill and Southwood (1978) cite several examples of the role of nitrogen levels in plants on phytophagous insects. Latterly the long term study of herbivores on Holcus mollis, by McNeill and colleagues

(mentioned in McNeill and Southwood 1978) has shown the effect of the host plant on individual numbers. Here the spring and autumn peaks of nitrogen result in both greater numbers of individuals and herbivorous species on Holcus mollis at these times. The influences of nitrogen may not necessarily be in the accepted periods of amino acid mobilisation, (i.e. during periods of growth, flowering or senescence) but may occur during periods of stress, resulting in conditions which allow outbreaks of numbers to occur (White 1969, 1974, 1976). These increased populations can also be attained by improving the food quality of the plant with fertiliser. Prestidge (1980) has shown that such fertiliser treatment can result in a four-fold increase in the numbers of leafhoppers between control and experimental sites. These increases in population size are due to a combination of increased productivity and dispersal of individuals from one site to another (Waloff 1980, Waloff and Thompson 1980).

A long term study on the viburnum whitefly, Aleurotrachelus jelinekii (Frauenf.) (Homoptera : Aleyrodidae) was started by T.R.E. Southwood in 1962 at Imperial College at Silwood Park. The study sites are three bushes of Viburnum tinus (Caprifoliaceae) which in 1962 were of similar size and are described in Southwood and Reader (1976) (Figure 1.1).

Bushes A and B occupy similar positions approximately 130m apart. A is situated in a small copse surrounded by Cedrus, Ilex and Rhododendron. B is slightly more exposed since some Rhododendrons were removed from the east side, and is surrounded by Cedrus, Buxus and Rhododendron.

Bush C is in a more shaded position in beech woodland and is likely to compete with the surrounding Fagus and Rhododendron for light, nutrients and water. Over the past four years, increased pressure from

FIGURE 1.1 The study sites at Silwood Park.



A



B



C

the surrounding trees and shrubs has caused the leaf numbers to drop, and it seems unlikely that this bush can survive long under the present conditions.

The relative densities of the fourth instar larvae in 1964 were 12, 1.5 and 1 on bushes A, B and C respectively, with Bush C taken as unity. This ratio continued in the same pattern over several years gradually becoming exaggerated until by 1974 the following ratio had been achieved. 491, A; 9, B; and 0.7, C. (see Figure 1.2). Using key factor analysis, (Varley and Gradwell, 1960; Podoler and Rogers, 1975), Southwood and Reader (1976) found that the key factor on all bushes was the failure of adult females to lay the maximum complement of eggs and or adult mortality.

The aim of this thesis is to dissect this key factor. In so doing it is hoped to identify those aspects that have the greatest influence on the population dynamics of this insect, and that account for the different population densities on the three bushes.

The aleyrodids cover a wide spectrum of associations between insects and their host plants from those which can be regarded as 'opportunist insects with transient populations' (Mound and Halsey 1978) to those whose life cycle mirrors that of their host plant. Trialeurodes vaporariorum (Westwood) the greenhouse whitefly, is an example of the former group. It is polyphagous, and although found on a large number of host plants, which are representatives of many families, these are usually soft leaved with few hairs. An introduced tropical species, it is found mainly in greenhouses where it is often a pest due to the suitable environment, causing mainly cosmetic damage by covering the crop plant with honey dew on which sooty moulds can develop.

FIGURE 1.2 Leaves from bushes A and B showing differences in scale of larval populations.



The viburnum whitefly, although found on Arbutus unedo and other hard leaved evergreen Ericaceae, lives principally in large numbers on Viburnum tinus. Aleurotrachelus is essentially a Mediterranean species first reported in Britain in 1940, and southern England represents the northern edge of its range. It has one generation a year. The first adults emerge towards the end of May in synchrony with the onset of new growth in the host plant. The numbers begin to decline in early July and the population has completely crashed by the end of August. The males usually appear a few days before the females and a peak in the total population is reached one to two weeks after the first emergence.

The adults are found mainly on the undersides of the leaves, and it is here that the eggs are laid. Like all aleyrodids the first instar is mobile, which serves to redistribute insects on the leaf, rather than allowing plant to plant or even leaf to leaf, migration. Found from July onwards, the first instar moults after two to three weeks to the black stationary second instar. The insect overwinters as the 4th instar. It seems likely that feeding takes place throughout the year, and that the stylets remain inserted throughout larval development, possibly only being removed during moults. Food in the form of plant sap is taken through the stylets which penetrate the phloem vessels (Pollard 1955, 1971).

The viburnum whitefly is therefore an ideal experimental animal, since its life history enables censuses to be easily obtained on populations which are relatively isolated from one another. In addition, because of the large proportion of the population sampled, sampling error is reduced. Particular cohorts can be followed and because the larval remains stay on the leaf the causes of mortality can be readily

identified (Figure 1.2).

This thesis has been organised into chapters assessing the role of fecundity, migration and predation on the adults and their potential progeny. The impact on fecundity of the host plant through the nitrogen supply received by the insect is also discussed. In addition, and where applicable, the results from Aleurotrachelus will be compared with those from the greenhouse whitefly which represents a very different life history strategy.

CHAPTER 2 - FECUNDITY

2.1 INTRODUCTION

Fluctuations in fecundity may be one of the regulating mechanisms in a population, if on a sufficient scale and if proven to be density dependent. There are several examples in the literature where it is, at least, a significant part of the key factor (cited in Southwood 1975a). There are also several known examples where fecundity has been shown to be density dependent (Watt 1960). Influences throughout the life history of a female can affect fecundity, since the quality (in terms of size and potential egg number) of a female is a result of her larval development; egg production may also be affected by conditions which surround the adult, such as the state of the host plant, population density and climate.

This chapter deals with factors which influence these stages in Aleurotrachelus and, for comparison, in Trialeurodes. It has particular importance since the evidence of Southwood and Reader (1976) suggests that variations in fecundity of Aleurotrachelus are one of the main variables in the life table, and may partially account for the different population levels on bushes A, B and C.

2.2 LARVAL CONDITIONS

2.2.1 Introduction

The impact of larval conditions on fecundity appears to be less well documented than those influencing adult females, with shortage of food being the most likely factor to depress, subsequently, adult fecundity. This can act in two ways. (1) By altering the larval developmental rate so that a univoltine species may be out of synchrony with the host plant

at the most favourable time for egg laying or, in a multivoltine species the maximum potential number of generations may be reduced. (2) By causing a reduction in weight of the adult female resulting in fewer eggs. Iheaghwam (1974), working with the cabbage whitefly, found some correlation between weight and fecundity, and Dixon (1966) noticed weight changes in the sycamore aphid with differences in nutritive status.

The most obvious mechanism underlying food shortage is larval crowding in relation to the amount of food available, but here conflicting evidence is found. Clark (1963a)working with Cardiaspina albitextura could see no effect of crowding during larval development on the subsequent number of eggs laid even when their density was sufficient to cause damage to the leaves. Hodjat (1968), on the other hand, showed the reverse effect with Dysdercus fasciatus.

To explore the effects of larval development on the fecundity of the subsequent females, experiments were carried out to observe the influence of length of larval development, density, temperature and weight of adult.

2.2.2 Methods and Results

The long life history of Aleurotrachelus caused considerable difficulty in rearing insects on potted plants, since the nutritive status of the plant could not be maintained over the necessary period. Because of this, manipulation of larval conditions proved impossible, and only situations found in the field were observed. The shorter life cycle and more polyphagous habit of the greenhouse whitefly enables it to be easily cultured, making experiments much easier.

The influence of the following on fecundity was tested:

1) length of larval development,

2) density during development,

3) temperature during development and

4) the weight of the female at emergence.

1) Length of Larval Development

a) Aleurotrachelus: The fecundity and longevity of females was compared between adults emerging at the start of the season with the onset of leaf growth, and those emerging last of all (approximately 11 days later). These and all subsequent experiments on fecundity were carried out in a similar way.

Cages were constructed as in Figure 2.1 from plastic hair rollers approximately 1.5 cm in diameter and from metal hair clips. The sides were covered with muslin to allow ventilation and the tops with cellulose acetate to facilitate counting, a rim of foam rubber was placed between the leaf and the cage to prevent damage to the leaf surface. For field experiments the roof was replaced with one of nylon which still allowed vision but which prevented the formation of condensation on which the insects' wings stuck.

Because of the evidence of Dalmat (1950), Ribbands (1950) and Simpson (1954) which suggested that some anaesthetics could cause premature ageing of insects, it was originally decided to move insects mechanically by means of a fine brush. This method, however, not only damaged the insects but also made sexing difficult as the ventral surface was not easily displayed. Some form of anaesthetic was clearly necessary and carbon dioxide proved the most suitable. It was given to insects either from a pressurised cylinder or from a Sparklets$^{(C)}$ CO_2 cork remover. The latter was most efficient, as the amount of gas could be easily regulated, and the size of the container made it practical for work both in the laboratory and in the field.

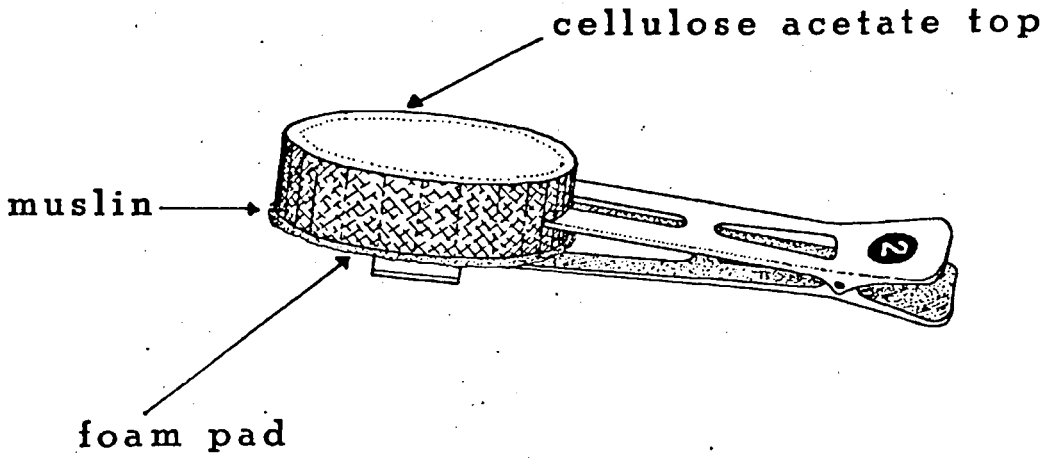


FIGURE 2.1

Design of cages used in fecundity experiments.

Newly emerged adults were used for all experiments. The adults usually emerge in the morning and are easily distinguished from older insects by their wings which do not have the brilliant waxy white colour achieved after the first day of life. Females tend, on the whole, to be larger than males but, to be confident of their sex, whiteflies were removed from the plant by placing a tube over them and tapping gently. This caused the insects to jump into the tube, where they could be sexed, anaesthetised and placed in a cage.

The cages were examined daily and removed when all adults were dead. No significant difference had been noted in the longevity of males and females.

After the cages were removed the dead females were preserved and later dissected to obtain an estimate of the number of mature eggs retained at death. As the mean number per female never exceeded 1.5 these results have not been included.

The comparison between fecundity and longevity of female Aleurotrachelus which emerged at the beginning and end of the season can be seen in Figure 2.2., the respective t - values for fecundity and longevity were 1.37 and 0.62 (not significant). It therefore seems likely that any differences in development time obtained are insufficient to show any effect on fecundity.

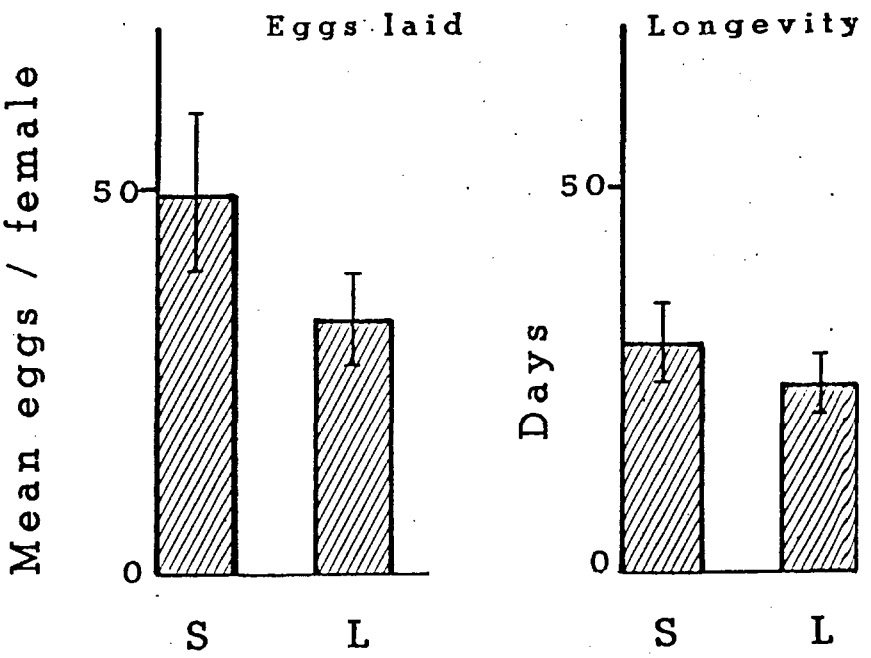
b) Trialeurodes: For comparison a similar experiment was carried out on the greenhouse whitefly. These were cultured in a greenhouse on tomato plants (variety Money-cross) and for experiments plants of the same variety approximately 20 cm high were used. These were potted in John Innes 2 potting compost.

To assess the effect of developmental period eggs of a similar age, but reared at 15°, 20°, and 25°C were allowed to develop. These

FIGURE 2.2 The effect of length of development on the fecundity of Aleurotrachelus. (±S.E.)

S - Adults emerging at the beginning of the season

L - Adults emerging at the end of the season



emerged over a period and the fecundity and longevity of females resulting was measured. The variations at these three temperatures can be seen in Figure 2.3., and on no occasion was a significant difference found between the means.

2) Density during Development

While it was not possible to manipulate larval densities in Aleurotrachelus, larvae of Trialeurodes were reared on tomato plants at 20°C from eggs which had been laid over a period of three days. These achieved the following densities of pupae/cm^2; 9.1, 7.3, 6.3, 4.7 and 3.3. Ten pairs from each density were tested for fecundity and longevity and the results are expressed in Figure 2.4. An analysis of variance proved insignificant for both fecundity and longevity ($F = 0.32$ and 1.23 respectively) and no correlation between density of pupae and eggs laid ($r = 0.10$), under these conditions, could be found.

3) Temperature during Development

No experiments on the effects of temperature on larval development and subsequent fecundity were undertaken with Aleurotrachelus. Using Trialeurodes, the effect of temperature was tested by allowing eggs to develop on potted plants at 15°, 20° and 25°C. The resulting offspring were tested for fecundity and longevity at the temperature of development and at differing adult temperatures. The results are shown in Figure 2.5. Neither fecundity nor longevity varied significantly when insects were kept at 15°C regardless of their origin (Figure 2.5 ●-F = 0.50 (ns) O-F = 2.62 (ns)). Insects reared at 25°C and kept at different temperatures showed no variation in fecundity (Figure 2.5 C-F= 0.30 (ns)) whereas their longevity did differ significantly (F-F = 11.21 ($P < 0.01$)). Insects reared at a lower temperature laid less eggs and had shorter lives when kept at 25°C than those reared at 25°C

FIGURE 2.3 The effect of length of developmental period on the fecundity of Trialeurodes. (±S.E.)

S - Short developmental period
L - Long developmental period

(reared and kept at the temperatures stated)

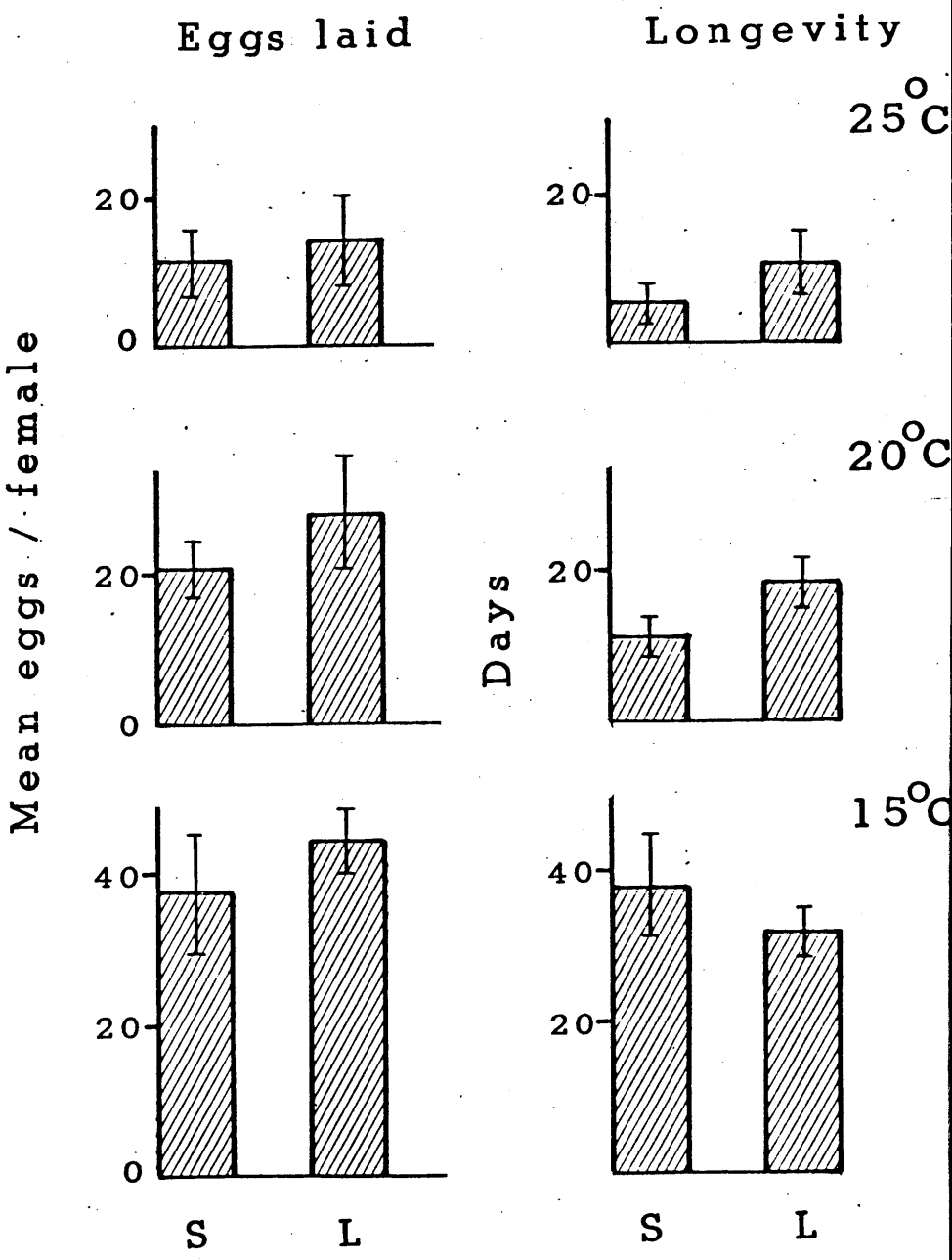


FIGURE 2.4

The effect of larval density on the fecundity of *Trialeurodes*.

FIGURE 2.4

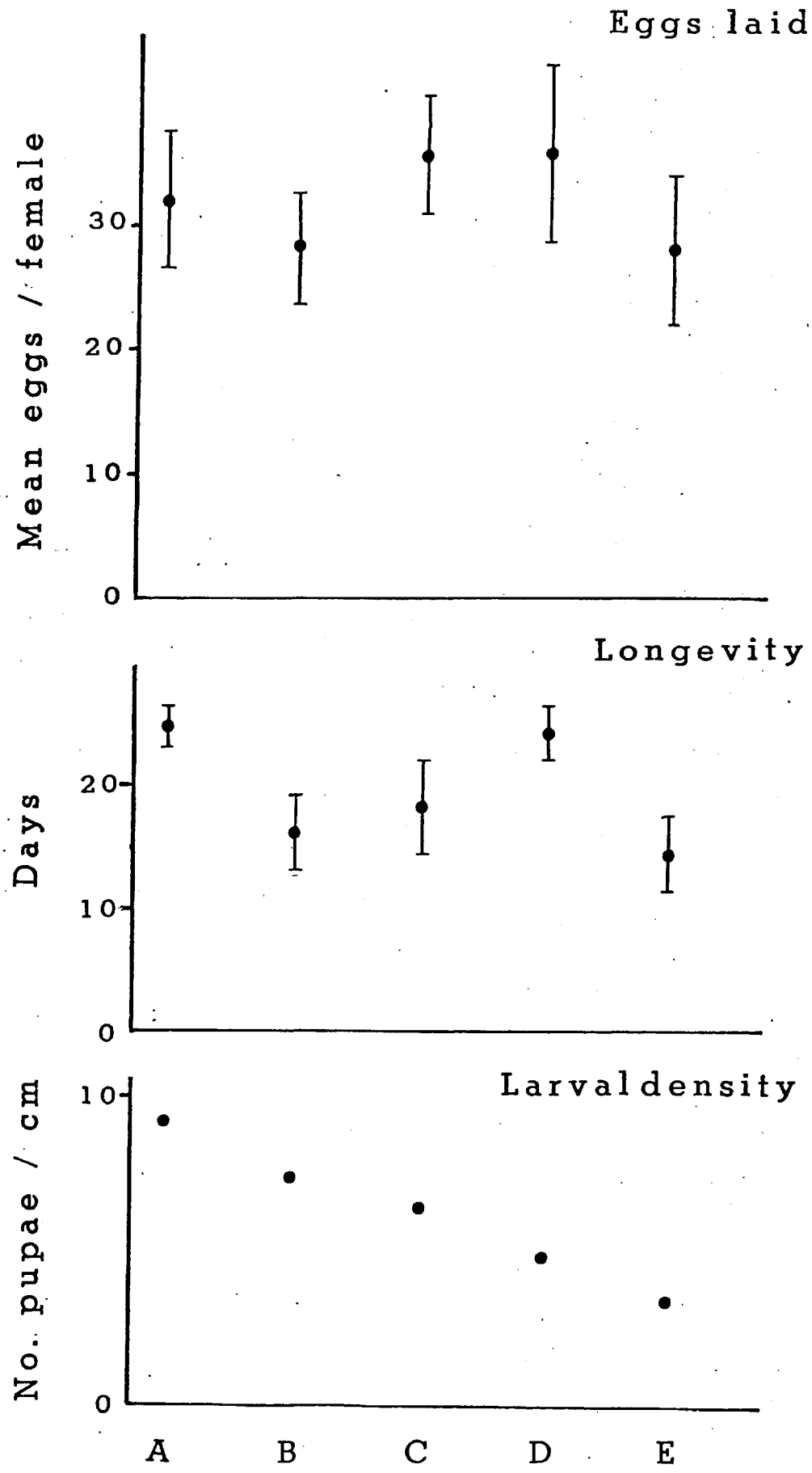
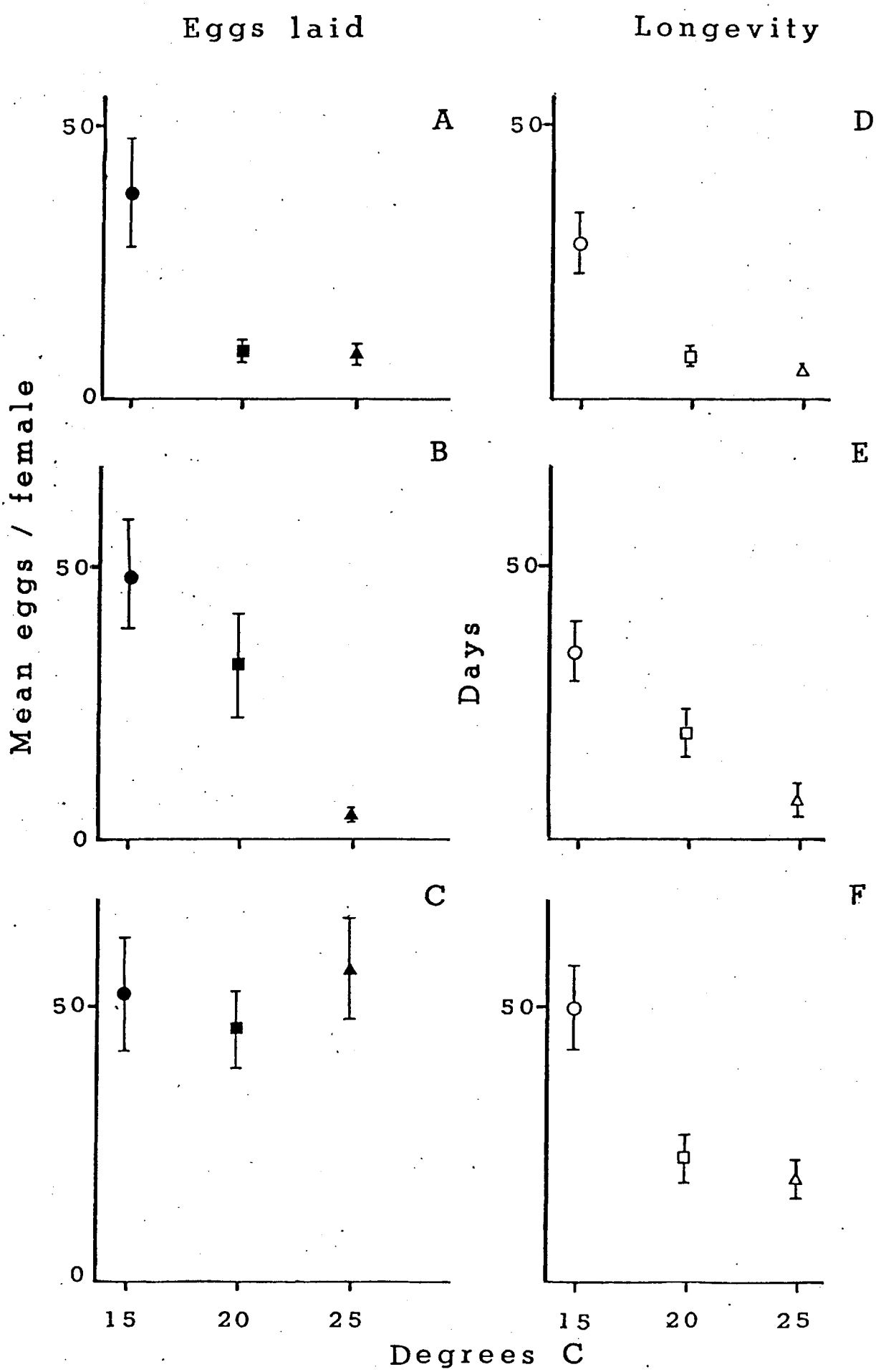

Eggs laid
Mean eggs / female
30
20
10
0
Longevity
Days
20
10
0
Larval density
No. pupae / cm
10
0
A
B
C
D
E

FIGURE 2.5 Effect of temperature during development on the fecundity of Trialeurodes

●	o	kept at 15°C
■	□	kept at 20°C
▲	△	kept at 25°C
A	D	reared at 15°C
B	E	reared at 20°C
C	F	reared at 25°C

FIGURE 2.5


Eggs laid
Longevity
A
B
C
D
E
F
50
0
Mean eggs / female
Days
15
20
25
Degrees C

(▲ - F = 29.25 ($P < 0.01$) Δ - F = 16.65 ($P < 0.01$)), whiteflies kept at 20° and reared at 20° or 25° showed no difference in fecundity (t = 1.18 (ns)), whereas significant differences were found between insects kept at 20°C but reared at 25° and 20° or 15°C (t = 4.75 ($P < 0.001$) t = 2.23 ($P < 0.05$)). Insects reared at any temperature appeared to be able to lay similar numbers of eggs at 15°C, whereas insects reared at 20° only laid a greater number at 20° and 25°C, and those reared at 25°C produced the maximum number at this temperature. Whiteflies reared and kept at the same temperature showed a tendency for more eggs to be laid at 25°C.

4) Weight of Female at Emergence

The weights of adult Aleurotrachelus were compared during two years. On both occasions and on both bushes A and B the differences between male and female weights were significant. (See Table 2.1.)

TABLE 2.1 Weights of male and female whitefly from Bushes A and B t tests all significant at the 1% level. (± S.E.).

Year	Wts.(mg.)				t	
	A		B		A	B
	♀	♂	♀	♂		
1971	0.961 ± 0.022	0.547 ± 0.010	0.901 ± 0.020	0.521 ± 0.015	17.42	15.51
1972	0.925 ± 0.016	0.476 ± 0.011	0.853 ± 0.024	0.457 ± 0.015	23.37	11.24

The differences between female weight on the two bushes A and B were not significant (1971, t = 2.08; 1972, t = 2.49;), and size was therefore not thought to contribute to variations in fecundity and hence to the large population differences between the two bushes.

A trial experiment was carried out with Trialeurodes in which newly emerged adult females were weighed on a Caln electro microbalance

before being caged on tomato plants at 20°C. No correlation between weight and fecundity (r = 0.18) was found.

2.3 ADULT CONDITIONS

The need for feeding before the maturation of the ovaries appears to vary considerably amongst insects, but there seems to be less variation within the aleyrodids. El Khidir (1963) working with the cabbage whitefly, Aleyrodes brassicae (Wlk.) noticed that the ovaries of the emergent female are immature, and that the eggs begin to mature during the first day of adult life. I have observed the same in Aleurotrachelus and Trialeurodes,

The choice of oviposition sites and the fertilisation of the females occupy the next period of development. The former can be linked with migration and will be discussed later. Mating is not a prerequisite for egg-laying in aleyrodids and much work has been carried out on the ability of virgin greenhouse whitefly to produce fertile eggs, leading to the splitting of the species into two races, with the American race producing males (Morrill 1903) and the English race developing into females (Hargreaves 1914). It is not known which sex unfertilised females of Aleurotrachelus produce, but both Thomsen (1925,1927) and Butler (1938) showed that unfertilised eggs of the cabbage whitefly produced haploid males. In this section the effect of the host plant (including its leaf age and variations between seasons and individuals), density of adults and climate are considered.

2.3.1 Host Plant

Van Boxtel et al (1978) showed that the larval food plant of the female greenhouse whitefly played a significant role in its fecundity and lifespan. In fact, Trialeurodes is found on a wide variety of plants. Russell (1963) lists some 206 species of 143 genera, which vary in

suitability from Lantana canera on which the survival rate was 90.48%, to Strelitzia reginae on which mortality was complete (Vitarana 1977). Aleurotrachelus is found on several evergreen species of Viburnum and on a limited number of unrelated evergreen shrubs, but is selective and does not colonise seemingly acceptable adjacent shrubs.

The age of leaf colonised varies with different species and their nutritive requirements. The majority of whitefly studied have shown a decrease in the number of eggs laid with leaf age (e.g. Hussey and Gurney (1960) working on Trialeurodes vaporariorum, Iheagwam (1974) on Aleyrodes proletella and Trehan (1944) on Bemisia tabaci). Other insects show different responses. Bernays et al (1975) observed that the survival of Locusta migratoria migratoriodes on seedling grasses was less than on mature plants. The aphid Brevicoryne brassicae, however, is less fecund on old leaves, whereas Myzus persicae shows the converse (van Emden 1969). The nutritive quality of leaves of the same plant is not always consistent. As Wratton (1974) has shown in birch some leaves can be out of phase, allowing, at any one time, the more favourable leaves to be exploited. In the sycamore aphid (Dixon 1966), the reproductive rate decreases during times of poor nutritive quality and when these coincide with periods of high density, reproduction ceases.

To assess the impact of the host plant on the fecundity of whitefly and to see if in turn this would account for different population levels on bushes A, B and C three experiments were carried out:

1. The fecundity on old and new leaves was compared.
2. The level of fecundity on each bush was estimated over a period of years to give a 'potential' fecundity for females in that particular year.
3. The effect of host plant quality was assessed.

Methods and Results

1. Effect of Leaf Age on Fecundity

10 pairs of newly emerged adults were set up (as described on P. 23) on each of three leaf types - newly emerged, 1 year old and, in 1969 and 1970, leaves of more than 2 years old. The numbers of eggs laid and the longevity of adults from these experiments are shown in Tables 2.2 and 2.3.

TABLE 2.2 Comparison between numbers of eggs laid on new and 1 year old leaves on Bush A. (± S.E.)

*** P < 0.001 ** P < 0.01

leaf type	$\bar{x}$ eggs/♀			longevity		
	old	new	t	old	new	t
1968	0.0	14.6±4.24	-	2.2±0.13	8.6 ± 1.54	4.15***
1969	5.8±2.60	67.6±13.90	4.61***	6.0±1.78	24.6 ± 3.80	3.58**
1970	16.1±6.55	110.9±16.41	5.37***	8.5±2.85	26.4 ± 5.03	3.09**
1971	10.8±2.62	66.4±7.67	5.91***	16.2±1.23	33.4 ± 2.59	5.24***

It is apparent from these data that not only do whitefly live longer on young leaves, but they also lay substantially more eggs.

TABLE 2.3 Comparison between numbers of eggs laid on 1 year old and older leaves, all t values not significant. (± S.E.)

leaf age	$\bar{x}$ eggs/♀			longevity		
	1 yr	2 yrs +	t	1 yr	2 yrs +	t
1969	5.8±2.60	3.0±1.22	0.97	6.0±1.28	4.0±0.47	1.08
1970	26.8±11.54	5.4±1.63	1.84	11.6±5.63	5.4±0.27	1.15

It appears that new leaves are the preferred site for egg laying and that, although some eggs are laid on old leaves, these are significantly fewer than on new ones. All categories of old leaves showed

similar results. This confirms the observed pattern on the bush where adult females emerge on old leaves and may lay some eggs there before moving to the more favourable new leaves.

When the fate of eggs on old and young leaves is examined, survival levels are found to be comparable (Table 2.4) $\chi^2 = 5.90$ (n.s.).

TABLE 2.4 % of 1st and 2nd instar on labelled leaves surviving to living 4th instar (i.e. just prior to adult emergence).

Year	% reaching 4th instar in May	
	old leaves	new leaves
1970/71	23.4	13.6
71/72	36.0	22.6
72/73	30.4	22.8
73/74	20.9	38.2
$\bar{x} \pm s.e$	27.68 ± 3.43	24.30 ± 5.11

These categories were chosen because they are most readily identified on old leaves. Further analyses of larval mortality will appear at a later date.

Thus, although actual survival does not differ, the number of eggs laid per leaf is far greater on new leaves. There could be three reasons for this. First, and probably most important, the new leaves have high nitrogen levels at this time and provide the female with a greater potential for increased fecundity than on old leaves. Secondly, old leaves are much tougher than new ones and it may be more difficult for the eggs to be fixed on the leaves, and thirdly space is limited on old leaves by the previous years' larval remains.

2. Seasonal Variations in Fecundity

During the period 1968 - 1976 the fecundity of female whitefly

was estimated for each season on all three bushes. These data can be seen in Figure 2.6, where considerable variation between years occurs on all three bushes. A trend can be observed, however, in which a build up from low to high fecundities occurs in the first three years, after which the potential fecundity fluctuates around a mean. This mean (shown in Figure 2.6) consists of data from 1971 onwards (i.e. after the peak in fecundity) and is used to provide an average level of abundance. Although throughout the whole period the fecundity of A is significantly higher than B ($t = 3.68$ $P < 0.001$), during the period of greater stability the potential fecundity of A is not significantly greater than that of the other bushes. This will be considered later in regard to the different population levels, but from these results it appears that the high population on A is not just due to the greater potential fecundity of the females on this bush.

3. Effect of Host Plant

The hypothesis was tested that the number of eggs laid is determined primarily by the influence of the host bush on oviposition, rather than the effect on the female before emergence. This was done by comparing the fecundity of females on their original host with that of females moved to another host as soon as practical after emergence. The results are shown in Figure 2.7. Bush C has been included in the Figure, but as on no occasion were there sufficient females to cage from this bush the results have been omitted from the analysis.

When the comparisons over four years were tested, only on one occasion was there any significant difference in the number of eggs laid on the same plant. (Bush B 1973 ($t = 2.51$ $P < 0.05$)). The hypothesis appeared true for 1970 and 1972 and in the other two years a trend for greater egg production on A was observed.

FIGURE 2.6 Seasonal variations in the numbers of eggs laid and the longevity of Aleurotrachelus on bushes A, B and C.

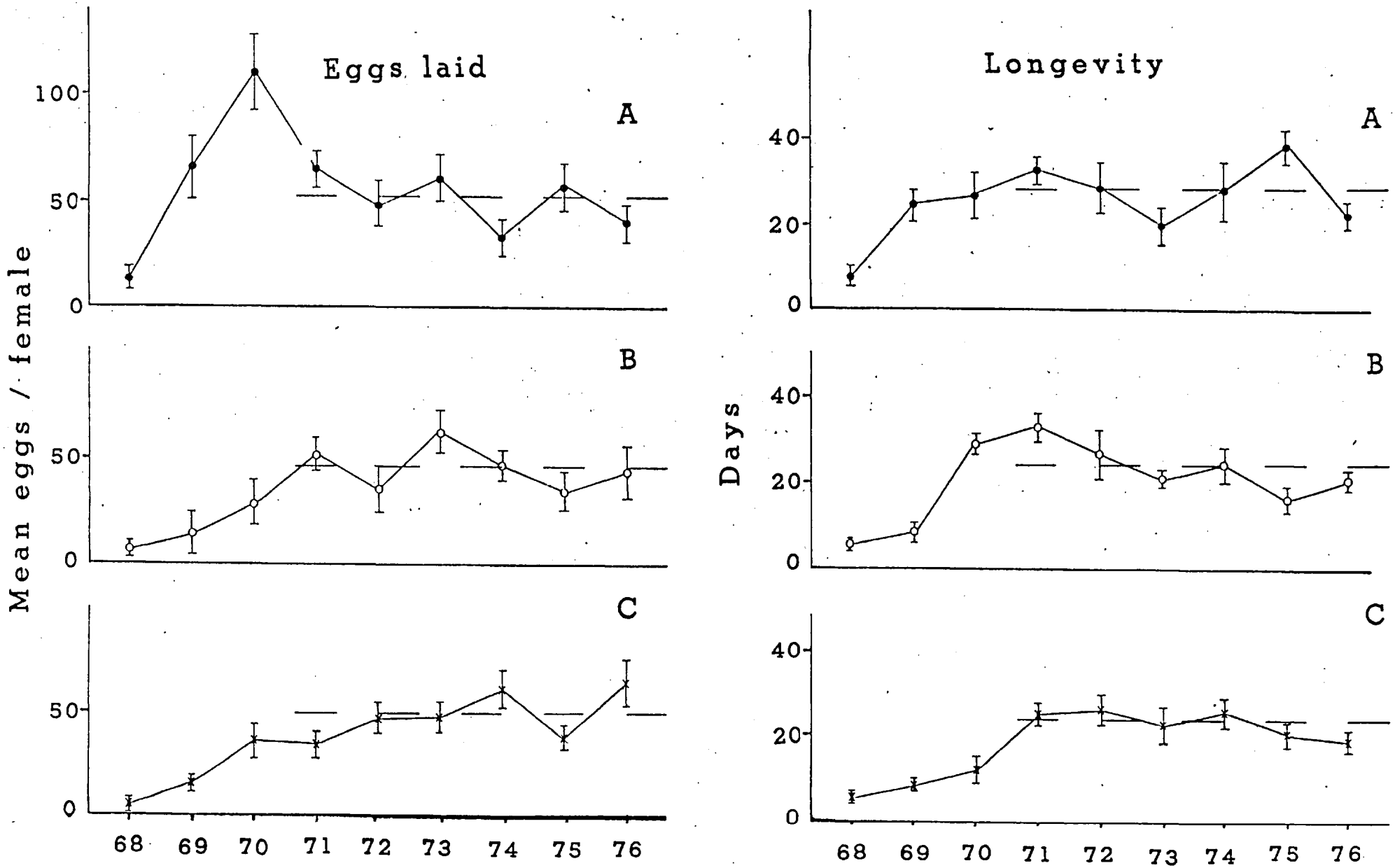

Eggs laid
Longevity
A
B
C
Mean eggs / female
Days
Years
100
50
0
40
20
0
68
69
70
71
72
73
74
75
76

FIGURE 2.6

FIGURE 2.7 Effect of the host plant on the fecundity and longevity of Aleurotrachelus over 4 seasons

A/A reared and kept on A

A/B reared on B and kept on A

B/B reared and kept on B

B/A reared on A and kept on B

C/A reared on A and kept on C

FIGURE 2.7

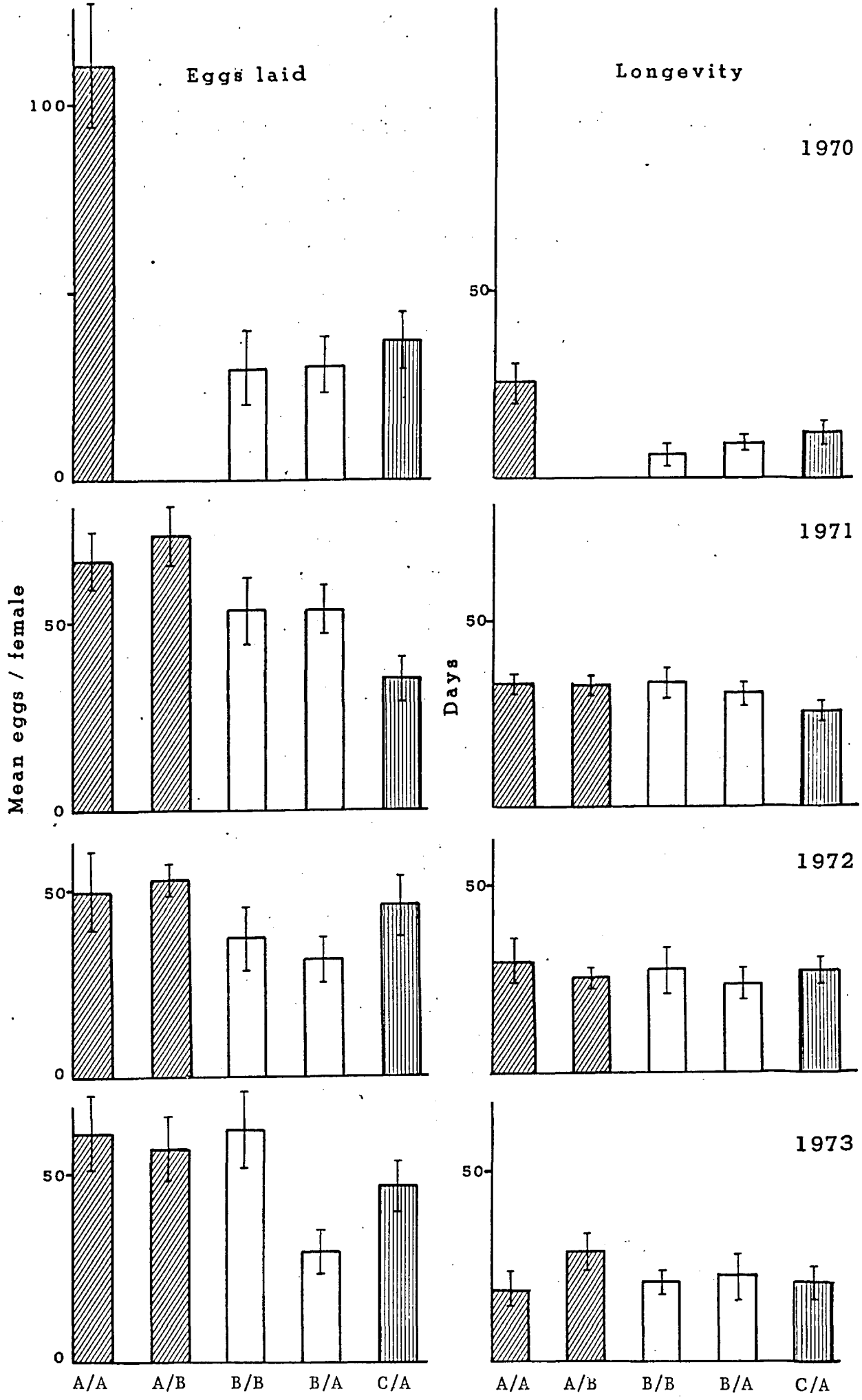

Eggs laid
Longevity
1970
1971
1972
1973
Mean eggs / female
Days
100
50
0
A/A
A/B
B/B
B/A
C/A

TABLE 2.5 t values obtained from differences in egg numbers laid on A and B.

Year	t	prob.
1970	5.63	<0.001
1971	1.99	0.1 - 0.05
1972	2.24	<0.05
1973	1.11	n.s.

When the data are taken as a whole for the four years a value of $t = 4.82$ ($P < 0.001$) is obtained which seems to suggest that the bush on which the eggs are laid is primarily important, and that A is a better oviposition site than B.

Figure 2.7 shows that longevity was not affected by the host plant, and from the evidence of the dissections it would appear that the difference in egg numbers laid on each bush is due to fewer eggs maturing rather than large numbers being retained.

2.3.2 Density

The effect of population density on the fecundity of insects has been well examined and reviewed by Watt (1960). A variety of reasons have been put forward as an explanation for the reduced number of eggs laid at higher densities. These include interference between individuals, reduction of food available, and competition for total space, which could affect rest, copulation, oviposition and the amount of oviposition sites available (Crombie 1942).

This section deals with the effect of density on fecundity in both *Aleurotrachelus* and *Trialeurodes*.

1. *Aleurotrachelus*

Methods and Results

Experiments on the effect of density on the fecundity of Aleurotrachelus were carried out in 1970. Pairs of newly emerged adults were caged on young leaves and allowed to remain in situ until all the adults had died. Cages containing 1, 3 and 5 pairs of white-fly were placed on Bush A and in the 20°C. controlled temperature room. No estimates were made on the fertility of these eggs.

The results from both field and laboratory experiments are shown in Figure 2.8. The latter proved insignificant, but the field data showed a significant correlation between the number of eggs laid per female and density. This contrasted with the other results from these data where neither longevity or the number of eggs per cage differed at different densities, and indicated that either the reduction in space, the presence of eggs or the interference from other individuals inhibited egg laying.

When the number of eggs laid on the bush is compared with the amount of available space per female (estimated from counts of new leaves taken throughout the seasons 1970 - 76 and mean measurements of leaves also taken throughout the season), the regression in Figure 2.9 is obtained, where the total number of eggs laid on bush A increases as the density of females rise. This is not apparent on the other two bushes, nor is there a relationship on any bush when total eggs are compared with total bush area rather than area per adult female.

If the number of females are compared with the log. eggs per female and the log.total eggs on the bush on all three bushes (Figure 2.10), no obvious trend is noted. On bush A (with the highest density of insects) a tendency is observed for the number of eggs laid per female to increase with density and then fall. This is coupled with a

FIGURE 2.8 Effect of density on the fecundity and longevity of Aleurotrachelus.

FIGURE 2.8

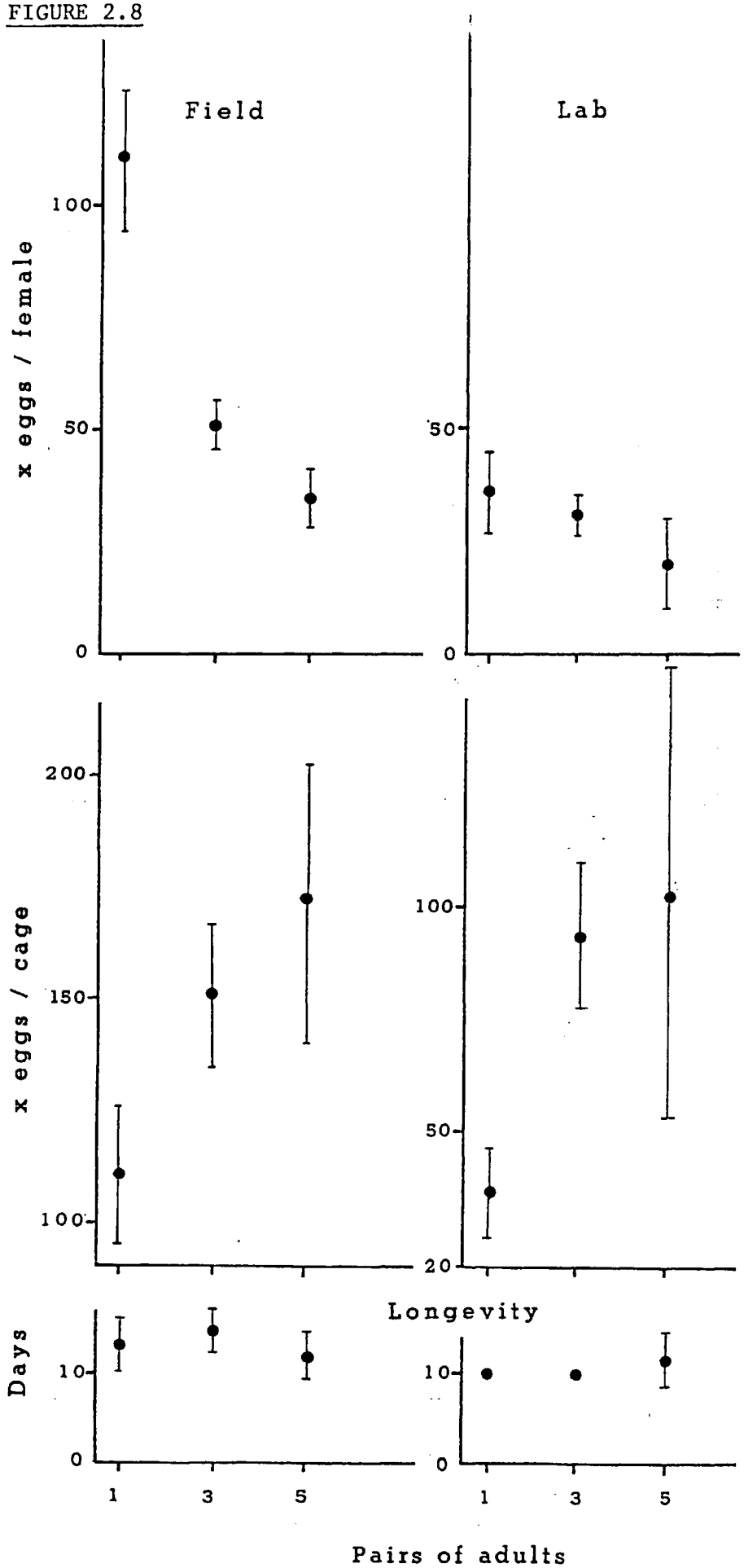

Field
Lab
x eggs / female
100
50
0
50
0
x eggs / cage
200
150
100
100
50
20
Longevity
Days
10
0
10
0
1
3
5
1
3
5
Pairs of adults

FIGURE 2.9 The numbers of eggs on bushes A, B and C compared with the total area available for each female.

A Y = 5.99 - 0.44 x r = 0.98 $p < 0.001$

B Y = 4.42 - 0.008 x r = 0.56 (ns)

C Y = 1.53 + 0.001 x r = 0.65 (ns)

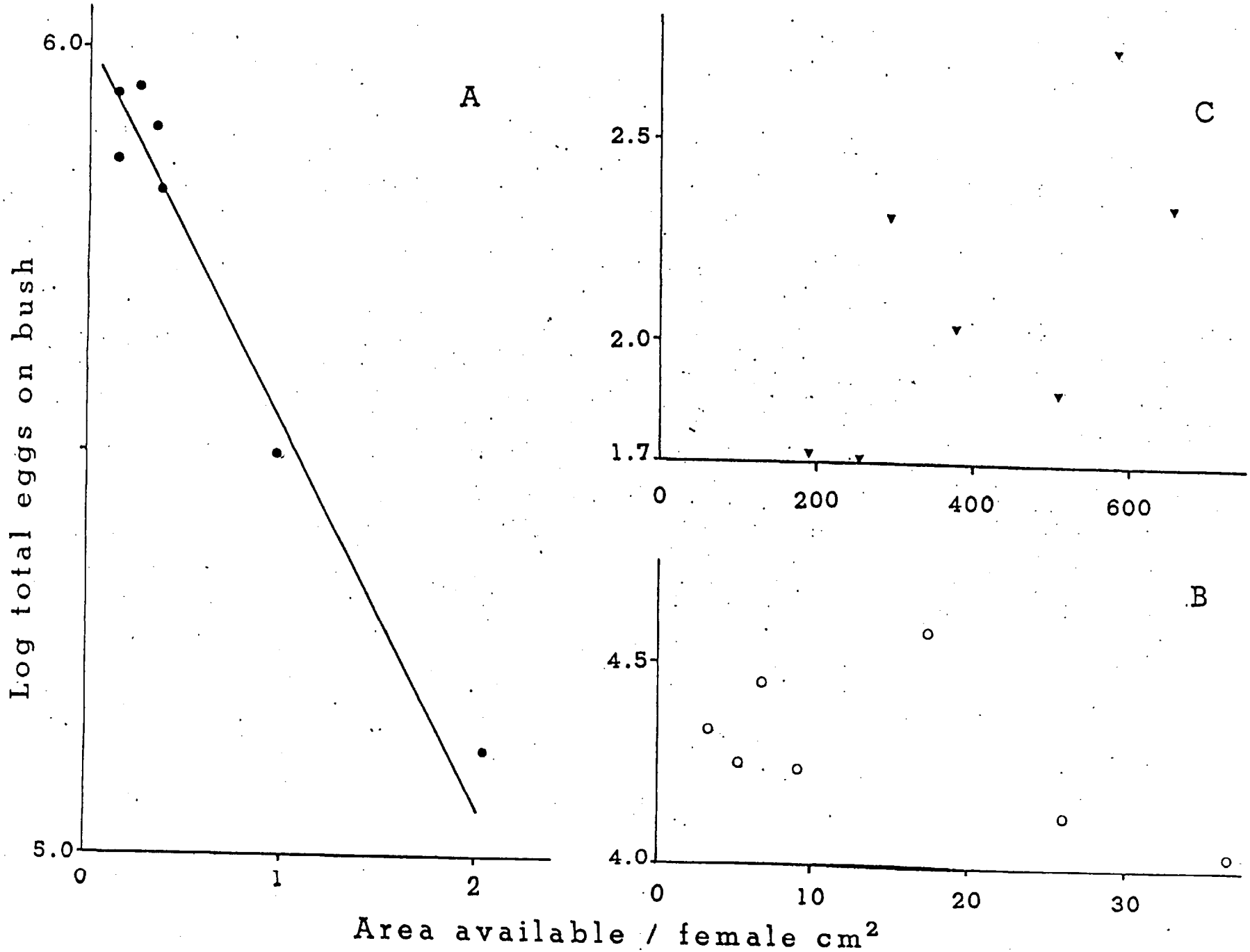

A
B
C
Log total eggs on bush
Area available / female cm²
6.0
5.0
0
1
2
2.5
2.0
1.7
0
200
400
600
4.5
4.0
0
10
20
30

FIGURE 2.9

FIGURE 2.10 Differences in log. numbers of eggs laid per female and log total eggs on the 3 bushes at different densities of adult females

• - Log. eggs/female

o - Log. total eggs.

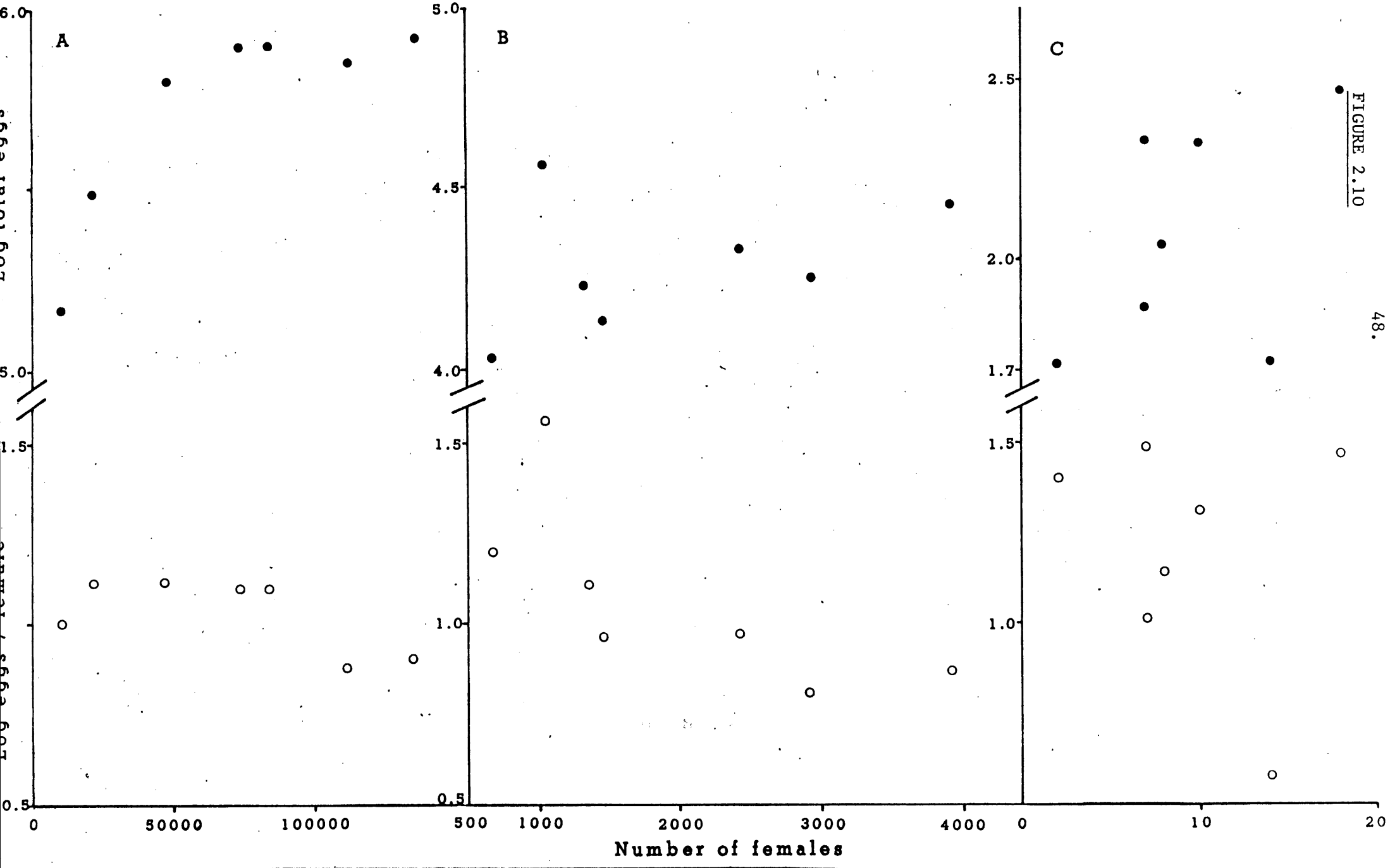

A
B
C
6.0
5.0
4.5
4.0
2.5
2.0
1.7
1.5
1.0
0.5
0
50000
100000
500
1000
2000
3000
4000
10
20
Log total eggs
Log eggs / female
Number of females

FIGURE 2.10

rise in total eggs, as the adult population rises, until a plateau is reached. This would be the expected pattern if density dependence were to play a role in the regulation of the population.

Bush B (with its intermediate population level) shows similar, if slightly more erratic, trends. If this is the case, it would indicate that on different host plants different population densities are limiting. Bush C showed no pattern, and this provides further evidence of the unstable condition of the population on this bush (Southwood and Reader 1976).

2. Trialeurodes

Similar experiments were carried out on the greenhouse whitefly. Five treatments of 1, 2, 3, 4 and 5 pairs of adults per cage were tested on both potted tomatoes and beans (variety The Prince). The results from these experiments are shown in Figure 2.11 and 2.12 respectively. Longevity did not differ on either host. On tomatoes the number of eggs laid per cage remained constant, but a difference was found in the number of eggs laid per female, which declined from the lowest density, following a 'Drosophila' type curve. The treatments on beans did not show this trend; in fact egg production was stimulated by increasing density and then declining - an 'allee' type curve.

When the area available for egg laying was increased by altering the diameter of the cages to 1, 1.5 and 2 cm, and although relatively few eggs were laid, more eggs were found in the increased space of the 2 cm cage (Figure 2.13), and when these were compared for a similar area no difference in numbers was noted.

Combined with the insignificant results when no effect of inter-

FIGURE 2.11 Effect of density on the fecundity and longevity of Trialeurodes on tomatoes.

FIGURE 2.12 Effect of density on the fecundity and longevity of Trialeurodes on beans.

FIGURE 2.11

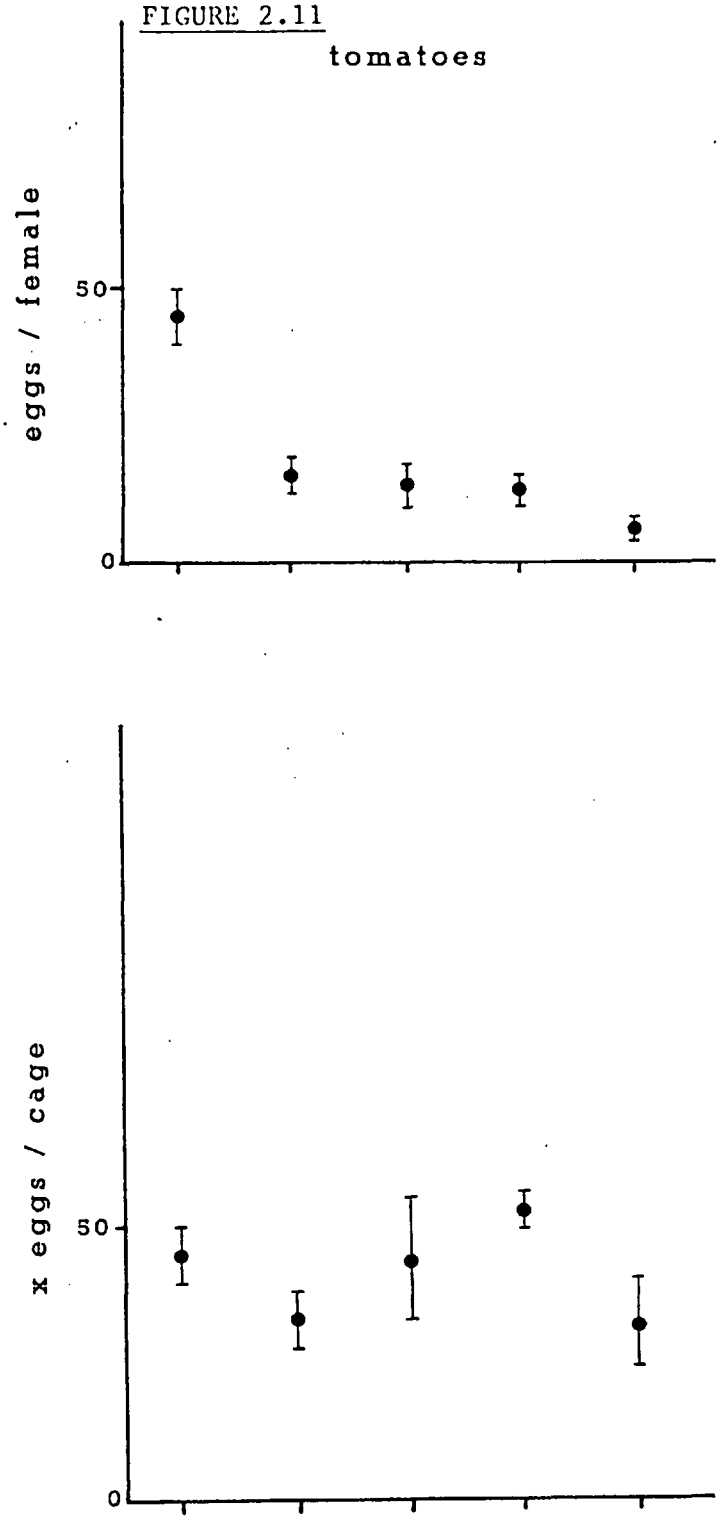


FIGURE 2.12

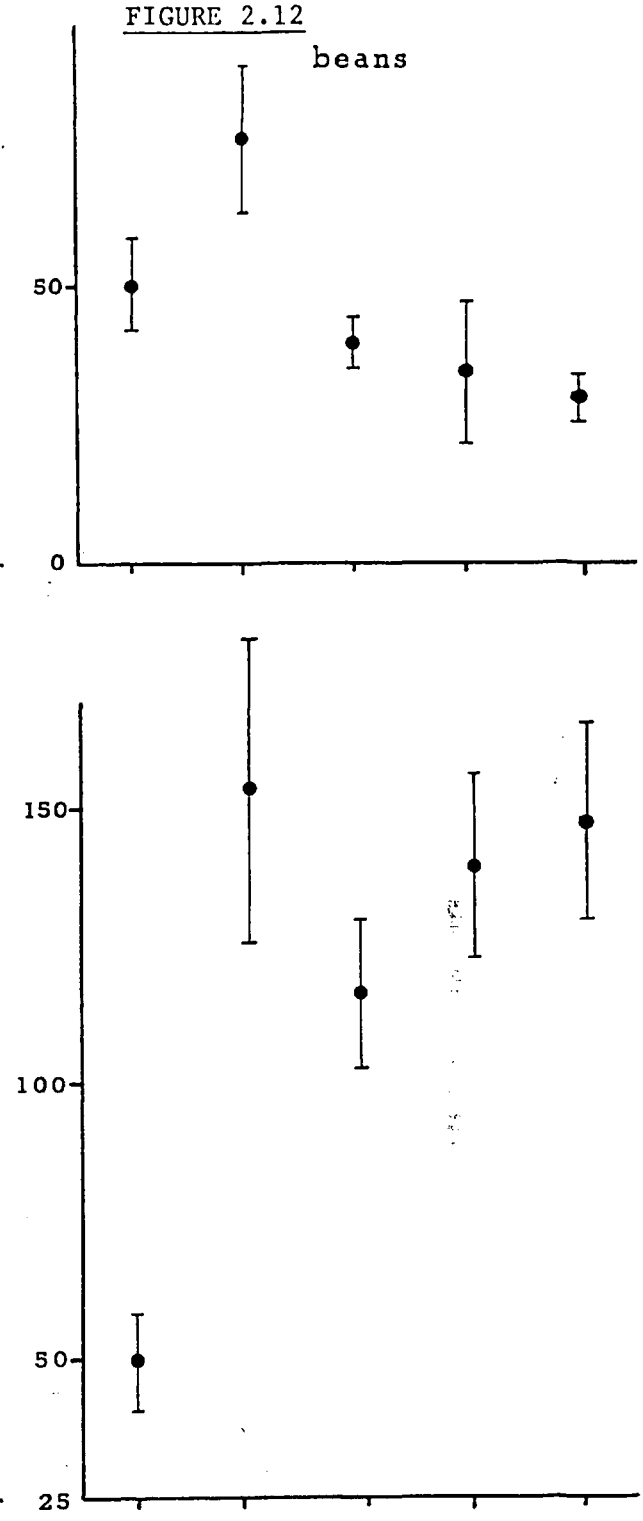
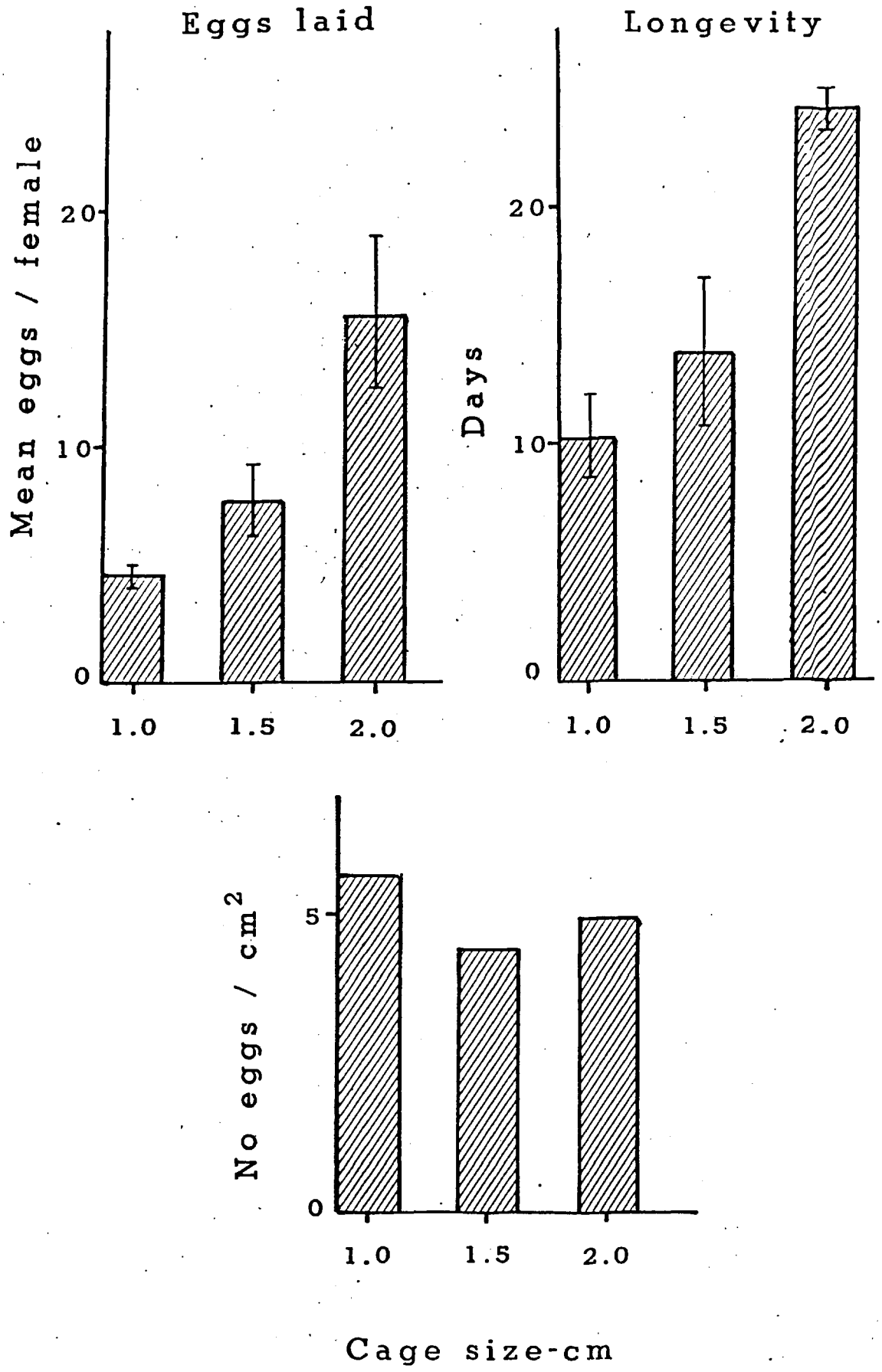


FIGURE 2.13 The effect of increasing the amount of available space on the fecundity and longevity of Trialeurodes

FIGURE 2.13


Eggs laid
Mean eggs / female
20
10
0
1.0
1.5
2.0
Longevity
Days
20
10
0
1.0
1.5
2.0
No eggs / cm2
5
0
1.0
1.5
2.0
Cage size-cm

ference by males or females at ratios of 1 : 1 was found, it would seem that space for oviposition sites is a limiting factor. The mean number of eggs produced per day can be seen in Figure 2.14. A peak in numbers laid per day is reached about twelve days after emergence, and although eggs are laid throughout life, the rate tails off after about twenty days. It appears that the first two weeks of adult life are the most important for egg production, for the number of eggs produced per female is higher (as also found by Iheagwam (1976) and after this time adult mortality begins to make an impact.

2.3.3 Climate

Climate plays a major role in the growth, development and productivity of insects. Of the three major components of climate, - temperature, windspeed and humidity - temperature will have most effect on univoltine insects such as Aleurotrachelus by its influence on fecundity rates. This will be discussed in this section. In addition insects at the northern edge of their ranges are often particularly vulnerable to low temperatures during winter. The key factor analysis did not suggest that this was a major cause of mortality, and this will be discussed in a future publication. The second effect - windspeed will be discussed later (Chapter 3). The impact of humidity on insects which live on leaf surfaces is not thought to be important if the plant is transpiring normally, as the atmosphere immediately above the leaf is almost saturated except when the wind velocity is very high. (Butler 1938). Evergreens, in general, have a low transpiration rate but this is still sufficient to maintain a high relative humidity up to 1 cm above the surface. (Ramsey et al 1938). Consequently, no experiments have been carried out on the influence of humidity on fecundity.

Methods and Results

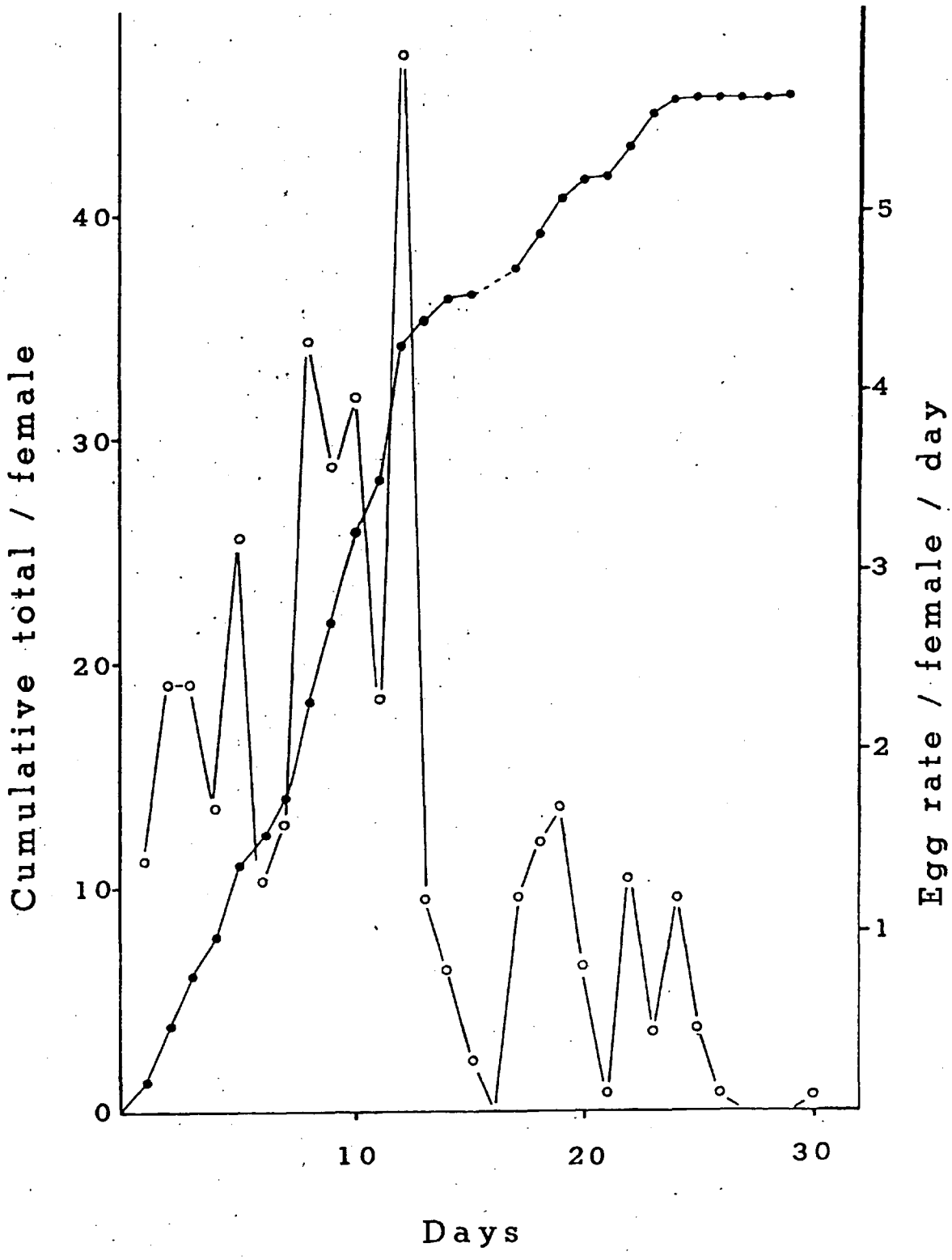
To test the effect of temperature on fecundity, paired adult

FIGURE 2.14

Cumulative total and egg rate per day of female *Trialeurodes*

- ● Cumulative total
- ○ Egg rate per female per day

FIGURE 2.14


Cumulative total / female
Egg rate / female / day
Days
0
10
20
30
40
1
2
3
4
5
10
20
30

Aleurotrachelus were set up on small potted Viburnum plants at 15°, 20° and 25°C. The same experiment was repeated in two consecutive years to provide greater weight to the first year. Both sets of data are shown in Figure 2.15. Not unexpectedly, in both years the rate of oviposition was increased by temperature, but data on the total number of eggs laid per female was less clear cut. In both 1969 and 1970, significantly more eggs were laid at 25°C than at 20° or 15°C (1969; 25°/20° $t = 2.51$ $P = 0.05 - 0.02$; 1970 25/20 $t = 2.14$ $P = 0.05 - 0.02$). The differences in numbers between 15° and 20° were not significant. From these data it is apparent that a threshold for increased fecundity is reached between 20 and 25°C. Longevity did not appear to be greatly affected by temperature in 1969, but in 1970 insects at 15°C lived significantly longer ($F = 4.03$ $P < 0.05$).

Similar information is available from the census data during the nine years 1968 - 1976. When the mean number of eggs per female is plotted against mean June temperature for that year (the time of maximum egg laying) for each of the three bushes, the trends in Figure 2.16 can be seen. Bushes B and C (those with lower populations) show no trend at all. While on Bush A the opposite case to that found in the laboratory is found. This conflicting result may just be an indication of the difficulty of applying controlled temperature results to fluctuating situations, but may also be the result of such factors as increased mobility and interference at higher temperatures which then result in a decrease in egg laying.

2.4 DISCUSSION

The fecundity of insects is a key component of any life table and hence crucial to population dynamics. In this chapter some factors which may affect fecundity in whiteflies have been assessed.

Both, in Trialeurodes with its short developmental period and

FIGURE 2.15 The effect of temperature on the fecundity of *Aleurotrachelus* during 2 seasons.

1969 $Y = -2.59 + 0.24x$ $r = 0.61$ $p<0.001$

1970 $Y = -4.89 + 0.44x$ $r = 0.69$ $p<0.001$

FIGURE 2.15

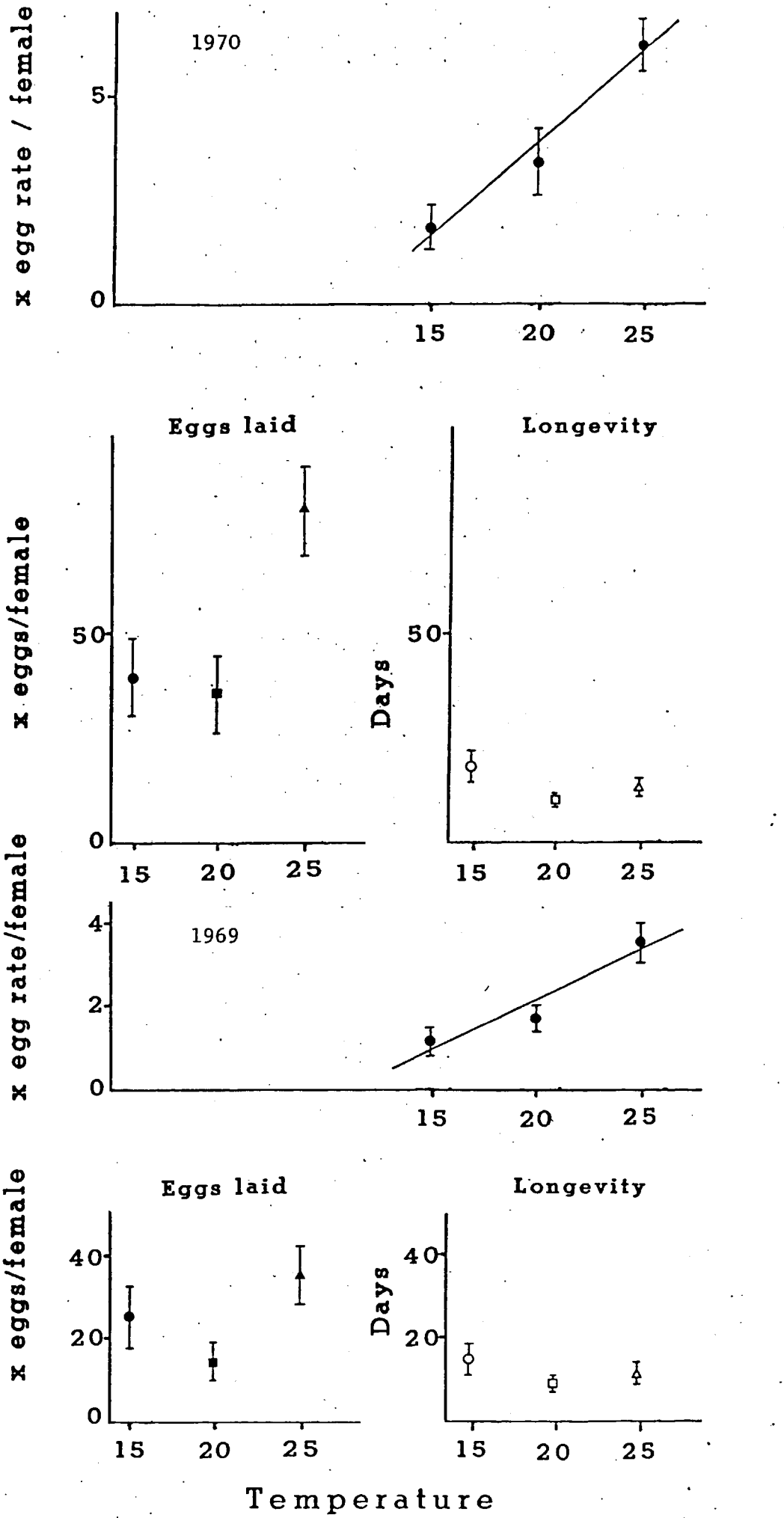

1970
x egg rate / female
5
0
15
20
25
Eggs laid
Longevity
x eggs/female
50
0
Days
50
15
20
25
1969
x egg rate/female
4
2
0
15
20
25
Eggs laid
Longevity
x eggs/female
40
20
0
Days
40
20
15
20
25
Temperature

FIGURE 2.16 Influence of the mean June temperature on the numbers of eggs laid per female during 9 seasons on the 3 bushes.

A . $Y = 27.52 - 1.17\,x$ $r = 0.67$ $p<0.05$

B . $Y = 5.52 + 0.64\,x$ $r = 0.12$ ns

C . $Y = 1.67 + 1.14\,x$ $r = 0.20$ ns

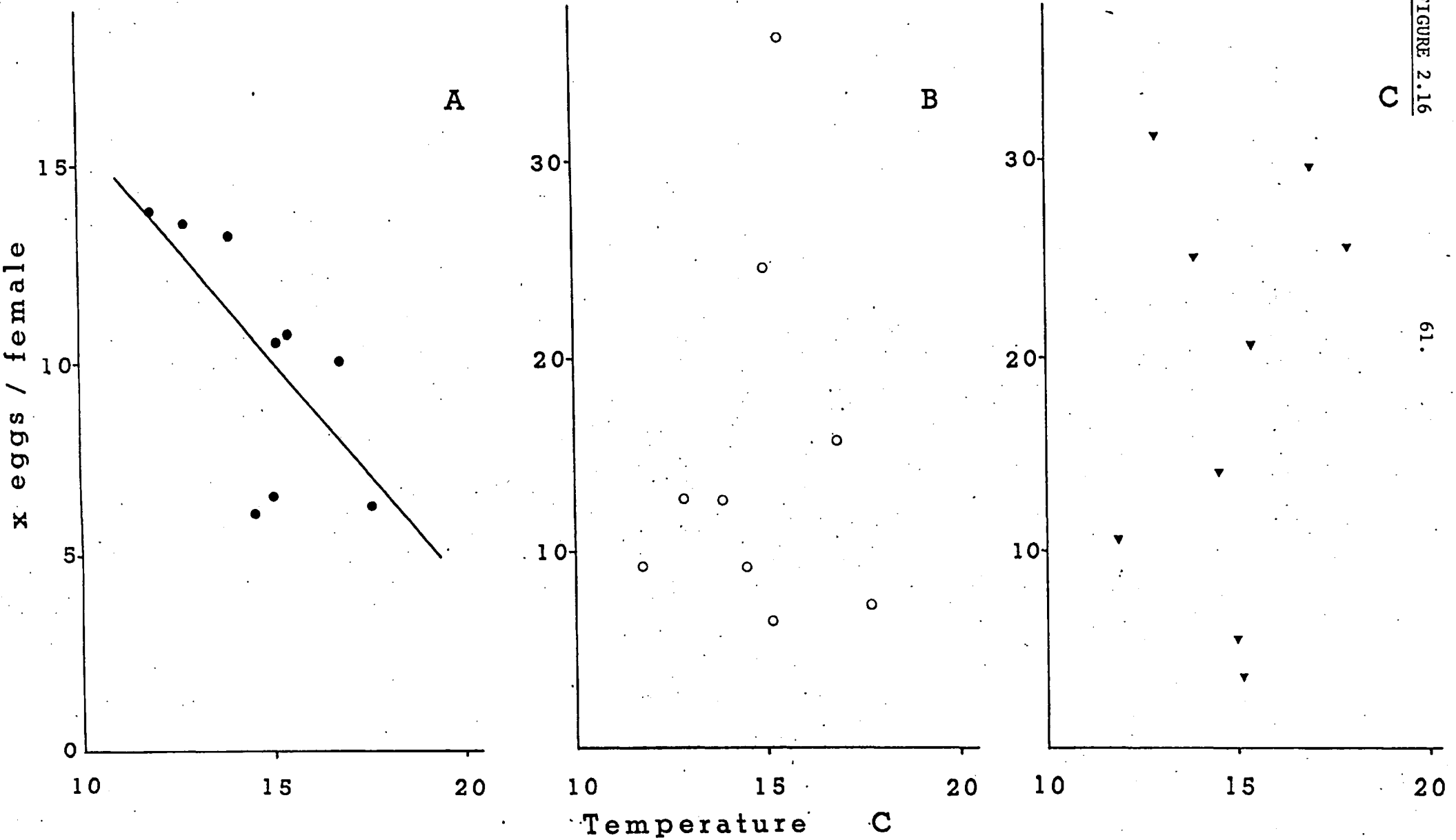


FIGURE 2.16

Aleurotrachelus with its annual life cycle, larval crowding did not appear to have any significant effect on fecundity. It may be that a 'sink' effect is produced in leaves at high densities, and only at extremes does mortality, or decreased larval development occur (Iheagwam 1976). What is important is the ability of the insect to synchronise with the host plant so that both egg laying and time of maximum development take place during optimum conditions of nutrition and density.

Climatic variations may be effective in four ways:

(1) by altering the timing and magnitude of amino acid flows:

(2) by inducing stress in plants by extreme conditions (White 1969, 1974), as Wearing (1967) found working with Brevicoryne brassicae and Myzus persicae, where water stress in young and mature leaves increased fecundity levels;

(3) by delaying the rate of development, as Iheagwam (1978) showed in the cabbage whitefly where the mean duration of development from egg to adult increased from 19.0 days at 25°C to 52.1 days at 15°C, (in a multivoltine insect this has the effect of reducing the number of generations per year); and

(4) by low temperatures lengthening the period of egg laying so that the time of maximum nitrogen availability is missed.

This survey reveals that Aleurotrachelus will lay eggs on old leaves (cf. Mound 1958) and that both males and females can feed on old leaves, so there can be no obvious physical deterrant to feeding, although old leaves are appreciably tougher. The nutritional advantage for the next generation is short-lived for nitrogen levels quickly revert back to their low levels (P.152). The advantage of laying eggs on new leaves would appear to be three-fold. Firstly, the fecundity of the female is increased by the improved food quality; secondly the old leaves provide a less favourable environment being both tough and

covered by the remains of the last generation. Moran and Buchan (1975), working with the psyllid, Trioza erytreae, showed that more than twice as many eggs were laid on soft rather than hard leaves. Thirdly, a new leaf has a greater probability of surviving for twelve months than an old one, an important consideration for a sessile insect.

Several workers have studied the influence of leaf age on fecundity. Iheagwam (1976) and Trehan (1944) found with the cabbage and cotton whitefly respectively that more eggs were laid on young rather than mature leaves. Wearing (1972) stated that in the absence of water stress mature leaves are nutritionally inferior to old and young ones, and further speculated that M. persicae may require the products of hydrolysis associated with senescence, and B. brassicae the amino acids associated with protein synthesis in new leaves.

On all bushes there was great variation in fecundity between seasons. Several examples of seasonal changes in nutritive quality have been described (e.g. Durzan 1968; Parry 1974) and the work of Prestidge and McNeill (1981)) has shown large variations between seasons. The maximum amounts of amino acids in Viburnum tinus are shown on P. 147 and these again show seasonal divergence. Thus it seems reasonable to assume that conditions of climate and stress affect the host plant and are important in the year to year fluctuations of egg populations. Bush C, with increased stress from surrounding plants and attacks by squirrels which drastically reduce the number of leaves, may undergo periodic surges and troughs in amino acid levels, which are not in synchrony with the other bushes.

The influence of the host plant on fecundity was specially apparent during the years 1970 and 1971. The remaining data display a more uniform level, which is probably caused by a combination of timing and the general level of the phloem flow both of which can influence

the fecundity of a species. This phloem flow involves a mobile pool of amino acids, varying (at best in grasses) in absolute values from 2000 - 5000μ moles/100 mg. dry weight. (Prestidge and McNeill, 1981). This variation means that all plants do not act in the same way each year, a fact which becomes more apparent in long term studies. It may be that Bush A is only particularly favourable in certain years and during this time the insects can maximise their potential fecundity. No experiments were carried out on the effect on Aleurotrachelus of different host plants. With Trialeurodes, when fecundity on bean and tomato were compared, no significant difference was noted. Hussey and Gurney (1958) found no significant differences in the fecundity of the greenhouse whitefly in different varieties of tomato. Dowell et al (1979) working on the citrus blackfly showed an increasing host range with density. The same was noted with the greenhouse whitefly by Vitarana (1977), where under high density conditions eggs would be laid on unsuitable hosts, but these then either failed to hatch or did not develop fully.

As Iheagwam (1976) has pointed out, the summer forms of the cabbage whitefly are unable to fly for long periods and therefore tend to remain on a leaf and lay as many eggs there as possible. In this it can be compared with the viburnum whitefly (see P.106). Under these conditions large numbers of individuals may accumulate on new leaves and the effects of density come into play. Iheagwam (1976) also notes that mobile insects rarely become crowded in nature because of their ability to redistribute themselves. With Trialeurodes this may be the case for in greenhouses either fresh plants are being added or new leaves are growing, thus opening up an expanding habitat. Aleurotrachelus is more limited by the simultaneous growth of the season's new leaves, which together with the limited flight of the insect, can produce conditions of high density. When Aleurotrachelus was tested experimentally, a correlation

between density and fecundity was observed. A similar response was noted with Trialeurodes on tomato, but as Watt (1960) states, the effect of density may vary in the same species on different hosts, as seen by the 'Allee' type curve on beans.

The role of density during the period of egg laying is important, from the increase of disease due to stress factors (Steinhaus 1958) to the decline in fecundity which has been noted by many workers (e.g. Clark (1963b), Dixon (1966), Iheagwam (1976) and Hargreaves and Llewelyn (1978)). Although the total number of eggs laid by Trialeurodes does not achieve the maximum forecast by Anon (1978) and Hussey and Gurney (1960), there is an indication that space for oviposition sites is a limiting factor. Tests for interference by males proved inconclusive following the pattern found by Clark (1963b) in which C. albitextura showed no reduction in fecundity until the number of males had become excessive. Whether this limitation is caused by the absence of suitable oviposition sites or the females are inhibited by the presence of eggs has been investigated by Day (1980). In a 24 hour experiment he suggests that adult density had no effect on oviposition rate whereas the number of eggs laid was at first stimulated and later depressed as the number of eggs already on the leaf was increased.

'Reproduction is adversely affected by extremes of temperature more readily than most other physiological functions' (Bursell 1974). The exact nature and range varies from species to species and covers the effects on numbers of eggs laid to the longevity of, and percentage of reproductive females. (Wadley, 1931; Graham, Glick and Ovye, 1967)

Aleurotrachelus illustrates one of the problems encountered in attempting to apply to field conditions data collected under constant

laboratory conditions (Thompson 1977); fecundity was shown to increase with temperature in the laboratory but no such evidence was seen under the fluctuating temperatures found in the field.

CHAPTER 3 - DISPERSAL

3.1 INTRODUCTION

It is essential for the survival of insects in temporary habitats that their life history can accommodate changing conditions. Migration is such an adaptation, for, as Taylor and Taylor (1977) state ' they (the animals) can neither function nor evolve unless they include the controlled mobility that enables them to select a place to live and so survive and reproduce'.

Temporal variations in habitats probably provide more constraints than absolute shortage of space (crowding), but if an insect is to maximise its fitness it must be able toleave an overcrowded or unsuitable environment. Indeed even insects in relatively stable environments may receive some evolutionary advantage by tolerating a certain level of dispersal (Hamilton and May 1977). Insect flight may be considered as movements of two types, migratory and trivial (Southwood, 1962). They can be distinguished by the response of the insect either to stimuli which induce flying - and so migration, or to vegetative stimuli which cause settling,feeding and oviposition. (Thorpe 1951, Kennedy and Stroyan 1959, Kennedy 1961, 1975, Johnson, 1969).

Johnson's (1969) definition that 'migration is essentially a transference of adults of a new generation from one breeding site to another' can be favourably compared with the rather generalist one of Baker (1978) who states that migration is the act of moving from one spatial unit to another.

Both external and internal factors cause insects to migrate, whilst physiological and behavioural features contribute to the overall mechanism summed in the life history. Aleurotrachelus has only one

generation a year and so, unlike the cabbage whitefly, cannot be seasonally dimorphic.

The ability to fly in many female insects appears to be influenced by the maturation of the ovaries. Many workers (Johnson 1959, Kennedy 1960, Dingle 1965 and 1966, Johnson 1969), have found that flight is a pre-reproductive activity. Waloff (1973) showed that the maturation of the ovaries in some leaf hoppers inhibited flight behaviour. Dingle (1965, 1966) found that in Oncopeltus the time of maximal flight occurred at the end of the teneral period. The cabbage whitefly shows a similar pattern, as the overwintering female moves to a new breeding site before the onset of egg-laying (El Khidir 1963). This prereproductive movement reaches its conclusion in many insects when the flight muscles begin to autolyse after migration has taken place (Dingle and Arora 1973, Johnson 1974).

Crowding, which can produce dramatic effects in aphids, can also alter the quality of food, and this in itself can influence the level of migration. Working with the bug Nysius vinctor, Kehat and Wyndam (1973) found that poor quality of food rather than the quantity available encouraged the flight of emerging adults. Similarly, Rose (1972) with species of Cicadulina, showed that flight was inhibited on young wheat seedlings, whilst the readiness to fly increased in non-gravid females on drying mature stems. Thus, if migrating females of Aleurotrachelus are to have the greatest reproductive value, migration should occur between the end of the teneral period and or even after pairing, but before egg laying. This represents a very narrow window of time, that can be further affected by the immediate weather conditions. It has been shown, for example by Waloff (1973), that increased temperature stimulates flight, whilst high windspeed inhibited flight.

Lewis and Taylor (1965), however indicated that the temperature rarely falls below the flight threshold for Aleyrodes proletella of 9°C, and peaks in flight depend on the numbers of mature insects rather than on weather conditions.

If the view of insect migration, outlined above, is accepted, then certain questions can be asked regarding migration of a particular species:-

1. What causes flight?
2. For how long is flight sustained, and is the range covered sufficient to reach a suitable host plant?
3. Can a suitable host plant be found on landing?

With these questions in mind, various experiments were carried out on the dispersal of Aleurotrachelus, the results of which are compared with those obtained from other species of whitefly.

3.2 METHODS

Evidence of migration in whiteflies, particularly Aleurotrachelus was sought by several methods.

1. Field experiments on a. potted trap plants
   b. sticky traps
2. Experimental assessment a. the effect of age on flight activity
   b. flight and landing in a flight chamber.
3. Dissection of trapped specimens.

3.2.1 Field experiments

a. Potted trap plants - During the years 1967, 1975 and 1976 potted Viburnum tinus plants, approximately 0.5m high, were placed at 2, 5, 8, 11 and 25 metres from Bush A in an easterly direction. They were examined daily and any adult whitefly found were removed and preserved. These were dissected at a later date. Whitefly on both the sticky traps

and potted plants were considered to originate from Bush A as there was no other source nearby.

b. Sticky traps - 24 - 26 cylindrical sticky traps of the type used by Broadbent et al (1948) were placed around the bush in annuli at 0.45m, 2.5m, 5m and 7.3m (Fig. 3.1). They were held on posts 0.15m, 0.75m and 1.4m from the ground and covered with greaseproof paper on which a resinous substance - "O - stick - O" - had been smeared. To prevent direct vertical migration, a muslin screen was placed 0.5m above the bush and the first annulus of traps. This was not thought to modify seriously the behaviour of the whitefly since few adults were observed either sitting on or flying towards the screen. Traps were examined daily and the whitefly removed and preserved for dissection; the sex of the trapped adults was also noted. The numbers collected were corrected for the effect of wind speed on the efficiency of the traps (Taylor 1962). An estimate of adult whitefly numbers on the bush on any particular day was made by counting the insects on 25 old and 25 new leaves and then determining the number of leaves on the bush.

3.2.3 Experimental assessment

a. The effect of age on flight activity - Newly emerged adult Aleurotrachelus were collected from Bush A and placed with the aid of a camel-hair brush onto old leaves of potted plants. All insects were in a similar condition: they had just emerged from the pupal case and could walk, although their wings were not expanded. The experiments were conducted at 20°C. An insect was picked up on the brush, which was gently tapped, until the whitefly either dropped or flew off. The first test was conducted 30 minutes after emergence and continued at 45 minute intervals until flight occurred. Insects of both sexes were tested.

FIGURE 3.1

Position of sticky traps round Bush A


area covered by muslin screen


position of bush

(1968 no outer traps, 1976 - no inner traps)

A - 0.45 m from bush

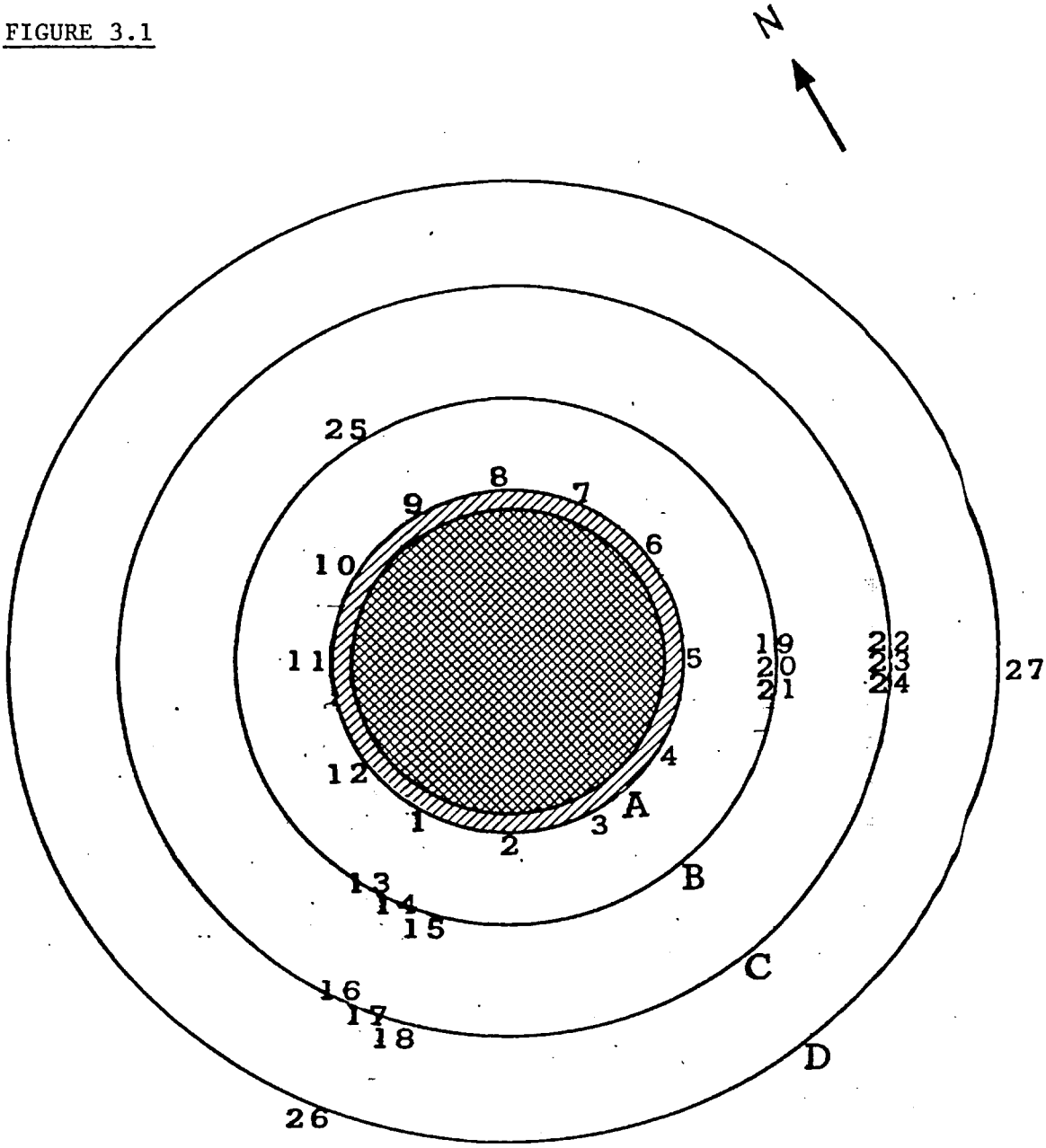
B - 2.50 m from bush

C - 5.00 m from bush

D - 7.30 m from bush

Height of Traps	Trap No.
0.15m	2, 6, 9, 11, 15, 18, 21, 24
0.75m	1, 4, 7, 10, 14, 17, 20, 23, 25, 26, 27
1.40m	3, 5, 8, 12, 13, 16, 19, 22

FIGURE 3.1


N
25
8
7
9
6
10
5
11
19
20
21
22
23
24
27
4
12
A
1
3
2
13
14
15
B
C
16
17
18
D
26

Female whitefly were tested daily to estimate the length of time they remained on old leaves before flight. Ten females of the same age were placed on old leaves of Viburnum tinus, in a darkened chamber. This method was used by Iheaghwam (1976). The sides of the chamber were sticky and the only source of light was at the top. After five hours the chamber was examined and the whitefly remaining on the leaves counted.

b. Flight Chamber Experiments - The flight chamber used was a vertical wind tunnel described by Kennedy (1974) and Kennedy and Ludlow (1974). This formed part of a closed-circuit airflow system in which the flow of air was not confined to the centrally illuminated square but extended on all sides.

The experiments were arranged so that observations on host preferences at landing and their willingness to fly could be made.

i) Duration of flight

Observations were made on adult whitefly to estimate flight duration and to note any flight activity which could be described as migratory. A rather arbitary flight period of 45 minutes by any individual was assumed to represent prolonged flight, after which observations would be discontinued. From the sticky trap data it appeared that insects flew throughout the day. It was therefore decided to fly the whitefly in the early afternoon to allow for a period of acclimatisation following removal from their natural conditions. Flight mature insects were taken from Bush A and kept on potted plants of the appropriate type. Prior to flight the plants and insects were placed in a lighted chamber at 20^{o} - 25^{o}C. They were individually transferred to tubes and released in the flight chamber. If the insects were reluctant to fly, the

number of flights required to achieve a total flight time of 40 seconds was recorded. It was assumed that the more starts required the less likely the insect was to fly.

ii) Host preference at landing.

Individual whitefly of two species, Aleurotrachelus jelinekii and Aleyrodes proletella were released into a flight chamber which had a fixed wind speed of 30cm/sec. A single plant was placed on the right of the chamber and the whitefly were released singly from tubes on the left. If voluntary take-off failed to occur after two minutes the insects were encouraged by gently touching them with a fine brush. The flight paths were observed and the place of settlement was noted. Three plants were used to examine settling preferences, Brussels sprouts (variety Evesham special), Tomato (variety Moneymaker) and Viburnum tinus.

3.2.3 Dissections - Five females were taken from those caught during each five day period on the sticky traps and potted trap plants, and dissected to reveal the condition of their ovaries. No assessment was made of the condition of the flight muscles.

3.3 RESULTS

3.3.1 Field experiments

1. Daily totals on sticky traps and trap plants - The numbers of whitefly, corrected for wind speed, caught daily from the first annulus of sticky traps for three consecutive years are shown in Figure 3.2. In addition the number of adults available on both young and old leaves are plotted, as are the maximum daily temperatures and windspeed at a height of 15 cm. The data indicate that Aleurotrachelus will fly throughout adult life, but there is a pronounced initial peak in numbers reaching the first annulus that coincides with the shift of the population

FIGURE 3.2 Numbers of whitefly trapped, corrected for windspeed, on the first annulus, with estimates of the population on old and young leaves in 1972, 1973 and 1974.

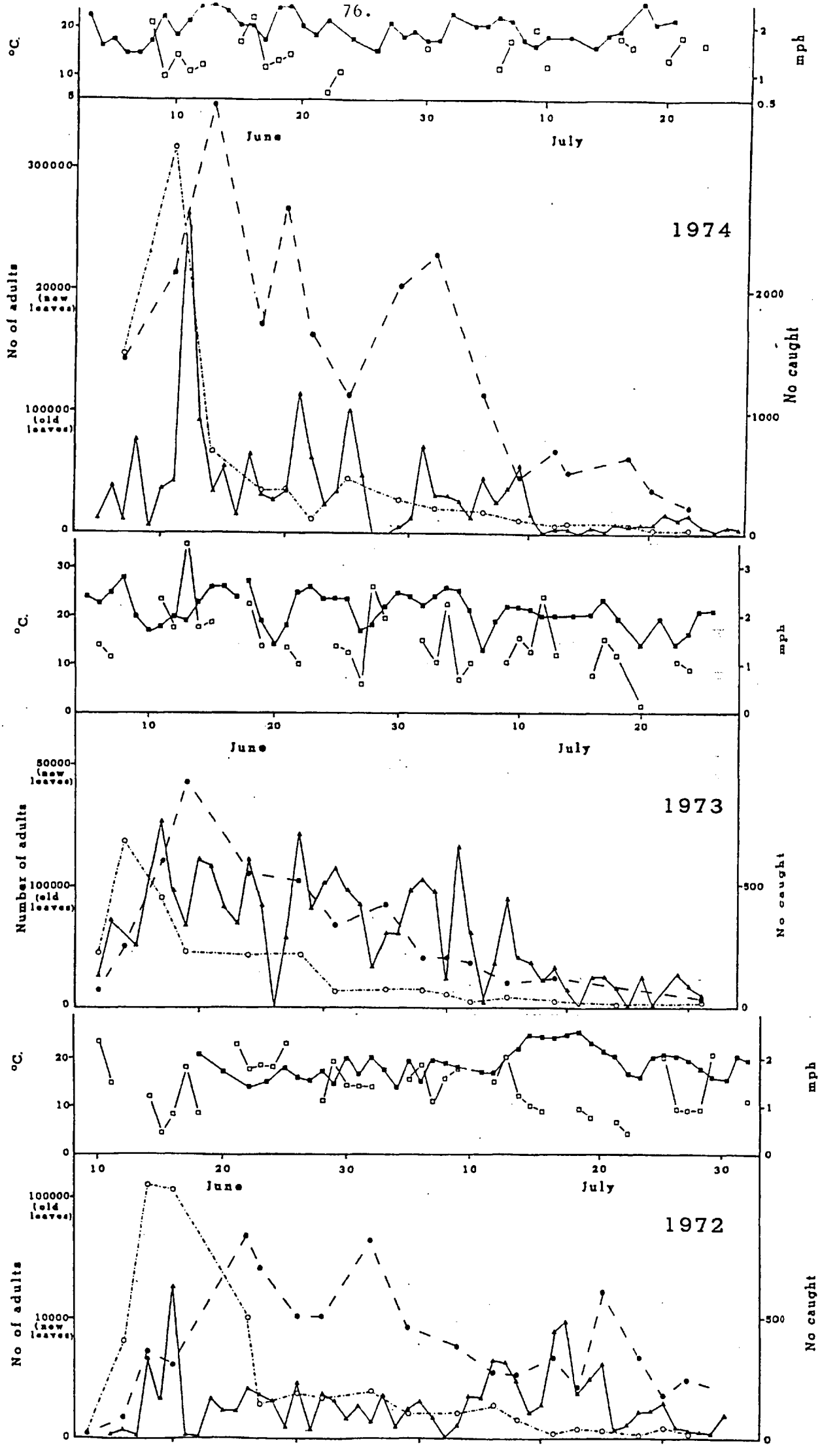
▲ numbers trapped

○ numbers on old leaves

● numbers on new leaves

□ windspeed in m.p.h.

■ maximum temperature


°C.
mph
June
July
1974
No of adults
(new leaves)
(old leaves)
No caught
°C.
mph
June
July
1973
Number of adults
(new leaves)
(old leaves)
No caught
°C.
mph
June
July
1972
No of adults
(new leaves)
(old leaves)
No caught

from a proponderance on old leaves following emergence, to one on new leaves approximately eight days later. Similar data from the trap plants are shown in Figure 3.3. with again a peak of movement approximately a week after emergence. Figure 3.4 shows the data from the same years from ten sticky traps from each annulus for the first twelve days after emergence. Here the trend seen in Figure 3.2 is repeated further from the host bush, with the peak again occurring about eight days after emergence. (This figure represents the mean for the years 1970 - 1976). The traps at 7.3m from the bush do not provide sufficient numbers to give a clear picture and have been omitted.

2. Climatic Effects on the total numbers caught. - No obvious trend could be established between the numbers caught on the traps, the maximum daily temperature and the mean windspeed at 15cm for each June day (the period of most active flight), although little activity was noted on cold or windy days. It may be that the variations in weather during these years were insufficient to show significant effects on the numbers caught.

3. Dispersal with Distance - The dispersal of small animals with distance has been expressed by two groups of equations which provide empirical descriptions of the relationship between numbers and distance (Freeman 1977, Taylor 1978). Those that Taylor (1978) suggests implying random movement with little effect of density are of the form:

$$N = a + bf(x) \qquad (3.1)$$

where N = number of insects, x = distance and a and b are constants. The equations which imply non-random dispersal and an effect of insect density are of the form

$$N = \exp(a + bx^c) \qquad (3.2)$$

which may be rewritten

$$\log_e N = a + bx^c \qquad (3.3)$$

FIGURE 3.3 Daily totals of males and females reaching the nearest trap plant (2m from the bush) in 1976.

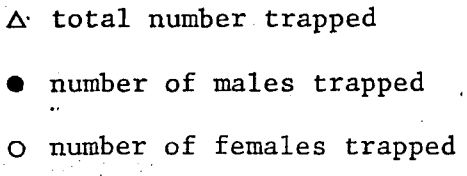


FIGURE 3.3

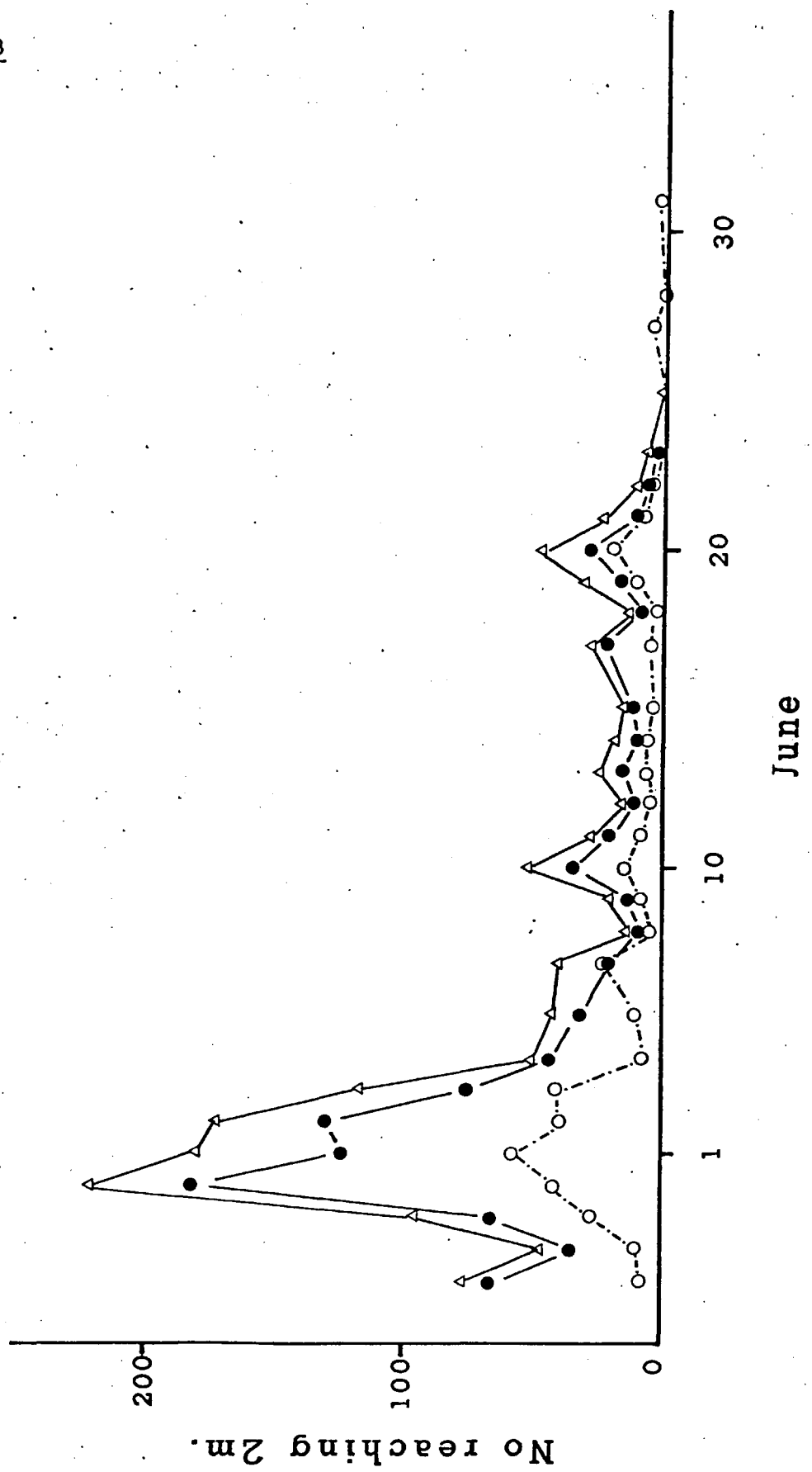


FIGURE 3.4 Numbers of adults caught, corrected for windspeed, on 10 traps and each annulus of sticky traps in 1972, 1973 and 1974.

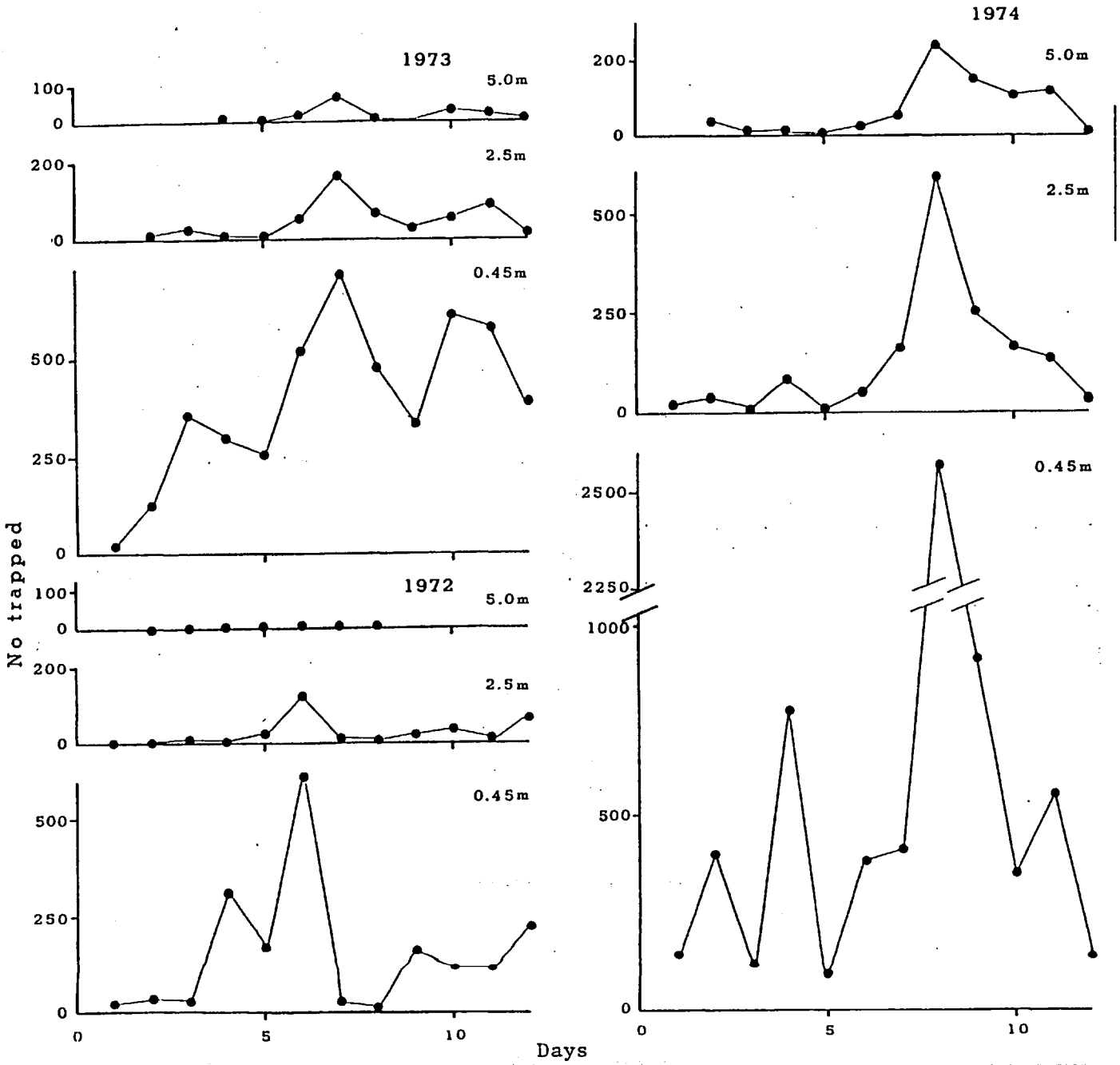

1973
5.0m
100
0
2.5m
200
0
0.45m
500
250
0
1972
5.0m
100
0
2.5m
200
0
0.45m
500
250
0
1974
5.0m
200
0
2.5m
500
250
0
0.45m
2500
2250
1000
500
0
0
5
10
No trapped
Days

FIGURE 3.4

Six particular forms of these equations are shown in Table 3.1.

TABLE 3.1 The six models tested for goodness of fit for density with distance

1.	$N = n + {}^{c}/_{x\log_e}$	Paris (1965)	group 1
2.	$N = a + b \log_e x$	Wolfenbarger (1946)	
3.	$N = \exp(a + {}^{c}/_{x})$	Taylor (1978)	group 2
4.	$N = \exp(a + b\sqrt{x})$	Hawkes (1972)	
5.	$N = \exp(a + bx)$	Gregory and Read (1949)	
6.	$N = \exp(a + bx^2)$	Dobzhansky and Wright (1943)	

Each of these has been fitted to the data in Table 3.2 which represents the total number of insects caught on ten traps during each season (corrected for wind speed) and Table 3.3, similar data from the trap plants. The fits of these equations is shown in Table 3.4 and 3.5.

TABLE 3.2 The numbers caught on ten sticky traps over the whole season corrected for windspeed (Taylor 1962).

Date	No. caught on 10 traps			
	Distance from bush			
	0.45m	2.5m	5.0m	7.3m
1968	699			
1969	815			
1970	909	190	61	120
1971	1946	521	260	320
1972	8150	2010	722	20
1973	15728	2617	1173	510
1974	17984	3517	2352	347
1975	12156	1214	792	230
1976		6916	2498	1125
$\bar{X}$ 1970/75	9478.8	1678.2	893.3	257.8

TABLE 3.3 Total number caught for the whole season on trap plants.

a) unpublished data of T.R.E. Southwood (1967)

b) data collected during 1975 and 1976.

		Distance from Host Plant.					
a)	Year	metres					
		1.4	4.1	9.5	20.0		Total
	1967	78	35	5	1		119
b)		metres					
		2.0	3.5	8.0	11.0	25.0	
	1975	225	25	32	1	1	284
	1976	1391	689	48	19	1	2148

TABLE 3.4 Fit of the six equations to the data from the sticky traps.

Year		Equation Y =	r	prob	Residual M.S.	prob
1970	1	$26.4+397/X$	0.99	<0.01	1784	<0.01
	2	$605-307\ \log X$	0.96	<0.05	19762	<0.05
	3	$4.44+1.08/X$	0.93	ns	0.239	ns
	4	$7.31-1.15\sqrt{X}$	0.88	ns	0.435	ns
	5	$6.42-0.309X$	0.80	ns	0.707	ns
	6	$5.88-0.030X^2$	0.63	ns	1.190	ns
1971	1	$170 + 800/X$	0.99	<0.01	3749	<0.01
	2	$1342 - 624\ \log X$	0.96	<0.05	63523	<0.05
	3	$5.64 + 0.884/X$	0.98	<0.02	0.068	<0.05
	4	$8.01 - 0.959\sqrt{X}$	0.93	ns	0.157	ns
	5	$7.29 - 0.261\ X$	0.86	ns	0.317	ns
	6	$6.86 - 0.027\ X^2$	0.71	ns	0.608	ns
1972	1	$-15.8+3705/X$	0.99	<0.01	261411	<0.01
	2	$5488-2975\ \log X$	0.98	<0.02	423470	<0.05
	3	$5.20 + 1.82/X$	0.71	ns	4.960	ns
	4	$11.30-2.66\sqrt{X}$	0.91	ns	1.640	ns
	5	$9.70 - 0.827X$	0.96	<0.02	0.792	<0.05
	6	$8.80 - 0.106X^2$	0.99	<0.01	0.272	<0.05
1973	1	$349 + 7240/X$	1.00	<0.001	14024	<0.001
	2	$10264-5660\ \log X$	0.97	<0.05	4594970	<0.05
	3	$6.69 + 1.37/X$	0.93	ns	0.414	<0.05
	4	$10.7 - 1.66\sqrt{X}$	0.99	<0.01	0.027	<0.01
	5	$9.53 - 0.477X$	0.97	<0.05	0.190	ns
	6	$8.86 - 0.055X^2$	0.89	ns	0.674	ns
1974	1	$70.9 + 8082/X$	0.99	<0.01	590061	<0.01
	2	$11974-6378\ \log X$	0.98	<0.02	4593888	<0.05
	3	$6.89 + 1.36/X$	0.83	ns	1.210	ns
	4	$11.1 - 1.77\sqrt{X}$	0.96	<0.05	0.317	<0.05
	5	$9.91 - 0.528\ X$	0.97	<0.05	0.241	<0.05
	6	$9.26 - 0.065X^2$	0.95	<0.05	0.398	ns
1975	1	$650 + 5742/X$	0.99	<0.01	142180	<0.01
	2	$7710-4428\ \log X$	0.95	<0.05	4283785	<0.05
	3	$6.00 +1.57/X$	0.94	ns	0.482	ns
	4	$10.5-1.84\sqrt{X}$	0.98	<0.02	0.172	<0.05
	5	$9.17 - 0.528\ X$	0.95	<0.05	0.410	ns
	6	$8.44 - 0.061X^2$	0.87	ns	0.996	ns

TABLE 3.5 Fit of the six equations to the data from the potted trap plants

Year	Equation, Y=	r	prob	Residual	prob
1975	1 $-39.7+ 459.3/X$	0.90	0.05	2187	< 0.05
	2 $200 - 74,1 \log X$	0.77	ns	4931	ns
	3 $0.131+11.0 /X$	0.87	ns	1.83	ns
	4 $6.62 - 1.46\sqrt{X}$	0.86	ns	1.92	ns
	5 $4.48 - 0.208 X$	0.81	ns	2.62	ns
	6 $3.46 - 0.0063 X^2$	0.69	ns	3.88	ns
1976	1 $-243+3230/X$	0.99	<0.001	9112	<0.01
	2 $1503-557 \log X$	0.90	ns	94443	<0.05
	3 $1.22 + 13.9/X$	0.89	<0.05	2.29	<0.05
	4 $10.1 - 2.07\sqrt{X}$	0.99	<0.001	0.128	<0.001
	5 $7.15 - 0.307X$	0.97	<0.01	0.781	<0.01
	6 $5.75 - 0.0099X^2$	0.88	<0.05	2.49	<0.05
1967	1 $-2.54 + 116/X$	0.98	<0.01	58.9	<0.05
	2 $82.5 - 30.2 \log X$	0.97	<0.01	113	<0.05
	3 $0.855+5.48/X$	0.84	ns	1.67	ns
	4 $6.08 - 1.37\sqrt{X}$	0.99	<0.001	0.0677	<0.001
	5 $4.42 - 0.234X$	0.98	<0.01	0.246	<0.05
	6 $3.61 - 0.0096X^2$	0.91	ns	0.968	ns

Overall in group 1 the best fit is given by Paris' (1965) equation which relates density to the reciprocal of distance. Among the density related group, which Freeman (1977) and Taylor (1978) found to give the least residual variance, it is clear that no single equation satisfactorily describes every set of data, but in general Hawkes (1972) provides the best fit. The value of c ($= \frac{1}{2}$) is less than 2, which according to Southwood (1978) indicates 'attraction between individuals inhibiting dispersal'. In Aleurotrachelus this is more likely to be the effect of the habitat than the influence of one individual on one another.

The fits of both Hawkes' and Paris' equations to the data of six years catches on sticky traps are shown in Figure 3.5 and from the trap plants in Figure 3.6.

Detailed studies by such workers as Wolfenbarger (1946) have shown

FIGURE 3.5

(a) Fit of Paris' equation to the data from the data of six year's catches of sticky traps.

(b) Fit of Hawkes' equation to the data from the sticky traps.

FIGURE 3.5(a)

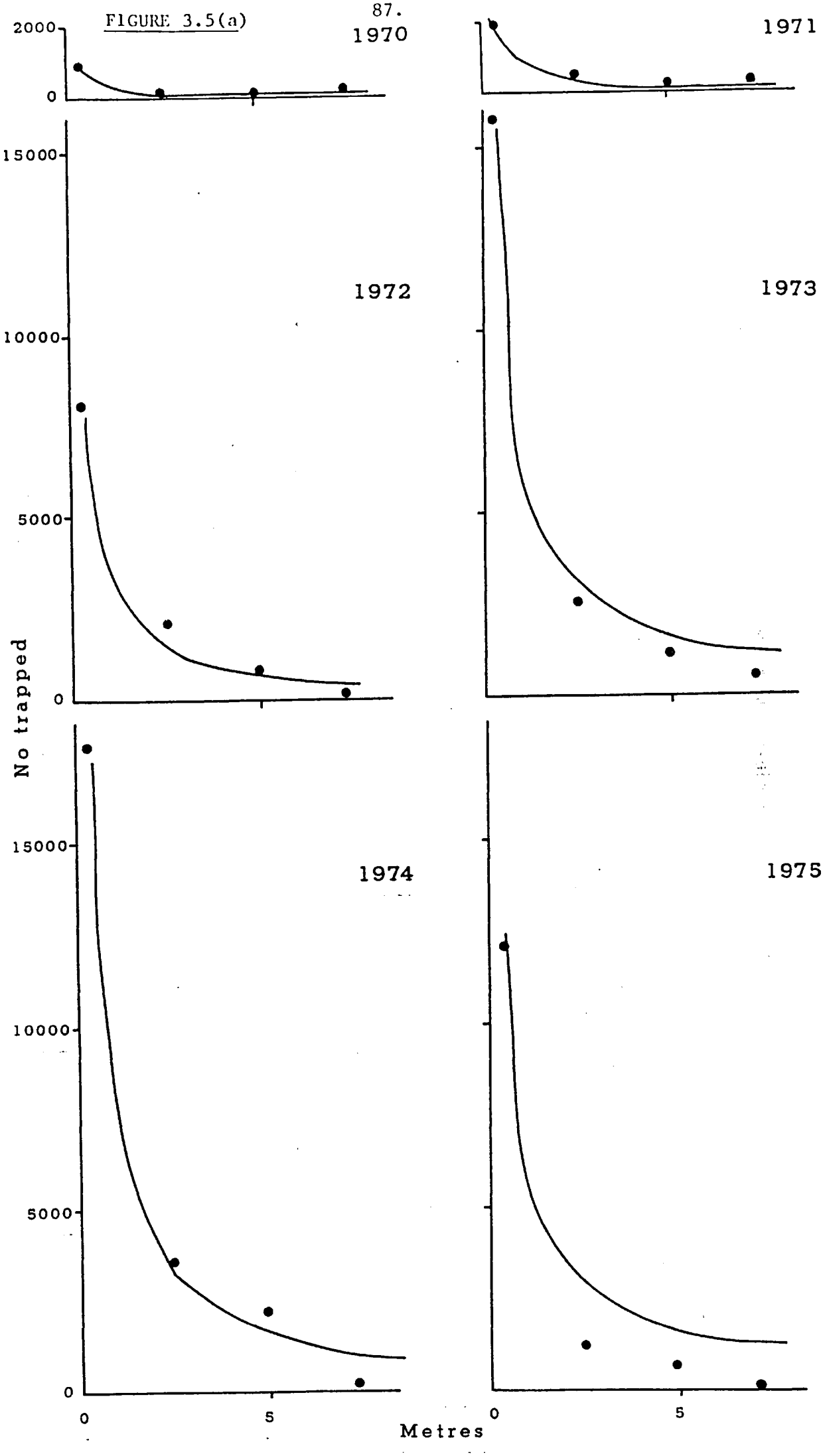

1970
1971
1972
1973
1974
1975
2000
0
15000
10000
5000
0
15000
10000
5000
0
No trapped
0
5
0
5
Metres

FIGURE 3.5(b)

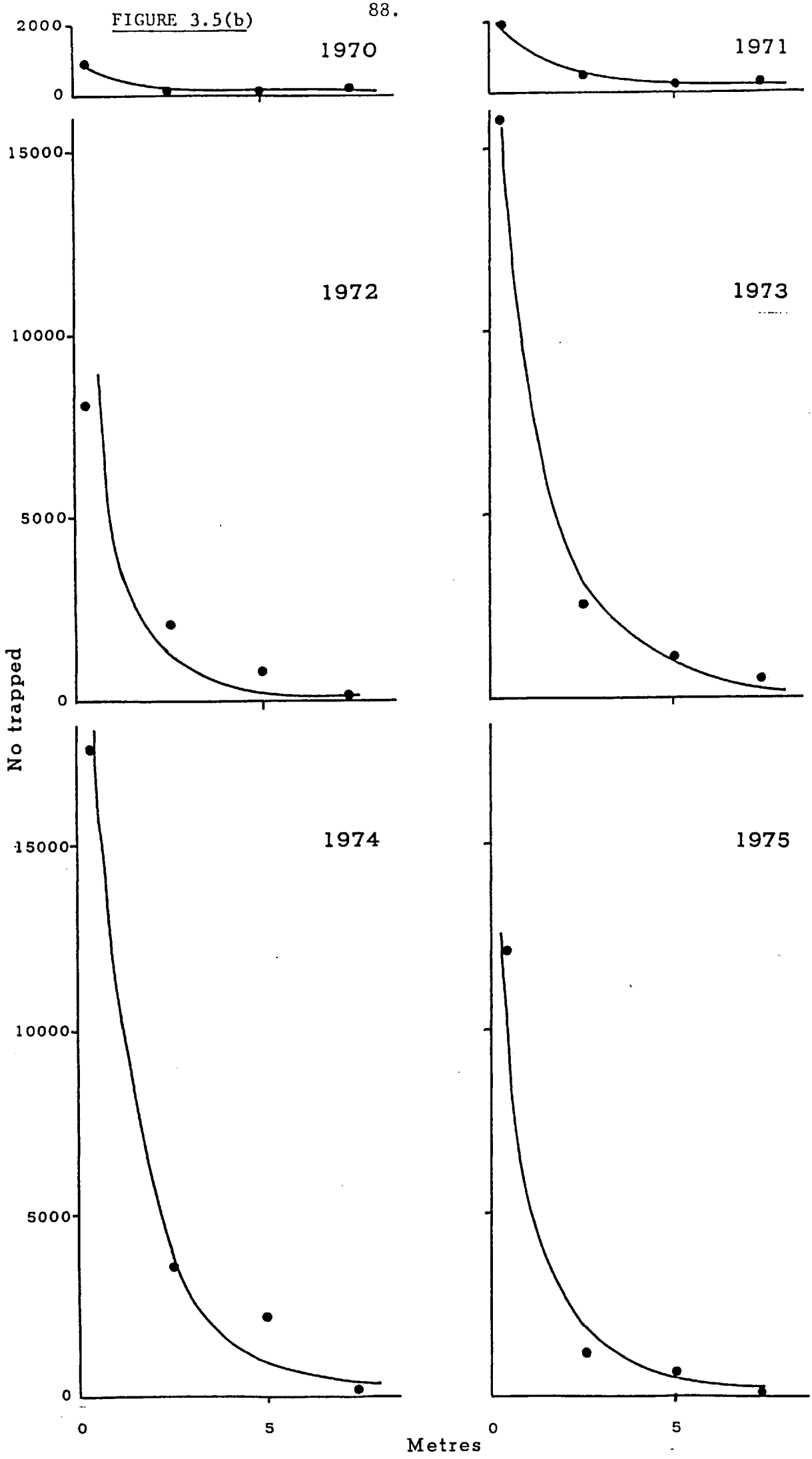

1970
1971
1972
1973
1974
1975
2000
0
15000
10000
5000
0
No trapped
0
5
Metres

FIGURE 3.6

(a) Fit of Paris' equation to the data from the trap plants.

(b) Fit of Hawkes' equation to the data from the trap plants.

FIGURE 3.6(a)

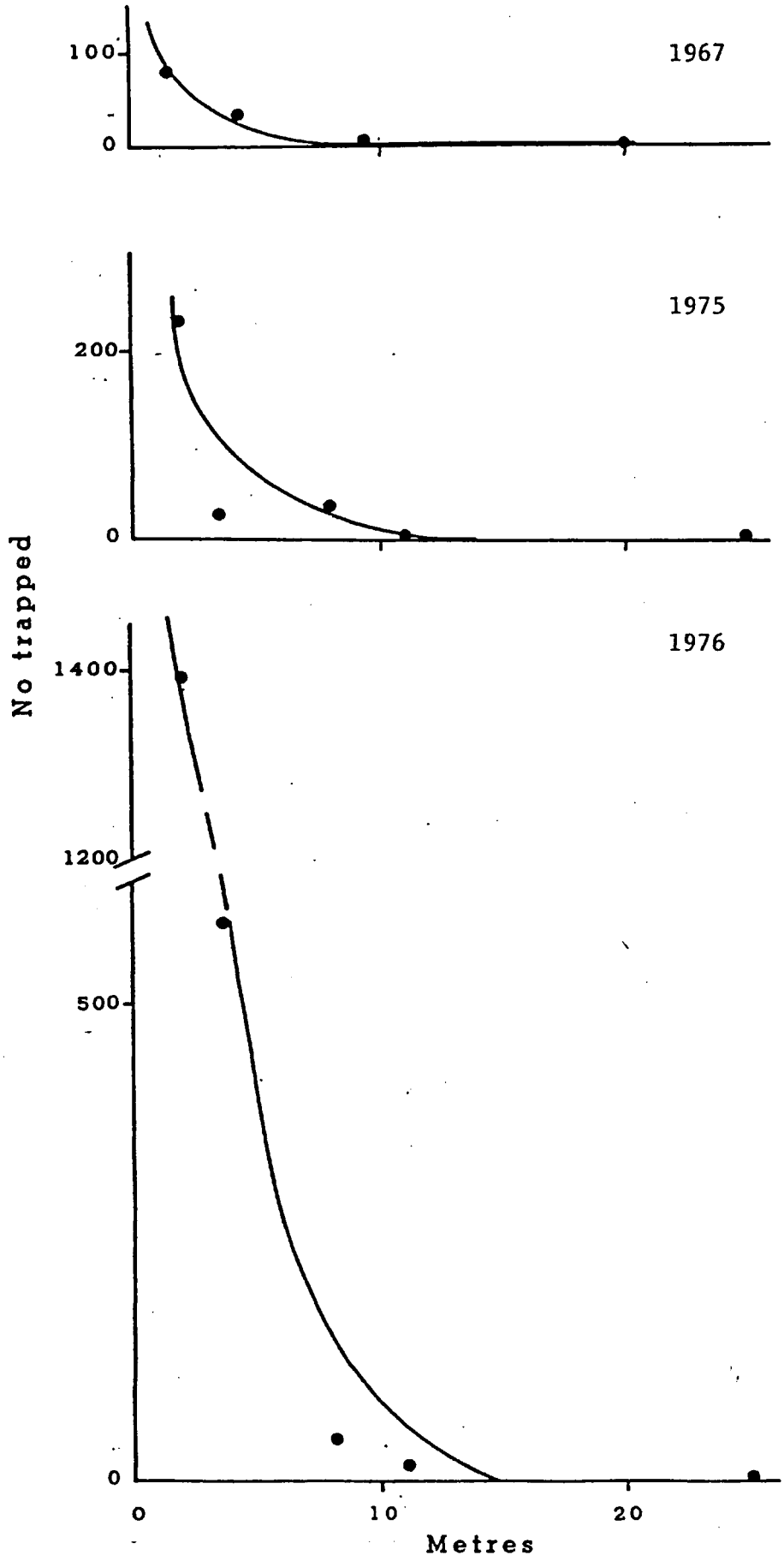
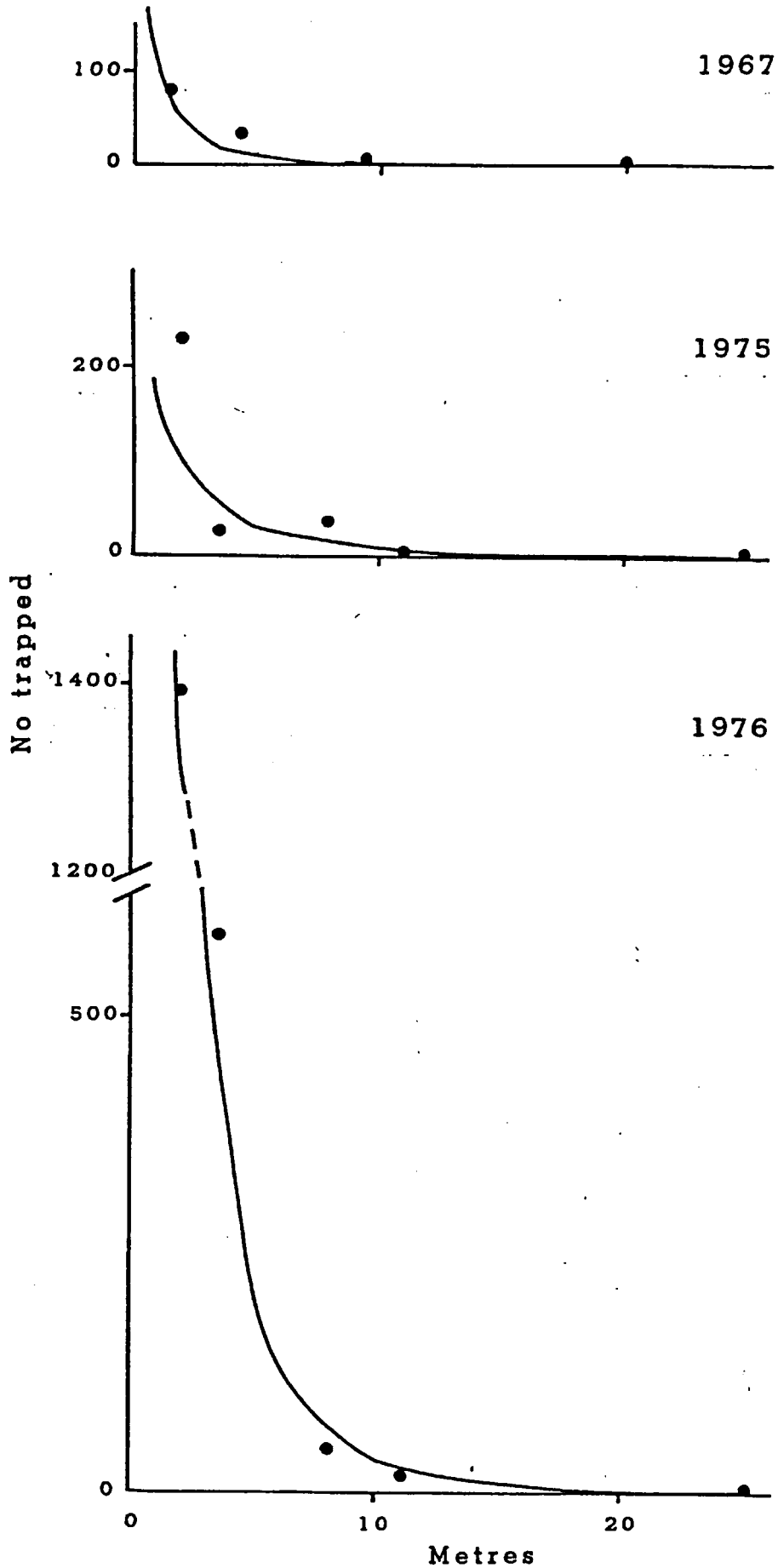

1967
100
0
1975
200
0
1976
1400
1200
500
0
No trapped
0
10
20
Metres

FIGURE 3.6(b)


1967
100
0
1975
200
0
1976
No trapped
1400
1200
500
0
0
10
20
Metres

that species have characteristic relationships between numbers and dispersal, this supports the derivation of an average slope for the years 1970 - 1975. The best fitting models have been applied to the average for these six years and are shown in Figure 3.7.

4. Numbers Caught at Different Heights - A comparison of the height density profiles for the five years (1971 - 1975) with complete sets of traps, corrected for wind speed and number of traps, is shown in Figure 3.8. Both numerically and proportionally less adults are caught on the higher traps. This absence of height in flight of adults of Aleurotrachelus found on the sticky trap data is confirmed by the flight experiment (P.110) when no insects were observed in upward flight. Furthermore the bush was covered by a muslin screen and at no time were any whiteflies seen settling on this.

5. Sex Ratio - The departure from a 50 : 50 sex ratio of adults caught on the sticky traps was tested with regard to population age and size (see Table 3.6).

TABLE 3.6 The departure from 50 : 50 of the sex ratio of whitefly trapped on sticky traps at 5 day intervals after adult emergence (inner traps only)

X o - significantly more males
T - low numbers trapped

Days from emergence	1970	1971	1972	1973	1974	1975
0 - 5	0.46	0.64^{T}	0.65^{xo}	0.81^{xo}	0.74	0.74^{xo}
10	0.67	0.71	0.63^{xo}	0.71^{xo}	0.79^{xo}	0.76^{xo}
15	0.68$_{T}$	0.64	0.69^{xo}	0.74^{xo}	0.65^{xo}	0.70^{xo}
20	0.32$_{T}^{T}$	0.56	0.52	0.54^{xo}	0.61^{xo}	0.60^{xo}
25	0.21$_{T}^{T}$	0.52	0.51	0.62^{xo}	0.60	0.64
30	0.21^{T}	0.47	0.40	0.64	0.67^{xo}	0.61^{xo}
35		0.44	0.48	0.55	0.66^{xo}	0.54
40		0.53	0.56	0.53	0.68	0.41$^{xo}_{\varphi}$
45		0.46	0.45	0.47	0.69	0.43$^{xo}_{\varphi}$
50		0.35	0.43^{xo}	0.47	0.53	0.28$^{xo}_{\varphi}$
55		0.54	0.43	0.59	0.31	0.20$^{xo}_{\varphi}$
60		0.50$_{T}$	0.38$_{T}$	0.39$_{T}$	0.41	0.15$^{xo}_{\varphi}$
65		0.15^{T}	0.32^{T}	0.00^{T}	0.40	0.13) ^{T}
70						0.07)

FIGURE 3.7 Fit of Paris' (1) and Hawkes' (4) equations (the best fitting models) to the average catches for the years 1970 - 1975.

(equations numbered as in Table 3.1 and in Southwood (1978)).

	r	p	Residual M.S.	p
1. $N = -125 + 4328/X$	0.99	< 0.01	36414	< 0.001
2. $N = 6231 - 3395 \log_e X$	0.97	ns	1492568	< 0.05
3. $\log_e N = 6.23 + 1.36/X$	0.90	ns	0.633	ns
4. $\log_e N = 10.30 - 1.69\sqrt{X}$	0.98	< 0.02	0.073	< 0.05
5. $\log_e N = 9.11 - 0.49X$	0.97	< 0.05	0.150	< 0.05
6. $\log_e N = 8.46 - 0.06X^2$	0.92	ns	0.517	ns

FIGURE 3.7

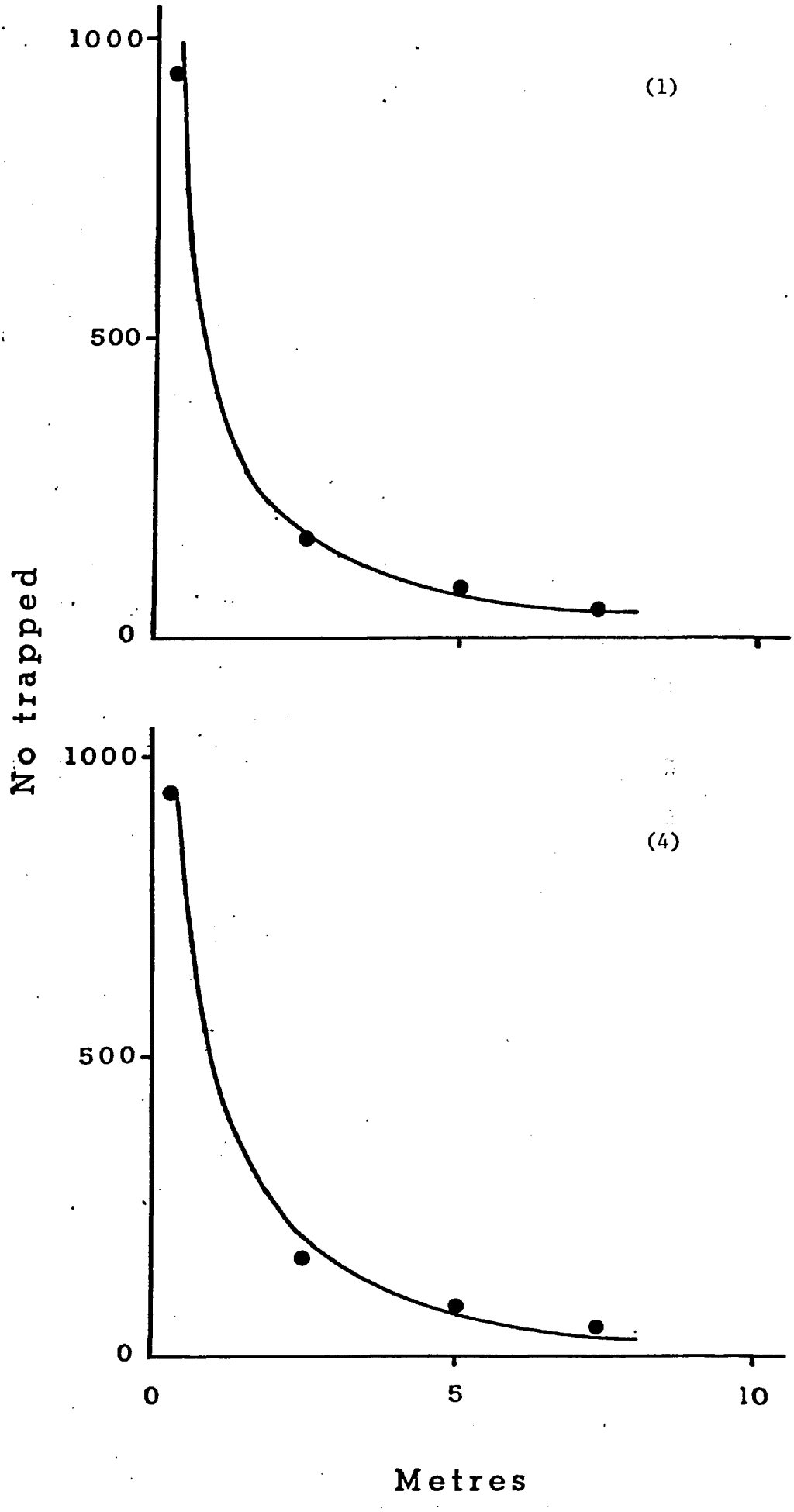
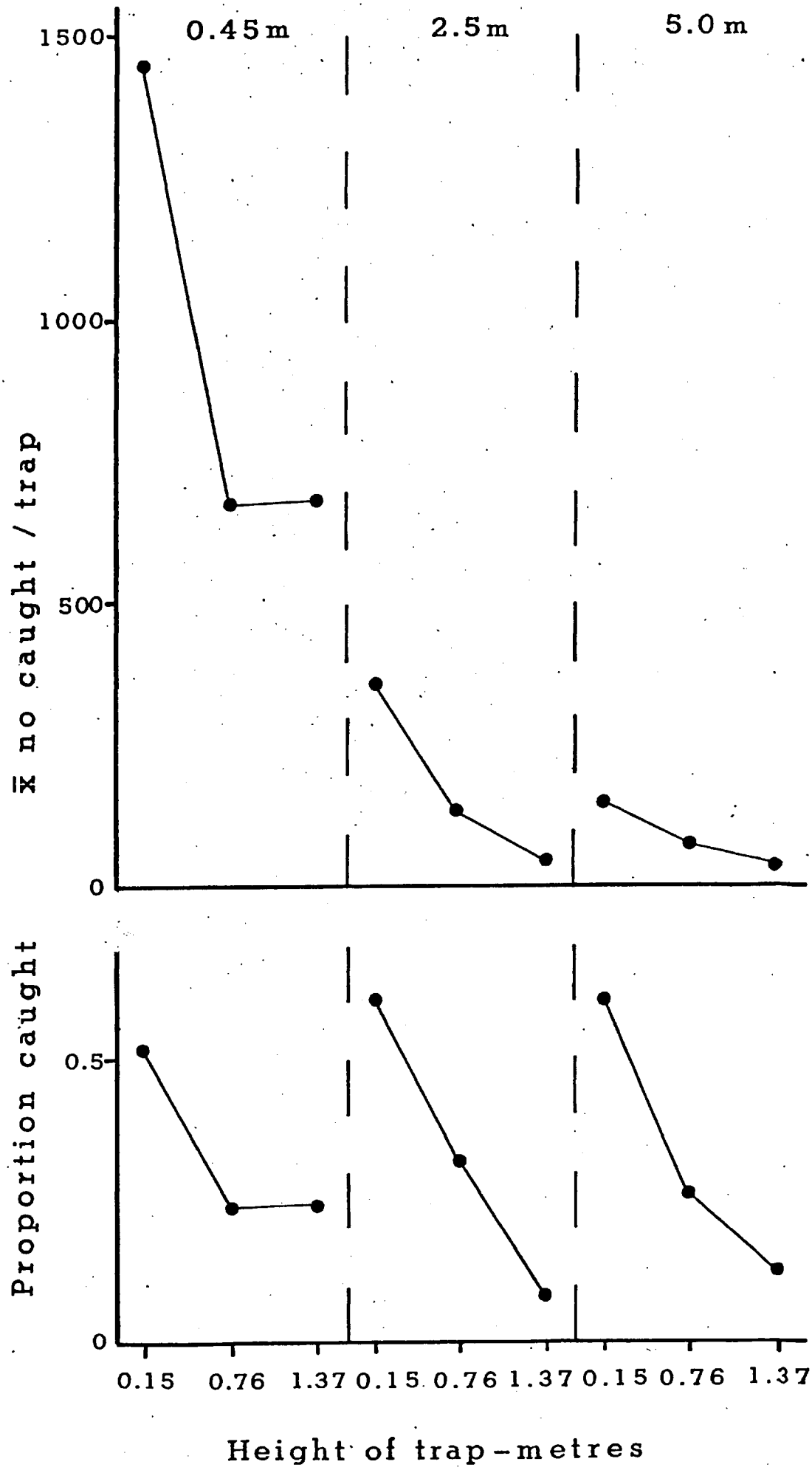


FIGURE 3.8 Numbers caught at different heights 0.45, 2.5 and 5 metres from the bush

a) mean per trap at each height

b) proportion of total catch at each height.

FIGURE 3.8


0.45m
2.5m
5.0m
1500
1000
500
0
x̄ no caught / trap
Proportion caught
0.5
0
0.15 0.76 1.37 0.15 0.76 1.37 0.15 0.76 1.37
Height of trap-metres

The numbers trapped show a significant preponderance of males caught when the population is young (i.e. soon after the beginning of adult emergence when males are in the majority) and relatively more females towards the end of the adult season.

When the sex ratio of adults caught on the inner and outer annuli of traps (see Table 3.7) is compared with the population density per year (Figure 3.9) it is clear that the proportion of males trapped tends to increase as the overall population size rises.

TABLE 3.7 The sex ratio of adults from the inner ring (a) and outer rings (b) of sticky traps
p - probability that no difference exists between the number of males and females

Year	No. migrating	No. males	Proportion of males	Total on bush	p
a)					
1969	110	58	0.53	16322	ns
1970	295	164	0.56	29267	ns
1971	735	345	0.47	46145	ns
1972	2737	1440	0.53	93964	<0.01
1973	5050	3275	0.65	162689	<0.001
1974	5606	3803	0.68	234931	<0.001
1975	5273	3002	0.57	149829	<0.001
b)					
1970	48	24	0.50	29 267	ns
1971	148	56	0.38	46 145	<0.01
1972	493	247	0.5	93 964	ns
1973	763	489	0.64	162689	<0.001
1974	1049	694	0.66	234931	<0.001
1975	495	265	0.54	149829	ns
1976	2186	1545	0.71	275368	<0.001

Similar data from the trap plants is seen in Table 3.8.

FIGURE 3.9 The relationship between the proportion of males caught on the inner traps (A) and outer traps (B) and the adult population on the bush.

A. $Y = 0.49+7.50^{-7}x$ $r = 0.83$ $p<0.02$

B. $Y = 0.40+1.13^{-6}x$ $r = 0.91$ $p<0.01$

FIGURE 3.9

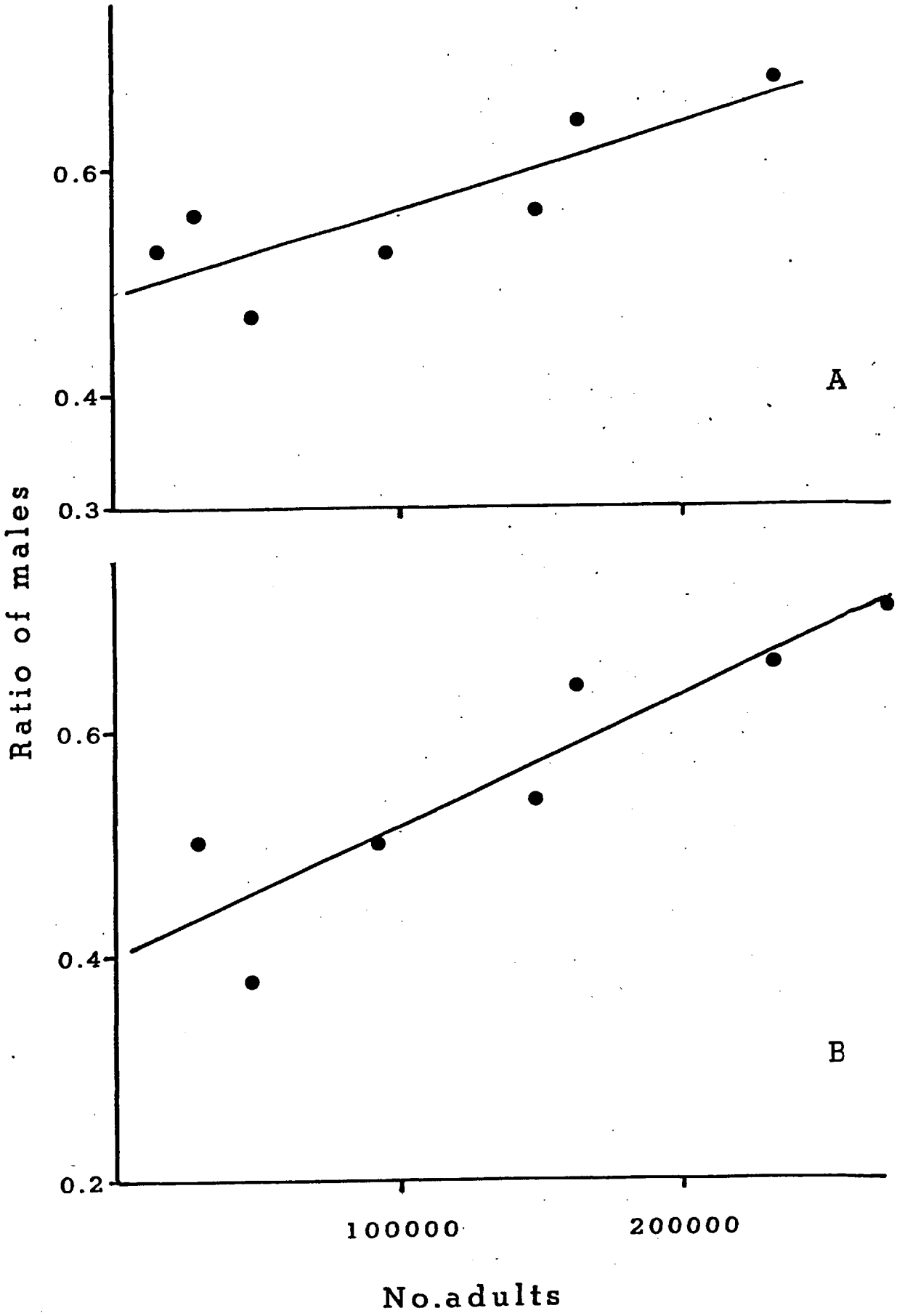


TABLE 3.8 Numbers of males and females caught on trap plants

		Distance of trap plant from bush (metres)					
Year		2.0	3.5	8.0	11.0	25.0	Total
1975	♀	108	13	18	1	1	141
	♂	117	12	14	0	0	143
1976	♀	395	287	16	6	1	705
	♂	996	402	32	13	0	1443

Differences from a 1 : 1 sex ratio gave

$$1975 \quad \chi^2 = 0.014 \quad \text{(ns)}$$

$$1976 \quad \chi^2 = 252.800 \quad (p<0.001)$$

Here the pattern is the same as on sticky traps where more insects leave as the population increases, but that this increase is made up of males.

6. The Influence of Population Size and Density - When the numbers of insects caught on the sticky traps are expressed as a proportion of the total population (see Figure 3.10) there is an indication that movement, at least up to 5 metres from the bush, is density dependent. It may be at higher densities the incidence of 'trivial' flights is greater, but that the insects remain in the vicinity of the bush. When the numbers caught on the three outer rings are compared with those trapped at 0.45m (see Table 3.9), there is no evidence that the proportion found at greater distances is higher at higher population densities, and that longer flights become more frequent as density increases.

FIGURE 3.10

The relationship between log. intensity of adult whitefly on new leaves and the percentage caught of the total population on 10 traps at 4 distances from the bush.

0.45m	$Y = 0.54 + 4.16x$	$r = 0.83$	$p < 0.01$
2.50m	$Y = -0.45 + 1.17x$	$r = 0.76$	$p < 0.05$
5.00m	$Y = -0.26 + 0.57x$	$r = 0.93$	$p < 0.01$
7.30m	$Y = 0.57 - 0.16x$	$r = 0.31$	p ns

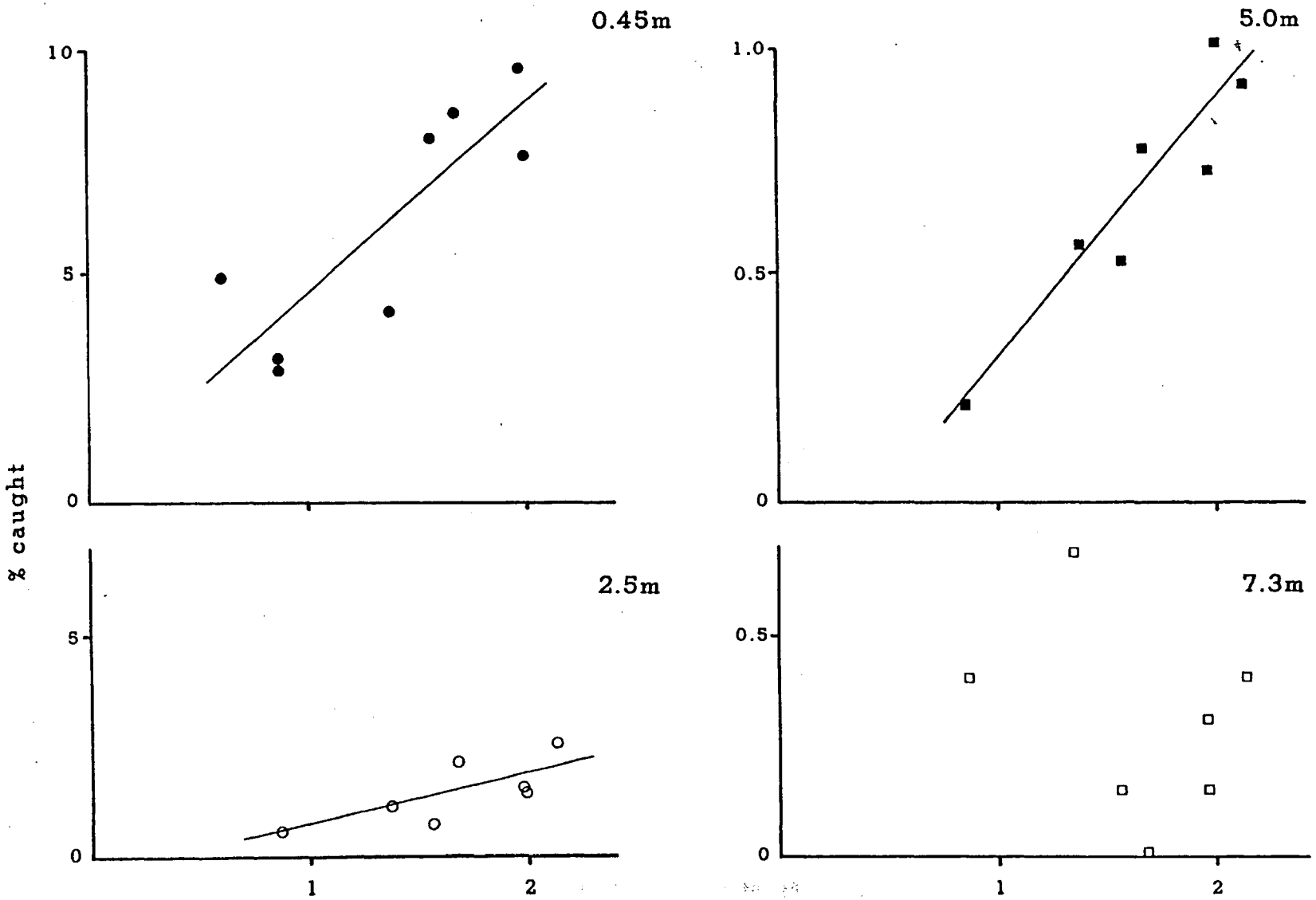


FIGURE 3.10

TABLE 3.9 Proportion of insects trapped on the 3 outer annuli and those at 0.45m.

	Proportion trapped		
Year	0.45/2.5	0.45/5.0	0.45/7.3
1970	4.78	14.81	7.59
1971	3.73	7.54	6.12
1972	4.05	11.26	433.50
1973	6.01	13.43	31.19
1974	5.11	7.66	51.07
1975	10.01	15.30	54.07
r	0.15 (ns)	0.34 (ns)	0.19 (ns)

The data for trap plants is shown in Table 3.10, and although only two years are included the same trend of an increased proportion caught at higher densities is observed.

TABLE 3.10 The percentage of the population caught on trap plants and the population density for the two years 1975 and 1976.

		Percentage of Population at				
Year	Pop. density	2m	3.5m	8.0m	11m	25m
1975	1.56	0.1500	0.0170	0.0210	0.0007	0.0007
1976	2.11	5.0000	0.2500	0.0200	0.0100	0.0004

3.3.2 The experimental assessment of flight and landing characteristics.

1) Effect of Age on Flight Activity - The development of flight activity from adult emergence is shown in Table 3.11 indicating that adult Aleurotrachelus are flight mature after approximately 3 hours.

TABLE 3.11 Flight development time

Time after emergence	Wing condition	Flight Ability
30 mins	partially expanded	nil
75	fully expanded	nil
120		fluttering
165		preliminary flight
210		normal

However, full readiness to take flight takes much longer. When whiteflies of differing ages were tested for take off, from old leaves during a five hour period, there was an asymptotic rise to take off by all insects after eight days (see Figure 3.11).

2) Flight and Landing in a Flight Chamber

a) The duration of flight

The average duration of flight is likely to be an important factor in population dynamics. A long flight may be migratory, but even with trivial or 'station keeping' flights the probability of being carried away from the immediate habitat by gusts of wind increases with flight length. This quality is here expressed as 'flight willingness', and was determined by measuring the mean number of flights in a vertical wind tunnel (see P.73) required to achieve a total flight period of 40 seconds (i.e. the lower the value the greater the 'flight willingness').

The effect of keeping 1 day old adults in various environments is shown in Table 3.12.

FIGURE 3.11. Effect of age on flight activity

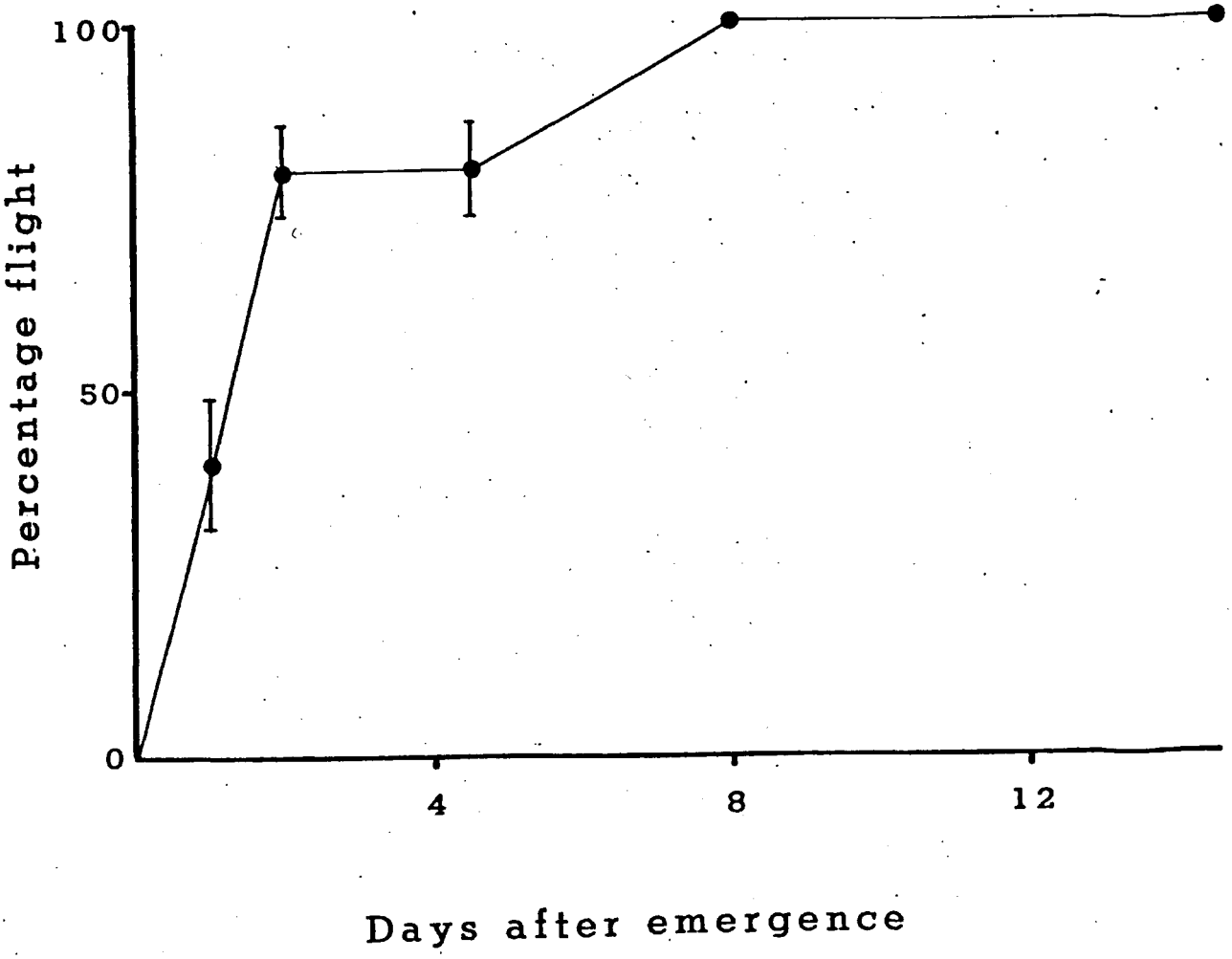


TABLE 3.12 Flight willingness of 1 day old adults in relation to their environment.

Leaf Type	N	Flight Willingness
Rhododendron	9	2.1 ± 1.05 S.D.
Starved	10	3.0 ± 2.00
Viburnum tinus (new leaves)	9	5.89 ± 3.86
Arbutus unedo (new leaves)	5	7.00 ± 3.05
Viburnum tinus (old leaves)	4	8.50 ± 3.11

Insects starved or on Rhododendron were significantly more flight-willing than those on old leaves of Viburnum ($t = 3.99$, $p<0.01$ and $t = 5.73$, $p<0.001$) respectively. Additionally adults from a non-host (Rhododendron) flew more readily than those from new Viburnum leaves. ($t = 2.84$, $p<0.02$). No significant differences in numbers of flights could be detected between adults from old, new or Arbutus leaves. It would therefore appear that Aleurotrachelus will leave an unsuitable or unfavourable environment.

Whiteflies emerge on old leaves, and as has been shown (Figure 3.11) a significant proportion do not fly for several days. The willingness of Aleurotrachelus to fly from old leaves is shown in Table 3.13.

TABLE 3.13 Flight willingness of whitefly of different ages on old leaves.

Age	N	Flight willingness
Newly emerged	8	8.0 ± 4.90
1 day	4	8.5 ± 3.11
2 days	4	5.0 ± 3.46
5 days +	5	2.4 ± 1.95

t-tests showed significant differences in flight willingness between old (5 day) and newly emerged and young (1 day) adults ($t = 2.41$, $p<0.05$; $t = 3.62$, $p<0.01$ respectively). However, no significant differences were found between the 5 day and 2 day adults, the insects preferring to leave old leaves during this time.

b) The length of individual flights

While many flights observed were of extremely short duration some individuals flights were over 10 seconds long and the pattern for these is shown in Table 3.14.

TABLE 3.14 The frequency of individual flight durations by females of more than 10 seconds duration in relation to age of individual

Age	duration of flight - seconds							
Days	11-20	21-50	51-100	101-150	151-200	201-250	$\bar{x}$	S.E.
2	1	1	2	1	3	1	120.8	26.3
3		5	2	3	1		76.5	14.9
6-8	7	10	2	1			33.4	5.5

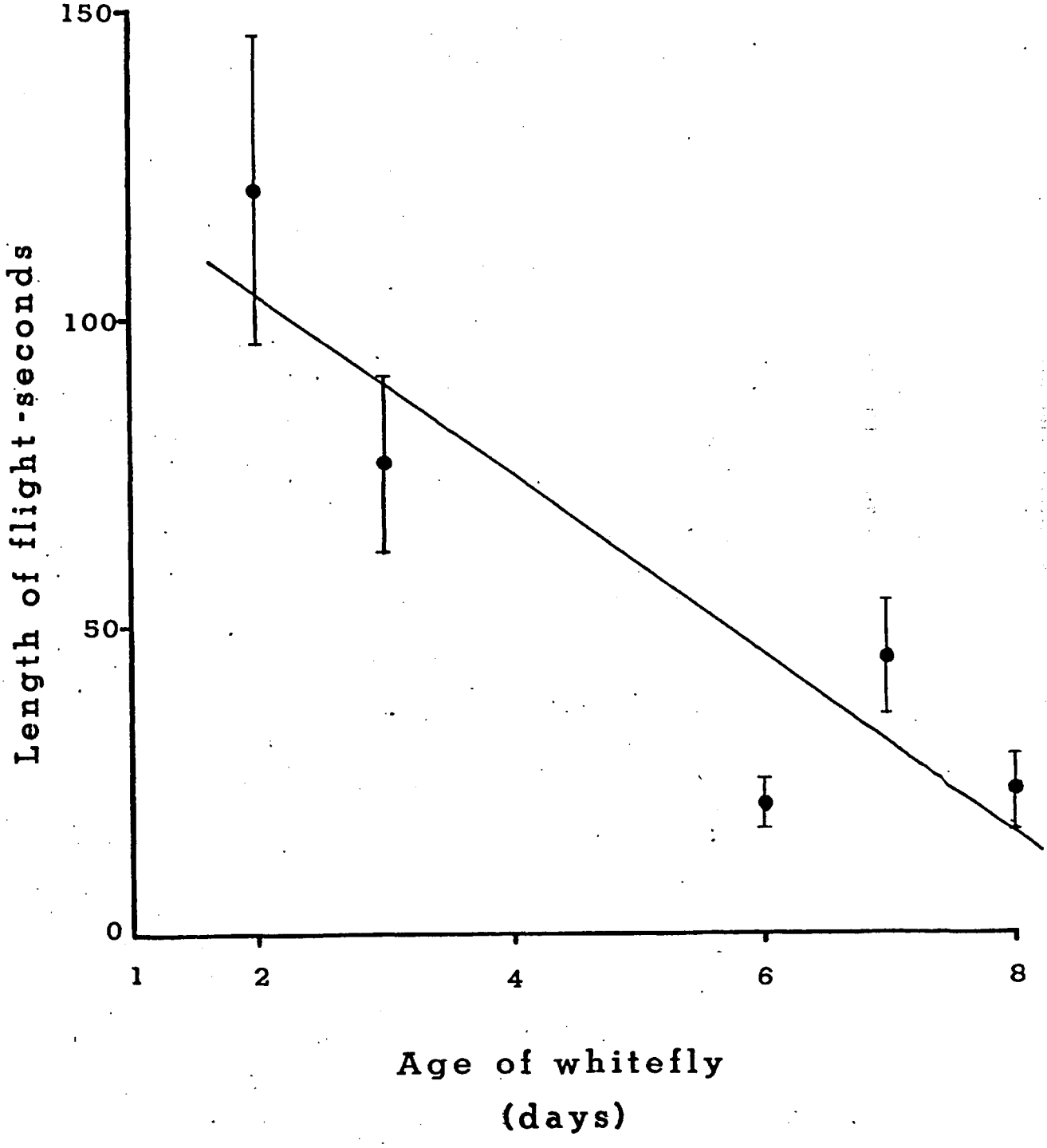
Thus it seems that longer flights occur with younger females, and this is further emphasized by the regression of mean flight duration and age shown in Figure 3.12. Only fourteen males could be flown for longer than 10 seconds and none for longer than 50 seconds. There was no significance with age and it may be that this reflects a tendency for males to be less migratory (Adesiyun and Southwood 1979, Cook, 1967 and Lawson et al 1951), or it may be (as with starvation and crowding in both sexes) no trend was seen due to the small sample.

In addition to these recorded flights, many tests were carried out on both Aleurotrachelus and Trialeurodes. Spontaneous take-offs

FIGURE 3.12

Relationship between flight length and age of female whitefly.

FIGURE 3.12


150
100
50
0
Length of flight-seconds
1
2
4
6
8
Age of whitefly
(days)

were few in Aleurotrachelus and, although on one occasion a flight of 3 minutes was recorded, the insect ranged round the edge of the illuminated centre of the chamber in an erratic manner, settling at the first opportunity. The behaviour of Trialeurodes was similar in most cases, and only one 15 day old male flew longer than the 45 minute prescribed period.

c) Landing site preference

A comparison was made in the flight chamber of the response of Aleurotrachelus and of Aleyrodes to various landing surfaces. Aleurotrachelus landed far more frequently on any plant than on walls or elsewhere (Table 3.15). This was not true of Aleyrodes.

TABLE 3.15 Landing site preferences of Aleurotrachelus and Aleyrodes

	Landing Site		
	Plant	walls/out	
Aleurotrachelus	77	15	92
Aleyrodes	19	29	48
	96	44	140

$\chi^2 = 26.5; \quad p < 0.01$

The difference between the two species was highly significant. The response of Aleurotrachelus seems to be to plants in general, since there was no evidence that more landed on the host plant (Viburnum tinus) than on any other plant (Table 3.16.),

TABLE 3.16 Effects of different host plant on landing preferences of Aleurotrachelus and Aleyrodes

	Type of Plant		
	Viburnum	Brussels sprout	Tomato
Aleurotrachelus plant	11	11	12
walls	3	3	2
Aleyrodes plant	5	10	4
wall/out	12.	9	8

whereas Aleyrodes displayed a tendency to land on crucifers.

3.3.3 Dissections

The state of the ovaries of female Aleurotrachelus jelinekii from both the sticky traps and the potted trap plants did not appear to differ as the population aged, and no trend for these females to represent a group of pre-reproductive individuals could be found.

3.4 DISCUSSION

It is evident that Aleurotrachelus adults are flight mature after approximately three hours (Table 3.12) and are able to fly throughout adult life. Younger females do appear to fly longer than older ones, but the typical flight was only 20 - 50 seconds duration of a somewhat erratic downwards movement, which could not be described as migratory. This is further emphasised by the dissection of females from potted trap plants throughout the season. The expected oogenesis flight syndrome (Johnson 1969) was not found; the ovaries of dispersed females resembled those of insects on the host bush and were in all stages of maturity with no pre-ponderance of immature females as might be expected.

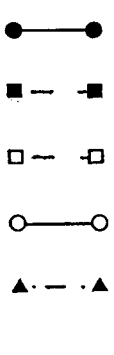
Aleurotrachelus displays no inclination either in the field or the laboratory to remain on old leaves for more than a few days after emergence (Figure 3.11). In fact the degree of favourability of leaves varies throughout adult life and again the laboratory results agree with the life history patterns in that adults prefer to remain on old leaves for the first few days and then move on to new ones which are favoured even under conditions of high density. Recognition of the host plant appears to occur after landing, presumably by probing, non-hosts then proving to be less acceptable.

When the catches are divided according to sex in five day periods for the first five years' data, no obvious trend is apparent, although taken as a whole the data show that significantly more males reach the outer circle of traps. This suggests that the increased number of insects moving and leaving the bush as density rises is made up chiefly of males and not females as one would expect in a migrating population. When Aleurotrachelus is compared with other insects, the decline in aerial density with distance appears to be the steepest known (Figure 3.13) and indicates that the Viburnum whitefly indulges in short flights which only take it short distances from the host plant. Little is known of the range of most whitefly. Iheaghwam (1977) found that winter morphs of the cabbage whitefly achieved a mean of 144 minutes of upward steady flight, whereas the summer morphs resembled Aleurotrachelus and achieved a mean flight of only 0.5 minutes, which lacked the upward steady flight expected in a migrating insect.

Aleurotrachelus appears to be less able than A. proletella to recognise its host plant by visual or olfactory means and must rely on probing after landing. It does however, land on any available green plant and in this resembles other whitefly species. Lloyd (1921) showed that Trialeurodes vaporariorum was attracted to yellow traps, and since then Vaishompayan et al (1975a) found a similar response in the same species to light in the yellow - green range. They assumed that visual orientation is a major factor in host finding behaviour of whiteflies, although odour may play a minor role in orientation and landing (Vaishampayan et al. 1975b). Van Lenteren et al (1977) and Verschoor-van der Poet et al (1978) obtained similar results again with Trialeurodes and found that it is after landing that the most important part of host selection occurs. This appears also to be the case in the citrus blackfly - Aleurocanthus woglumi (Dowell 1979).

FIGURE 3.13

Decline in aerial density with distance



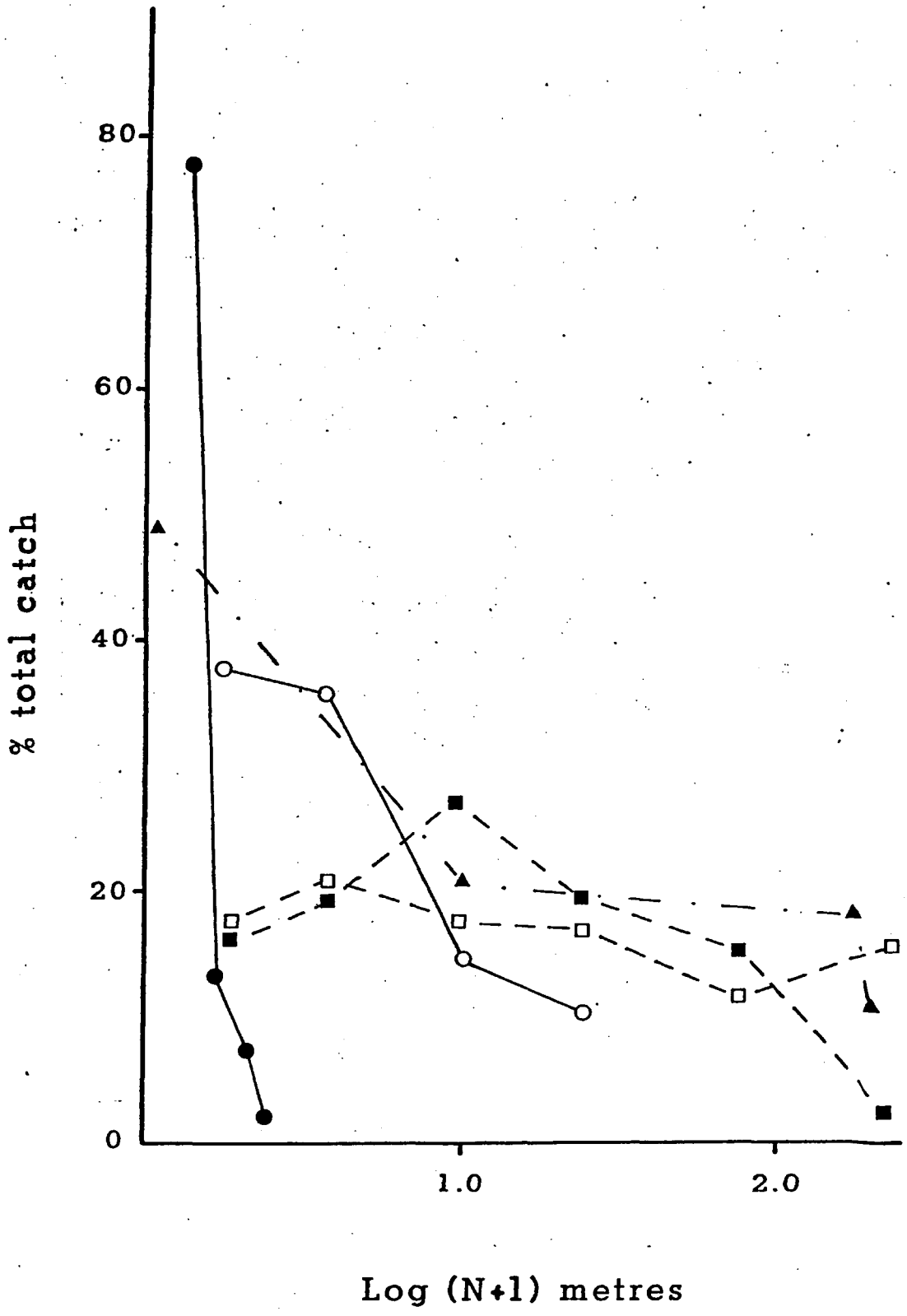
●——● – Aleurotrachelus jelinekii

■– –■ – Ascidema obsoletum)
) Waloff and Bakker (1963)
□– –□ – Orthotylus virescens)

○——○ – Cicadulina mbula — Rose (1971, 1973)

▲·– ·▲ – Oscinella frit — Southwood, Jepson and van Emden (1961)

FIGURE 3.13



The cabbage whitefly was found to be more likely to colonise a brussels sprout plant in bare ground than those surrounded by weeds (Smith 1969 a and b), while Trehan (1940) found this whitefly to be attracted to yellow light. Moericke (reported in Smith 1969b) found the influence of ultra violet on landing behaviour was greater than in most aphids. The tobacco whitefly was found by Mound (1962) to be sensitive to both ultra violet and yellow light and concluded the two provided a complementary balance between migratory (ultra violet) and vegetative (yellow) behaviour.

Dingle and Arora (1973) suggested four criteria which could be applied to migrating insects.

1. The type of locomotory behaviour, and whether or not this could be described as migratory.
2. The existence of a oogenesis flight syndrome which inhibits flight after oocyte development.
3. The fact that most migrants are 'denizens of temporary habitats'.
4. Most migrants have life history strategies which emphasise productivity.

When these are applied to Aleurotrachelus, no positive association could be seen, for at no time did Aleurotrachelus show any preference for long flights, they always landed as soon as possible on any type of plant and showed no evidence of host discrimination. These flights occurred throughout adult life and even females which flew a distance had ovaries in a similar condition to insects on the bush. Thirdly, Aleurotrachelus displays little mobility between habitats. This is shown both by the steep gradient in fall off in dispersal with distance and by the value of C (≤ 2) in equation (3.2) which implies an increased aggregation round the original source. This is further emphasised

by estimating the number of insects reaching 0.45m from the bush, which as density rises represents a greater number of insects than recorded for the total population, indicating that adults are 'flitting' in the vicinity of the bush in proportion to the density available. Finally, Aleurotrachelus' life history strategy is not one of rapid population growth, for it has one generation per year, and in the main preserves low population levels.

In conclusion, the only time Aleurotrachelus could be regarded as a migrating species according to Johnson's (1969) definition is during the movement from old leaves to new before the onset of egg laying, which constitutes a movement from one breeding site to another. This is followed by a long period of trivial flight akin to the situation found in the sycamore aphid (Dixon 1969) in which trivial flight is used to redistribute insects throughout the host plant, or from patch to patch (Hassell and Southwood 1978) and not from habitat to habitat. When density is high, some dispersal from the host plant may occur, but this appears to be unsuccessful when the different levels of populations on nearby bushes are examined.

CHAPTER 4 - PREDATORS

4.1 INTRODUCTION

Aleurotrachelus jelinekii is the only herbivore, and indeed the only small invertebrate, found in any numbers on the Viburnum tinus bushes at Silwood Park. It therefore seemed reasonable to assume that any predator found on the bushes was feeding almost exclusively on the whitefly. This chapter gives estimates of the numbers of these predators and examines some of their responses to population density in the field. The significance of these to the population dynamics of the insect is considered in Chapter 6.

The main predators of Aleurotrachelus found during the study were: spiders (predators of only the adult stage), a predaceous mirid and the larvae of a neuropteran. Spiders were found on all the bushes, the most common species being the web-spinning Linyphia triagularis, and Metasegmentata. The mirid, Campyloneura virgula (Herrich-Schaeffer), feeds on all stages (Southwood and Leston 1959) as does the coniopterygid, Conwentzia psociformis (Curtis). The phenology of these species in relation to whitefly life history is shown in Fig. 4.1.

The other predators found on the bushes are not thought to have a major impact on the adult population, both because of their low numbers and their infrequent appearance. Encarsia tricolor (Foerster), the parasitoid of the cabbage whitefly will also parasitise Aleurotrachelus, and after disappearing from the study site in the early 1960's has reinvaded the population on Bush A as the numbers of individuals there have increased. The effect of larval parasitism on the insect will be discussed in a future publication and here it is merely noted that adult Encarsia will act as occasional predators due to their host feeding activities (Gerling 1966, Nell et al. 1976). A few individual syrphid and drosophilid larvae (Acletoxenus formosus Loew) have also been found

FIGURE 4.1 Phenology of Aleurotrachelus and its 3 main predators.

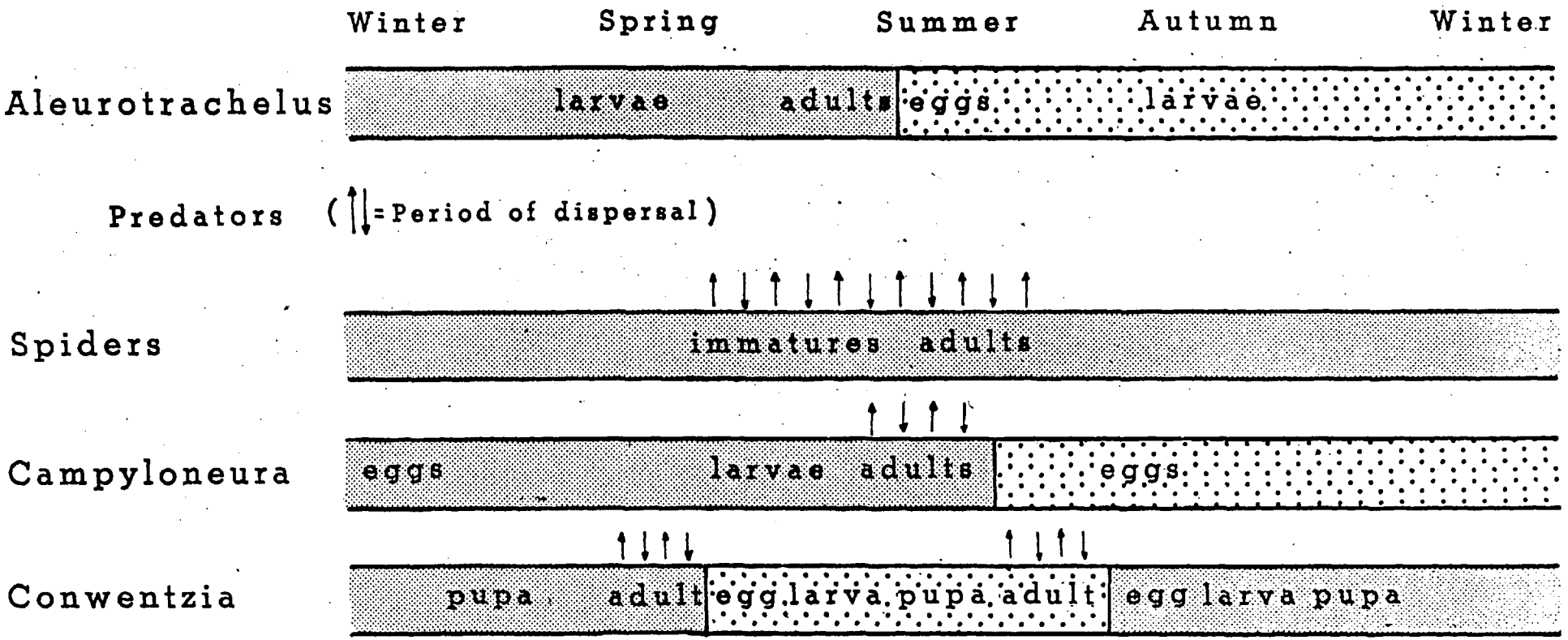

Winter
Spring
Summer
Autumn
Winter
Aleurotrachelus
larvae
adults
eggs
larvae
Predators
(↑↓=Period of dispersal)
Spiders
immatures
adults
Campyloneura
eggs
larvae
adults
eggs
Conwentzia
pupa
adult
egg
larva
pupa
adult
egg
larva
pupa

FIGURE 4.1

on bushes A and B.

4.2 METHODS AND RESULTS

Different sampling methods were used for estimating spider numbers from other predators.

1) Spiders. The number of webs on each bush was counted daily and each web was assumed to represent one spider. The whitefly caught in the webs were readily visible, and after counting were marked with rotor dye dissolved in acetone. This was applied with a hypodermic syringe, the acetone evaporating quickly leaving the insect clearly marked.

2) The other predators found on the leaves were estimated by counting all insects in a sample of 25 old and 25 new leaves. During the adult season samples were taken every two days. The estimate for any one year consists of a mean for all the sampling dates during the adult whitefly life.

4.2.1 Spiders

The mean number of spiders for each season compared with mean adult whitefly density per leaf for the same period is shown in Fig. 4.2. The numbers of spiders is variable and there is no discernable increase in their number as the population density of the whiteflies rises on either bush A or B. Furthermore the number of spiders found on both bushes did not differ significantly even with their markedly different levels of population density.

As expected the total number of whitefly trapped in webs is related to spider numbers (Fig. 4.3), but the number trapped per spider showed no such relationship (Fig. 4.4). These relationships are not surprising and merely confirm the lack of any interference between spiders

FIGURE 4.2 Mean numbers of spiders per season compared with prey density

A. $Y = 16.52 + 1.11x$ $r = 0.45$ (ns)

B. $Y = 16.07 - 0.14x$ $r = 0.18$ (ns)

FIGURE 4.2

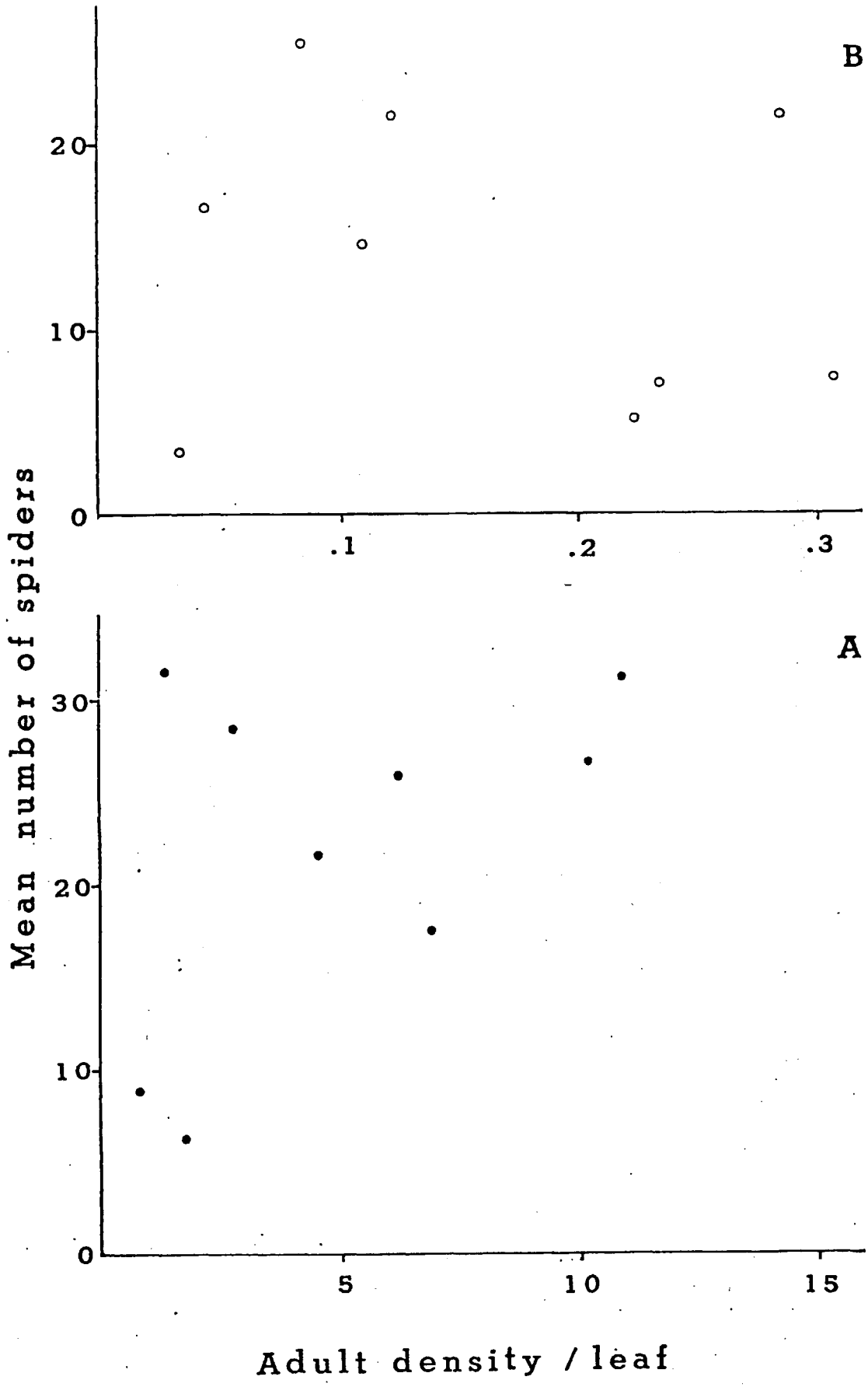

B
20
10
0
.1
.2
.3
A
30
20
10
0
5
10
15
Mean number of spiders
Adult density / leaf

FIGURE 4.3 Total number of whitefly trapped against spider density during the seasons 1968 - 1976 on bushes A and B.

●▼ - higher number than expected

●△ - lower number than expected

A. $Y = 80.37 + 11.44\ x \quad r = 0.77 \quad p<0.02$

B. $Y = 24.58 + 5.04\ x \quad r = 0.93 \quad p<0.001$

FIGURE 4.3

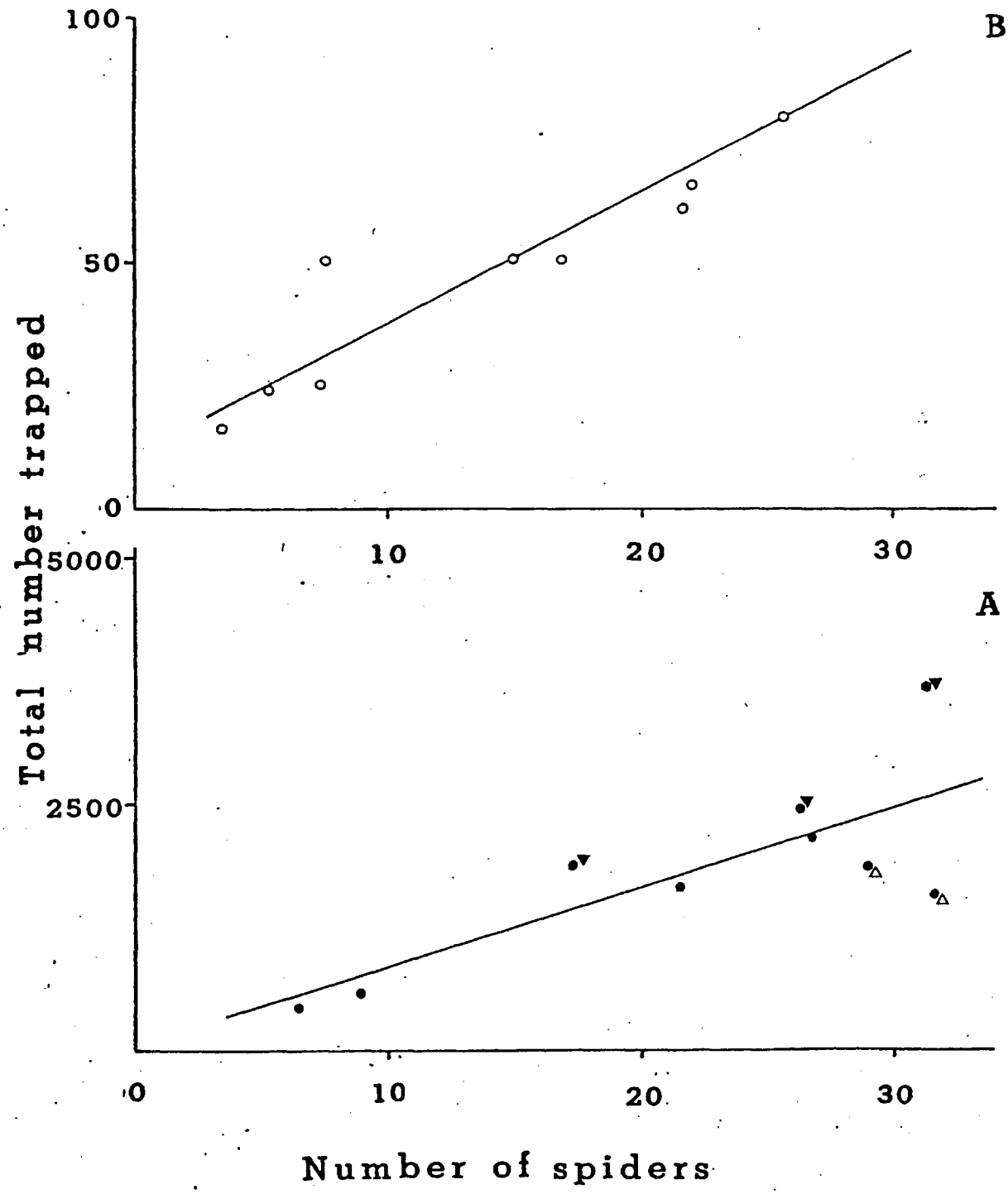
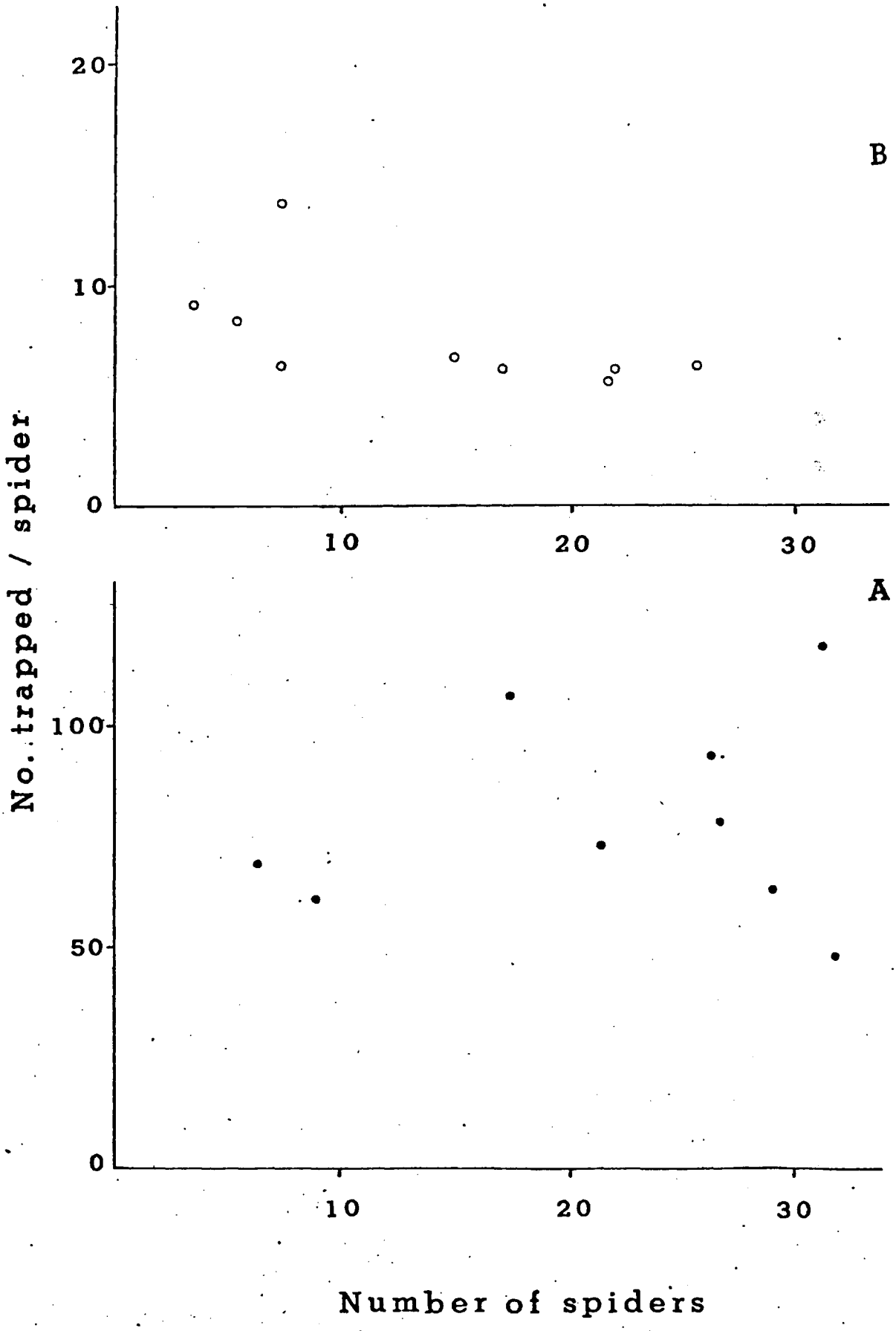

100
50
0
B
5000
2500
A
Total number trapped
0
10
20
30
Number of spiders

FIGURE 4.4 Mean number trapped per spider compared with the mean number of spiders for that season for years 1968 - 1976 on bushes A and B.

A. $Y = 71.13 + 0.38\,x \quad r = 0.16$ (ns)

B. $Y = 10.26 - 0.19\,x \quad r = 0.59$ (ns)

FIGURE 4.4


20
10
0
B
10
20
30
A
No. trapped / spider
100
50
0
10
20
30
Number of spiders

as their density rises. A more interesting relationship is shown in Fig. 4.5 in which the numbers trapped per spider rises with whitefly density on bush A alone. The points marked ▼ and ▽ correspond to the similarly marked ones in Fig. 4.3, in which respectively more, or less, whitefly were trapped than predicted by the linear relationship. The relative effect of these factors is clear from Fig. 4.6, which shows a declining percentage trapped as whitefly density rises. The relationship in Fig. 4.5 would have to be much steeper to be reversed to one of direct density dependence. Thus, neither on bushes A or B do spiders appear to contribute to the stability of the whitefly populations. This may be due in part to the very slow numerical response of the spiders, with only one generation per year. Additionally it is interesting to note that whitefly do not represent the main prey of spiders throughout the year and both bushes support similar spider populations.

4.2.2 Other Predators

When the total number of predator species is plotted against adult whitefly density (Fig. 4.7) for bushes A and B, A shows a positive correlation between adult density and species richness, whereas the two appear unrelated on the less dense bush - B. It may be that the lower densities on A show the same picture, and as the population rises it is exploited by an increasing number of predator species. The seasonal fluctuation in predator species number can be seen in Fig. 4.8.

If this species richness is converted into total number of individual predators no correlation is seen on either bush (Fig. 4.9). These data were then broken down into the three species which occurred in the highest numbers (i.e. C. virgula, C. psociformis and the syrphid larvae) (see Appendix 4.1) only the coniopterygids (C. psociformis) showed a positive relationship with whitefly density per leaf as shown

FIGURE 4.5 Mean number of whitefly trapped per spider compared with prey density on bushes A and B

A. $Y = 54.75 + 4.94x \quad r = 0.81 \quad p<0.01$

B. $Y = 7.11 + 0.03x \quad r = 0.13$ ns

●▼ - higher number than expected

●△ - lower number than expected

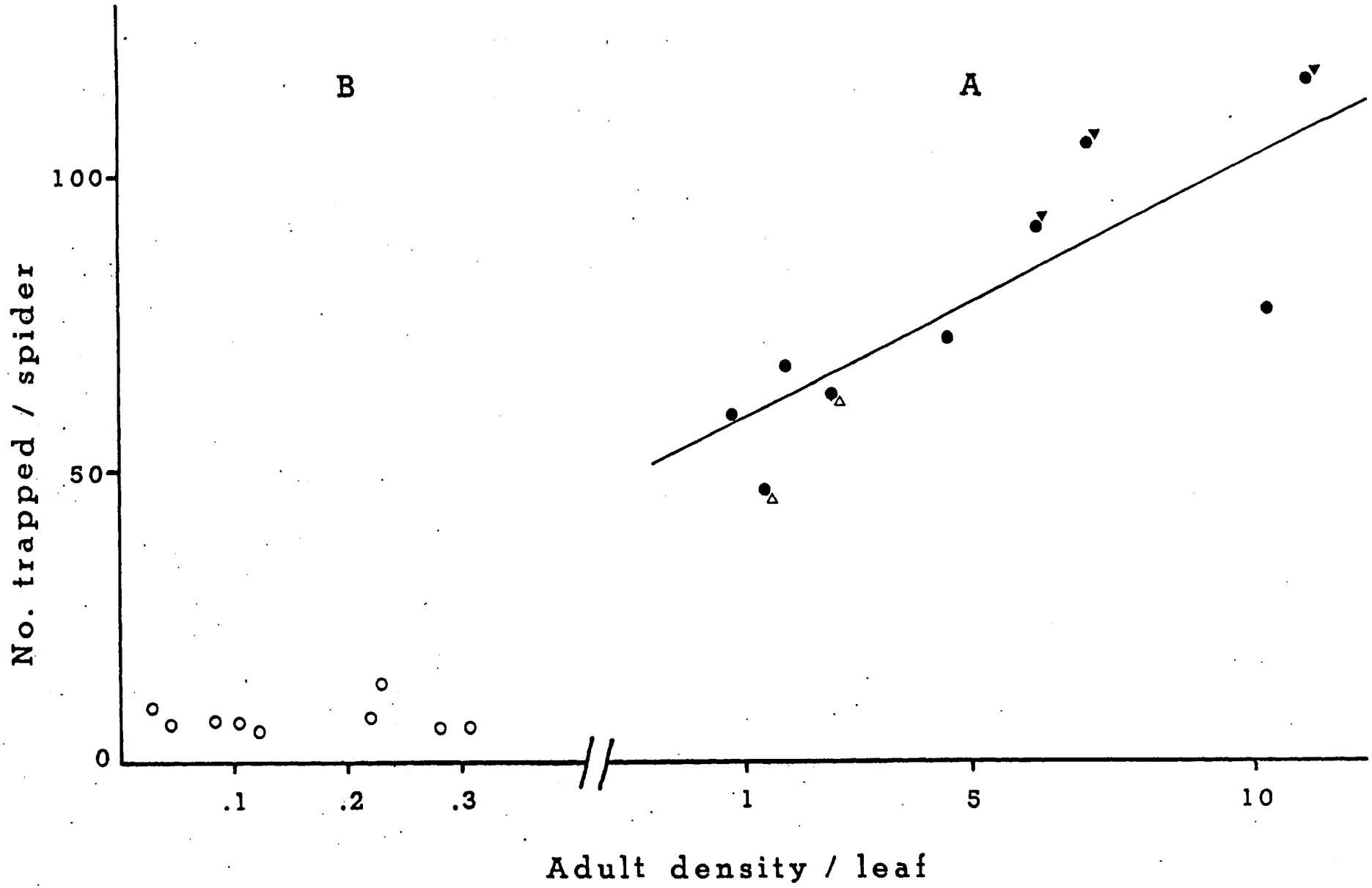


FIGURE 4.5

FIGURE 4.6 Percentage of the adult population of whitefly trapped by spiders compared with log. population density.

A. $Y = 20.54 - 13.34\ x \quad r = 0.76, \quad p < 0.02$

B. $Y = 4.93 - 3.77\ x \quad r = 0.88 \quad p < 0.01$

FIGURE 4.6

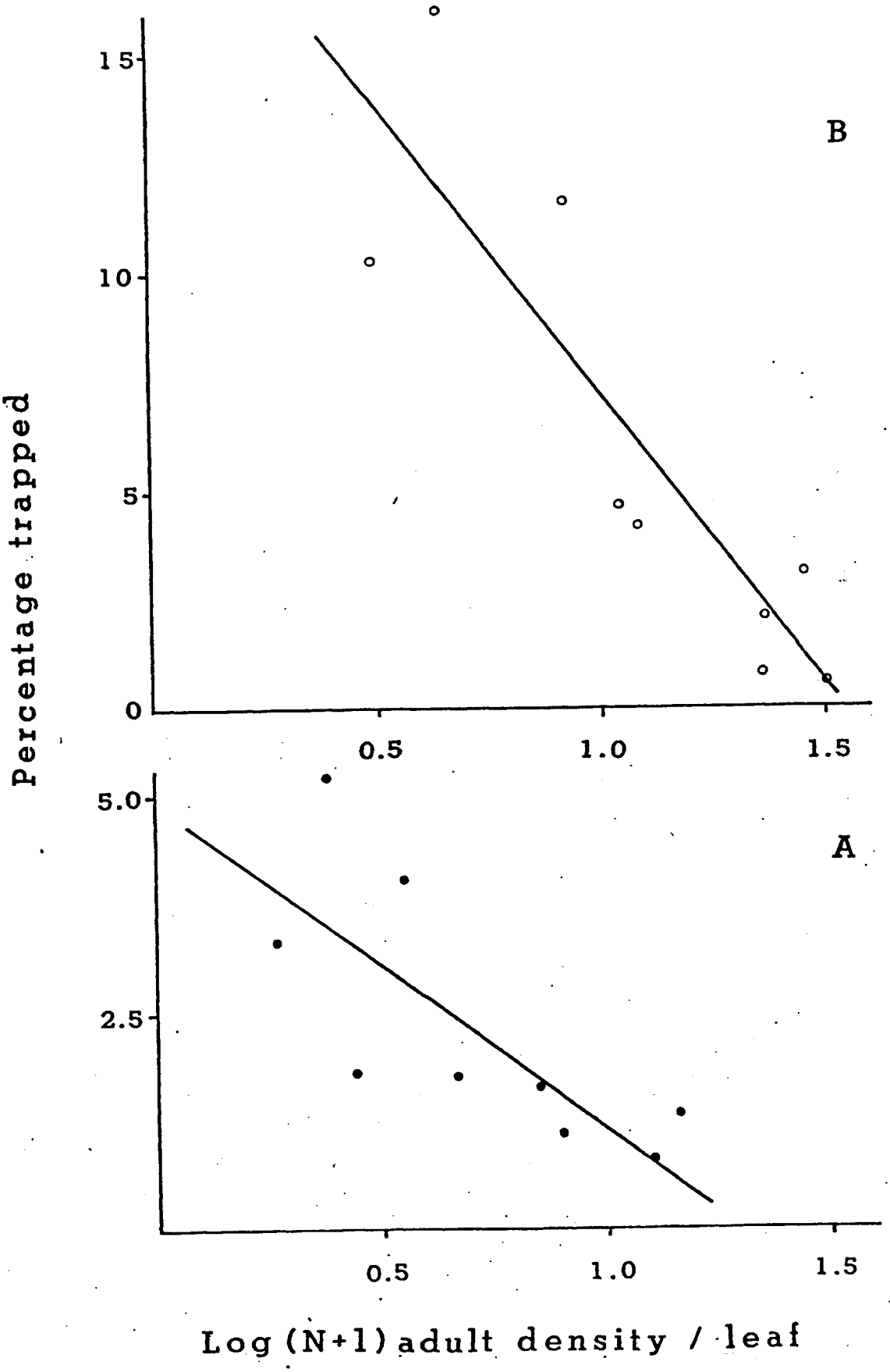

Percentage trapped
15
10
5
0
0.5
1.0
1.5
B
5.0
2.5
0.5
1.0
1.5
A
Log (N+1) adult density / leaf

FIGURE 4.7 Total number of predator species found at different densities of whitefly per leaf on bushes A - B

o = Bush B

● = Bush A

A. $Y = 1.15 + 0.41\ x$ $r = 0.87$ $p<0.01$

B. $Y = 2.36 + 1.51\ x$ $r = 0.23$ ns

FIGURE 4.7

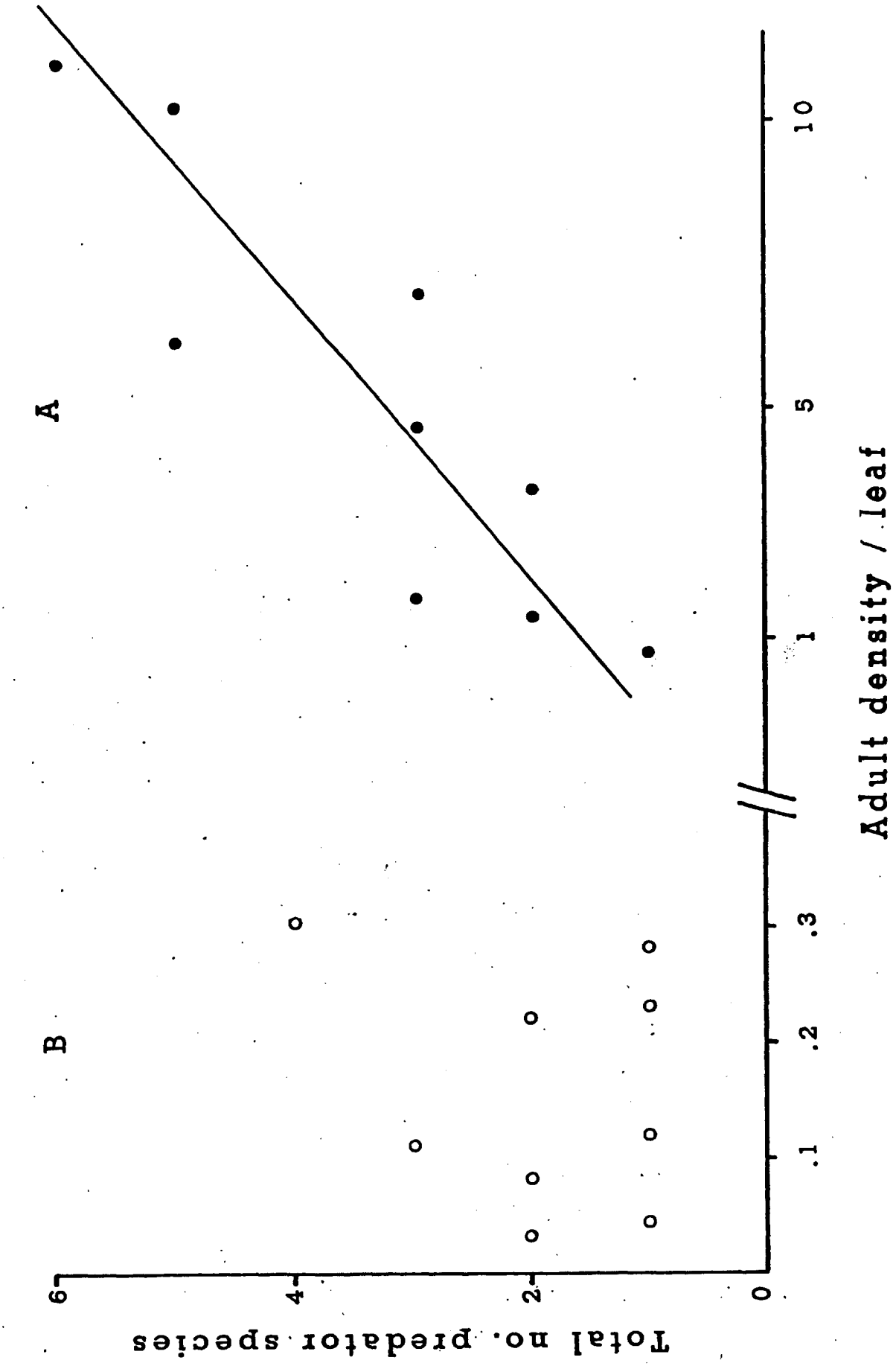

A
B
Total no. predator species
0
2
4
6
.1
.2
.3
1
5
10
Adult density / leaf

FIGURE 4.8 Seasonal variations in numbers of predator species.

FIGURE 4.8

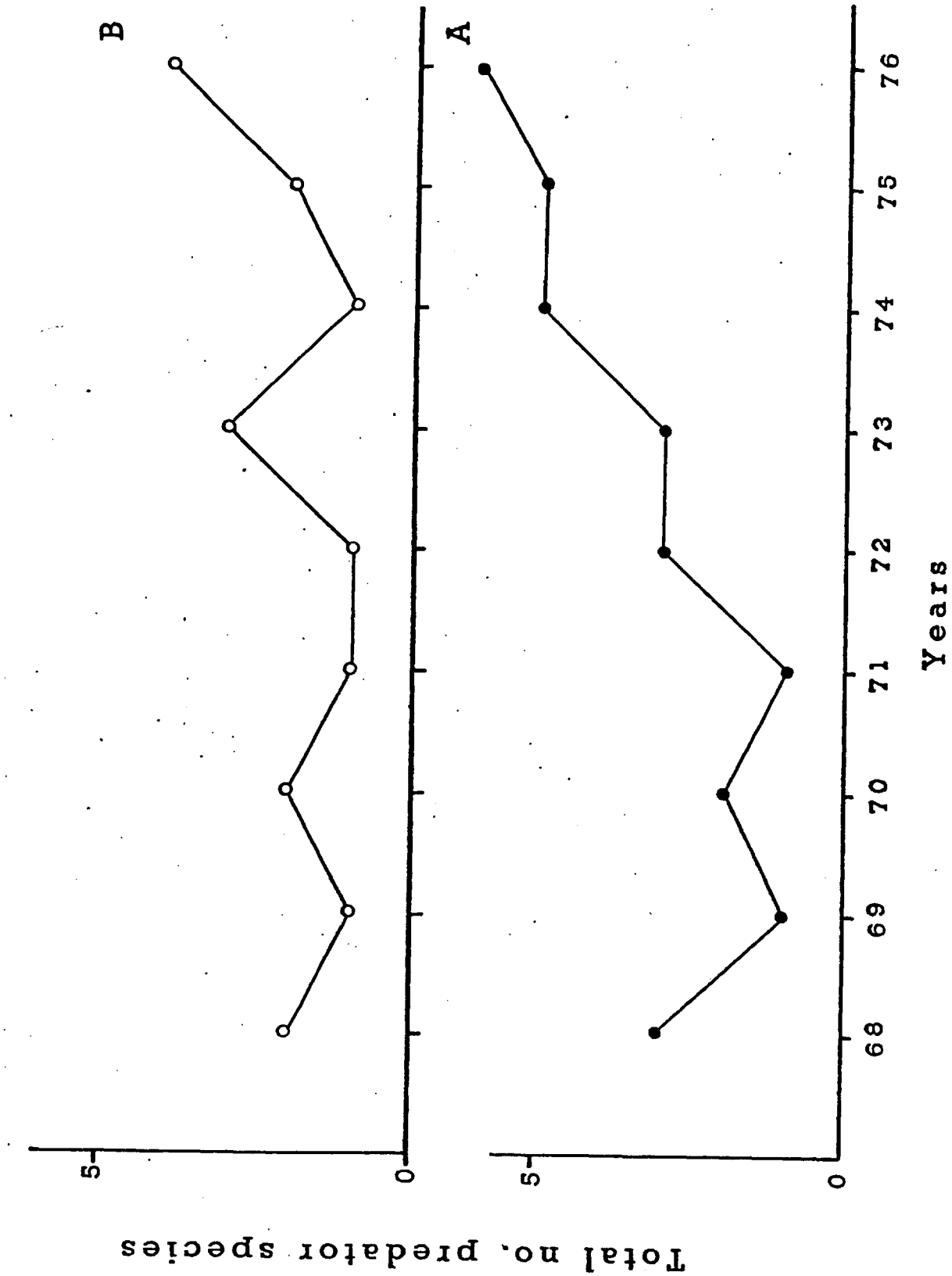
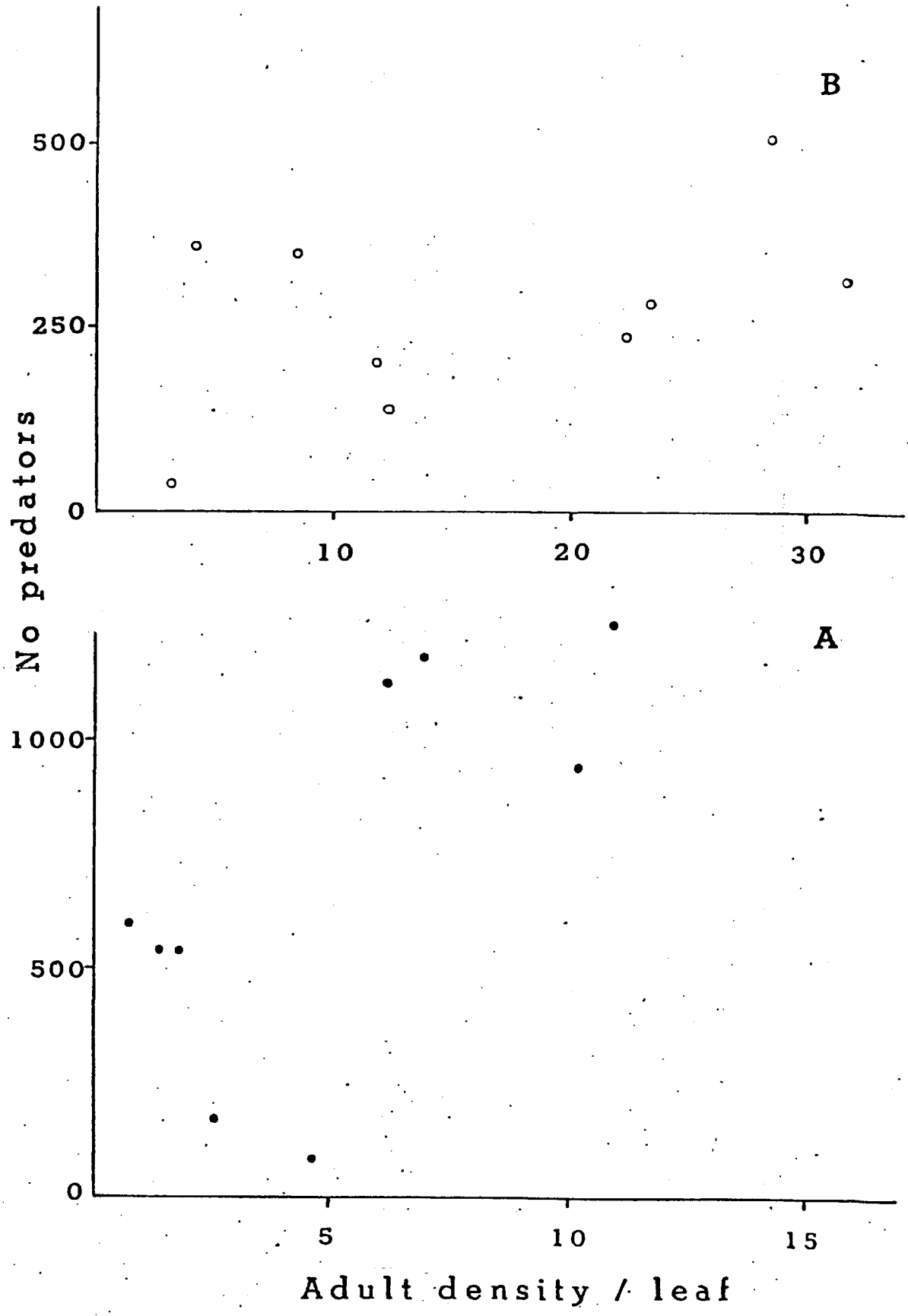

B
A
5
0
5
0
68
69
70
71
72
73
74
75
76
Years
Total no. predator species

FIGURE 4.9

Relationship between the total number of predator species and population density on Bushes A and B.

FIGURE 4.9


B
500
250
0
10
20
30
No predators
A
1000
500
0
5
10
15
Adult density / leaf

in Fig. 4.10. This could be a result of the life history of these insects, which have several generations a year, and therefore should have a more rapid numerical response.

4.3 DISCUSSION

Viburnum tinus appears to be an unattractive host for herbivores. Presumably this stems from its recent and relatively sparse introduction into Britain and its inherent characters including low nitrogen levels. This fact must be reflected in the number of general predators.

The actual impact of predators and their significance on the population dynamics of the whitefly is discussed in Chapter 6. The importance of spiders as predators found by Turnbull (1962), Solomon (1973) and Waloff (1980) has not been noticed here. Spiders seem to have a greater impact on population numbers at low densities where they could become important. Here, however, although there is an increase in the number of prey taken as their density increases, there is no corresponding response in spider numbers.

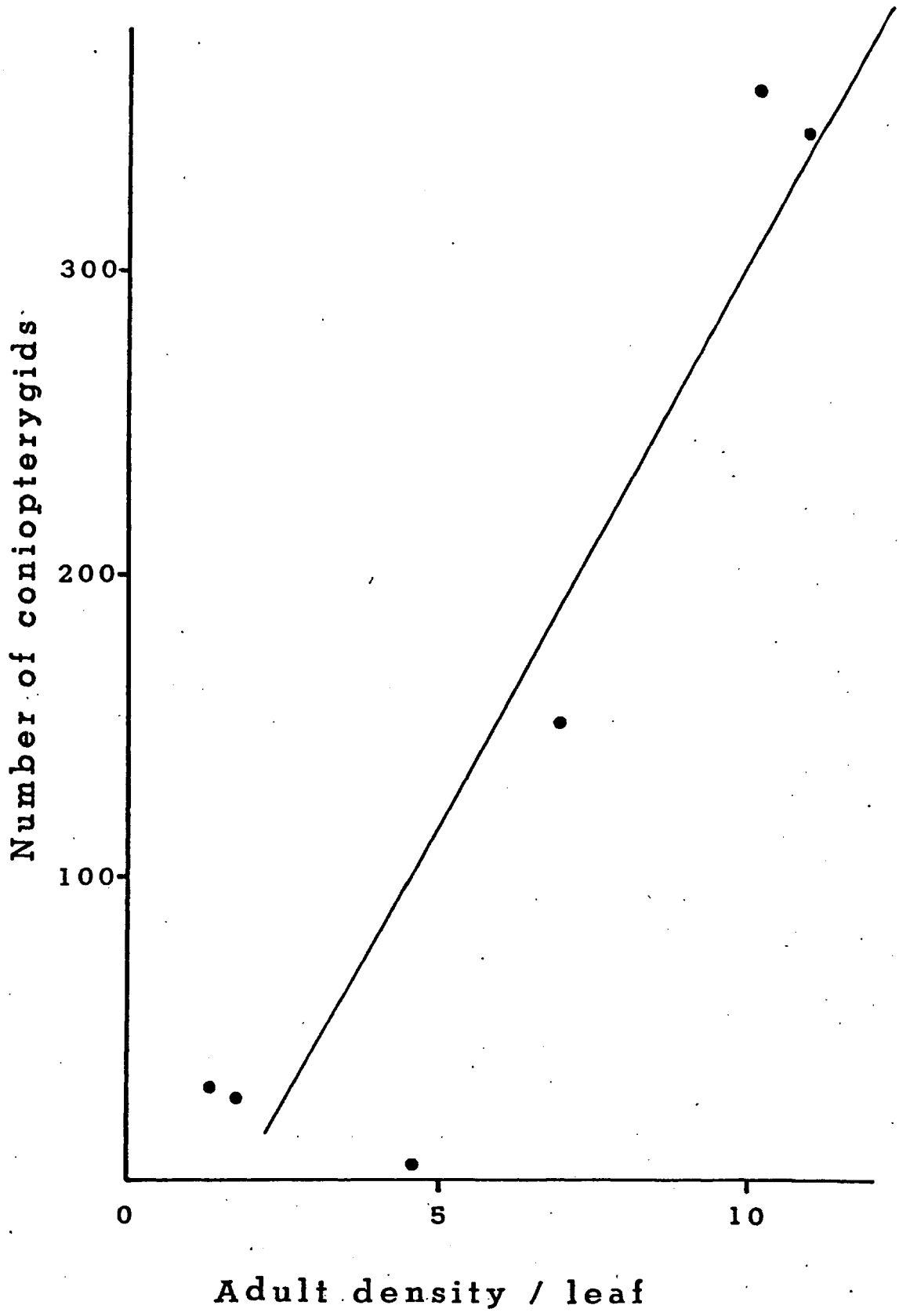
Only the Coniopterygids responded from year to year to whitefly density. Interestingly, this is the only multivoltine species amongst those studied, supporting the view of a numerical response to whitefly density occurring within a season; additionally there is the increased opportunity for immigration in years of high density (see Fig. 4.1).

Even though this relationship has been revealed between coniopterygids and whitefly numbers which can be accounted for in the life history, and although prey consumption was not measured in the field, the mirids must, by reason of their frequency of discovery and larger

FIGURE 4.10 Relationship between coniopterygid numbers and whitefly density.

$$Y = 69.36 + 37.45\,x \qquad r = 0.94 \qquad P<0.01$$

FIGURE 4.10


Number of coniopterygids
300
200
100
0
5
10
Adult density / leaf

numbers of individuals present, be regarded as the most important predator of the whitefly. It would seem that predators have some impact on the number of Aleurotrachelus adults but they are not the major means of regulation.

CHAPTER 5 - THE NITROGEN LEVEL IN THE HOST PLANT

5.1 INTRODUCTION

The general premise that nutrients can place limitations on the growth and development of plant-eating insects has been noted by several authors (e.g. McNeill 1973, Moss et al. 1975, Dixon 1976, Parry 1974, 1976) and, as Southwood (1973) states, the foliage of seed plants is often only marginally adequate nutritionally: one or more vital constituents may be close to the minimum levels. In addition, the inclusion in plants of secondary plant substances may place restrictions on the development of some insects. However, it seems more likely that specialist feeders such as Aleurotrachelus, are limited by either carbohydrate or nitrogen levels in the plant as they have overcome any chemical defense. Whiteflies are phloem feeders (Pollard 1955, 1971) and as plant sap is mainly composed of sucrose (Duckett 1974) the level of nitrogen is assumed to be the limiting factor. Indeed, many studies (van Emden and Bashford 1971, Parry 1974, 1976, Hill, 1976) have stressed the correlation between reproduction, insect growth and the availability of nitrogen.

The amount of soluble nitrogen found in plants has been shown to given an estimate of the amino acid levels in the phloem (Pate 1968, Prestidge 1980, McNeill and Broodbank unpub). It therefore seemed legitimate to carry out amino acid analyses on the three bushes involved.

The aim of this section is to look at the amino acid levels in the three bushes throughout seasons and during different years, and to relate these to the oviposition levels on the different host plants.

5.2 METHODS

The measurement of soluble nitrogen can be used as an estimate

of the amount of available nitrogen. A relationship between soluble nitrogen levels and amino acid amounts has been established. (Pate 1968, McNeill per. communication). All nitrogen analyses in this study have been confined to estimations of amino acid levels which provide a more sophisticated measure, as either individual or group effects of these can be estimated. These estimations were carried out on leaf samples, phloem extracts would have been more precise but these proved technically impossible.

Leaves were collected regularly from Bushes A and B. Collection from C was less frequent especially in later years, when the size of the bush was decreasing. All samples were taken at the same time of day, (approximately 11.30am.), as no experiments into diurnal rhythms of amino acids were carried out. Samples were picked and freeze-dried as soon as possible. Prior to 1978 the samples were plunged directly into frozen carbon dioxide to prevent any decomposition before analysis, but because of the short time involved between collection and preparation the results were not thought to be adversely effected and the practice was discontinued (Broodbank personal communication).

After freeze drying samples were ground in a ball mill and then extracted in 2.2 pH buffer solution. The resultant supernatant was analysed in a Locarte auto-amino-acid analyser on the 23 cm column. The amounts of amino acid present in each sample were calculated against a known standard. These standards provided seventeen peaks which could be readily identified. For unknown peaks a mean of the common amino acids (excluding proline cystine, lysine, histidine and arginine was used (as advised by the Locarte manual). This gave an estimate for acids which previously could not be included in the total and thus made it more meaningful. The amounts of essential amino acids were estimated without tryptophan, which tends to break down during extraction, and

arginine which was not always present. However, the absolute totals (i.e. all amino acids peaks found on the chart) do contain estimates of arginine. Named peaks are numbered in sequence (Table 5.1).

In 1977 Bush B was fertilised with dried blood at a rate of 2oz per sq. yard before the onset of new growth. This treatment was repeated in subsequent years.

5.3 RESULTS

5.3.1 Total Amino Acid Levels

The maximum amounts of amino acids found during the season in years in which samples were taken as shown in Fig. 5.1, together with the 10 essentials and the named amino acids (1 - 10). Four main points emerge from this:

(1) As the quantity of amino acids in the leaves rises, so the proportion of essentials increases.

(2) There is considerable variation between years on the same bush, resulting in a peak in 1977. Unfortunately Bush C was so depleted by the hot summer in 1976 that it was impossible to obtain sufficient samples during that year. It seems likely that this peak is due to two possible reasons. Firstly, a response to the stressful conditions in 1976 when water was in particularly short supply, resulting in an over compensation in nitrogen levels, or secondly, the nutrient supply to the plant may have increased following the dry summer and subsequent heavy rain.

(3) The total levels of amino acids in bushes A and B follow a similar pattern with amounts found in A being marginally higher than in B.

(4) Bush C displays its aberrant nature (Southwood and Reader 1976) still further in its amino acid levels by not following the patterns shown by the others.

TABLE 5.1 Amino acids identified during analysis

1.	aspartic acid	
2.	threonine	X
3.	asparagine + glutanine - amide	
4.	glutamic acid	
5.	proline	
6.	glycine	
7.	alanine	
8.	valine	X
9.	methionine	X
10.	isoleucine	X
11.	leucine	X
12.	tyrosine	
13.	phenylalanine	X
14.	γ amino-butyric acid	
15.	histidine	X
16.	lysine	X
17.	arginine	X

X indicates an 'essential' amino acid

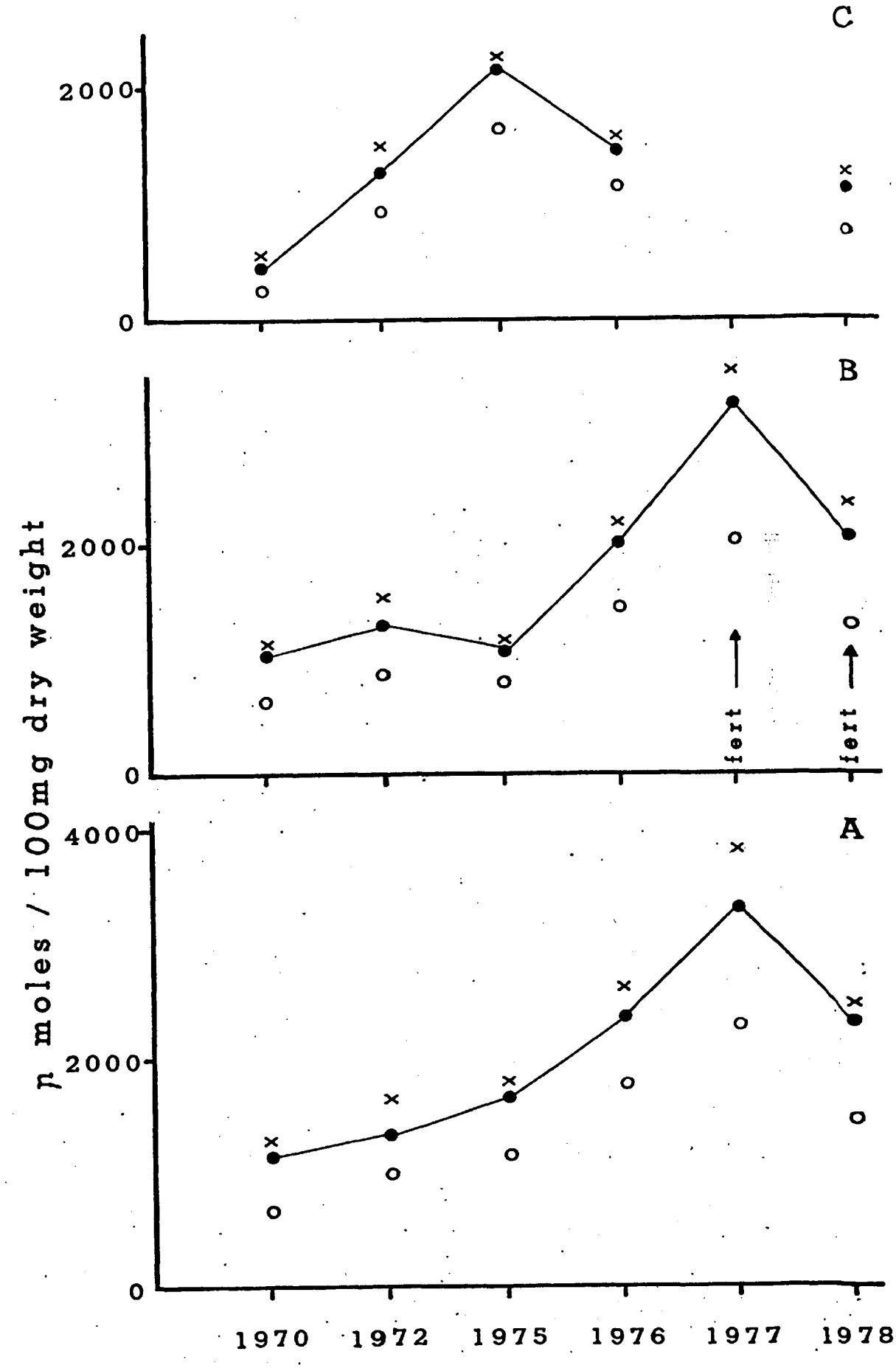
FIGURE 5.1 Maximum amounts of amino acids found in the three bushes during six seasons

x Absolute total

● Total of named acids

o 10 essentials

FIGURE 5.1


C
2000
0
B
2000
0
fert
fert
A
4000
2000
0
n moles / 100mg dry weight
1970
1972
1975
1976
1977
1978

When the data in Fig. 5.1 for A are plotted against the number of eggs laid per leaf for the six sampling dates, the curve in Fig. 5.2 is obtained. The number of eggs laid per leaf was taken as a gauge of fecundity on the bushes as this eliminated both the effect of adult density (P. 41) and bush size. Fig. 5.2 shows an increase in egg numbers until a level of approximately 1,500 η moles/100 mg dry weight is attained, after which the rise in egg numbers is less dramatic, and it seems likely that either the curve is asymptotic or at still higher concentrations of amino acids egg numbers could fall.

The two lowest points (circled) represent years in which the estimation of amino acids could be slightly lower than their actual maximum value. The 1970 result represents an August sample of the oldest preserved leaves to be analysed, and the 1972 value is estimated from a sample analysed on a different machine, in which the levels were determined from fresh weight quantities. Even so it is likely that the trend is correct.

The slope resulting from the data from Bush B (Fig. 5.2) shows a positive correlation between numbers per leaf and amino acid levels ($r = 0.97$ $p<0.01$). The same data for Bush C are plotted in Fig. 5.2 showing that this positive correlation is now not found. It may be that the very low numbers and consequent sampling errors for some stages (only 32 eggs in 1978) cause spurious relationships. It seems likely that the whitefly on this bush are subject to so many disturbances (Southwood and Reader 1976) that any differences due to nutritional status are masked.

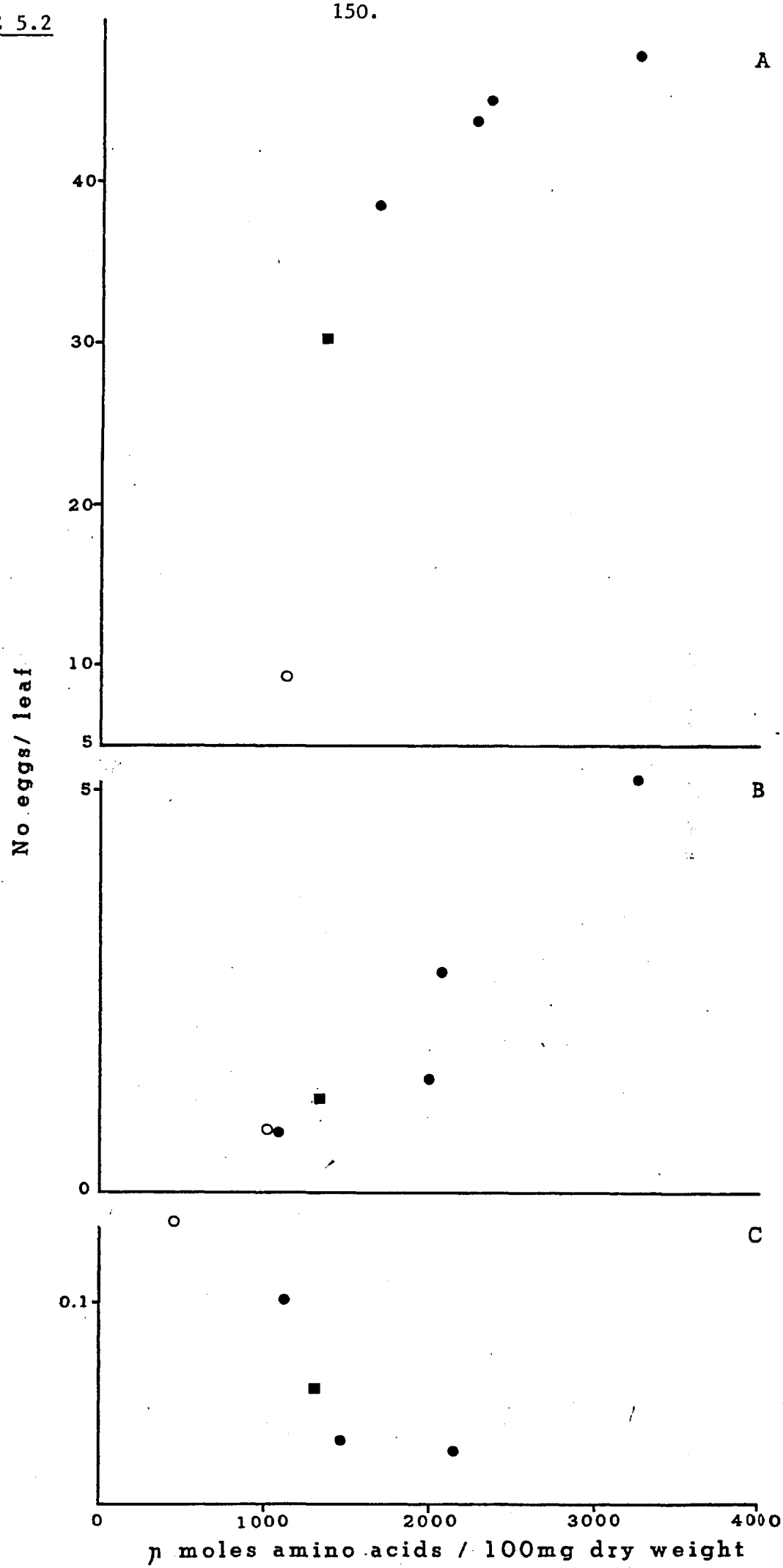
The possibility that whitefly can initiate a 'sink type' situation on this plant has been investigated by S.A. Hickman (unpub.). Insects from the low population on Bush B would be expected to have little impact

FIGURE 5.2 Maximum amino acid amounts compared with number of eggs laid per leaf on the 3 bushes

■ - represents samples analysed by S.A. Hickman

o - represents old samples.

FIGURE 5.2


A
40
30
20
10
5
No eggs/ leaf
5
B
0
C
0.1
0
1000
2000
3000
4000
μ moles amino acids / 100mg dry weight

on the host plant, whereas the higher initial population on A could stimulate further amino acid production.

Old leaves with varying degrees of infestation were analysed for amino acid levels just prior to adult emergence;the results found are shown in Table 5.2.

TABLE 5.2 Amino acid amounts found in old leaves of different infestations, results expressed in μ moles/gm fresh wt. (S.A. Hickman unpub.).

		Type of Infestation		
Bush		Low (1-10*)	Medium (11-50)	High (51 +)
A	Total	4854.3	4854.8	4281.2
	1-16	3688.2	3503.6	3231.0
B	Total	6218.7	4902.3	
	1-16	4139.4	4181.3	
C	Total	3299.8		
	1-16	2360.8		

*4th instar larvae

These results show no clear cut answers: the amounts found in C are characteristically low; the trend downwards in the 1-16 in A is reversed in B, and the high amount from leaves of Bush B with a low infestation is a result of a large quantity of arginine. It may be that these leaves were not picked at the best time to show a trend of the type envisaged. For although it is possible that individual leaves show variations in nitrogen levels in relation to levels of infestation, and the heavily infested leaves might have higher levels initially, both the population and senescence could exhaust leaves just prior to emergence.

Further investigations on this could prove interesting.

5.3.2 Individual Amino Acid Levels

When the data are split into individual component amino acids, the importance of each in the total curve can be seen (Fig. 5.3). It would be expected that the acids which were important in increasing egg numbers would be positively correlated with the curve in Fig.5.2 However, the major components are alanine (7) and γ amino butyric (14) which constitute between 6.60 and 51.73% of the total amount.

It would appear from this that the increase in fecundity is brought about by a gross rise in total amounts rather than by any obvious limitation of any of the essential amino acids, and it may be that whitefly, which contain symbionts in mycetomes (Steinhaus 1949) can, like Myzus persicae (Mittler 1970), survive without all the so called essential amino acids found necessary in work with artificial diets. No obvious trend is found in Bush B, only threoine and valine show any correlation with the total amounts.

5.3.3 Seasonal Variations in Amino Acid Levels

The variations in amounts of amino acids during the season 1977 in bushes A and B can be seen in Fig. 5.4. It would appear that a uniform level is maintained throughout the year, with a substantial peak in amounts in the early summer (June) when the new leaves are growing. When the percentage of each individual amino acid is observed over the whole season, no obvious trends can be seen (Fig 5.5 a and b). Using the classification of Prestidge (1980) Table 5.3, some pattern is noted. Here Group I represents acids which are positively correlated with insect performance (van Emden 1973) and Group II includes amino acids which are known to be unfavourable to insect performance (γ amino-

FIGURE 5.3a Individual amino acids compared with number of eggs per leaf on Bush A.

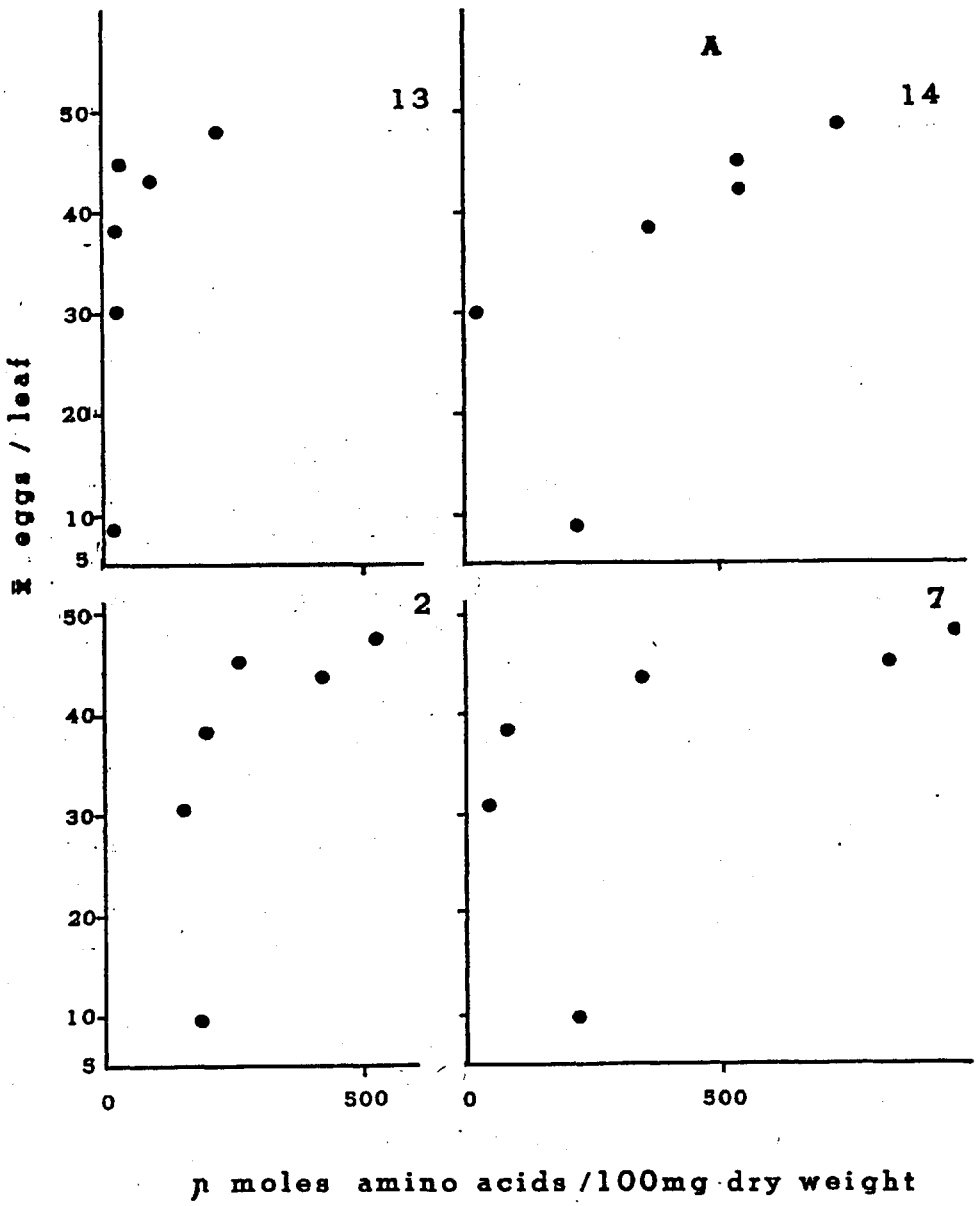


FIGURE 5.3b Individual amino acids compared with number of eggs per leaf on Bush B.

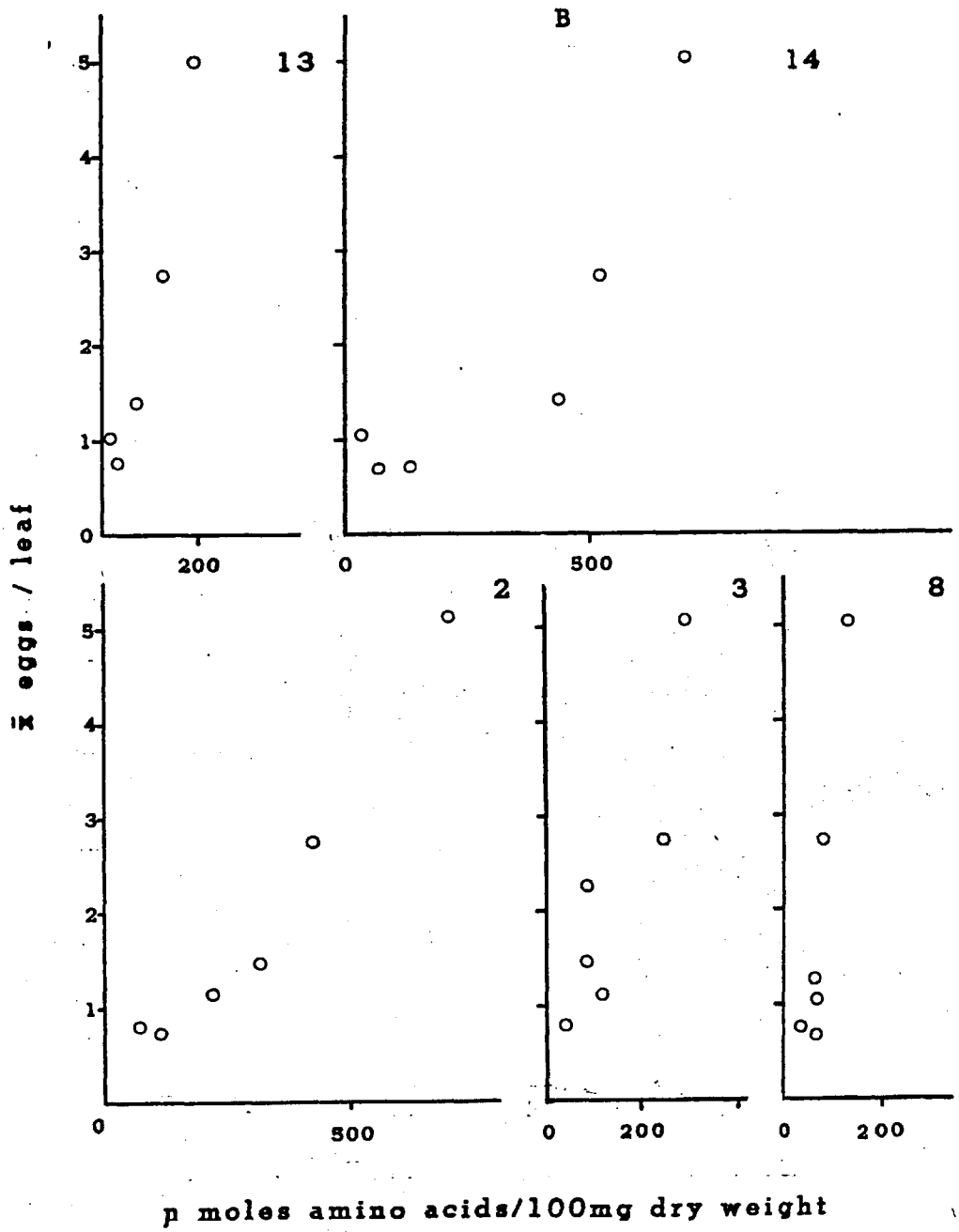


FIGURE 5.4 Seasonal changes in amino acid levels during the season (1977) on bushes A and B

● - amounts in old leaves

o - amounts in new leaves

FIGURE 5.4

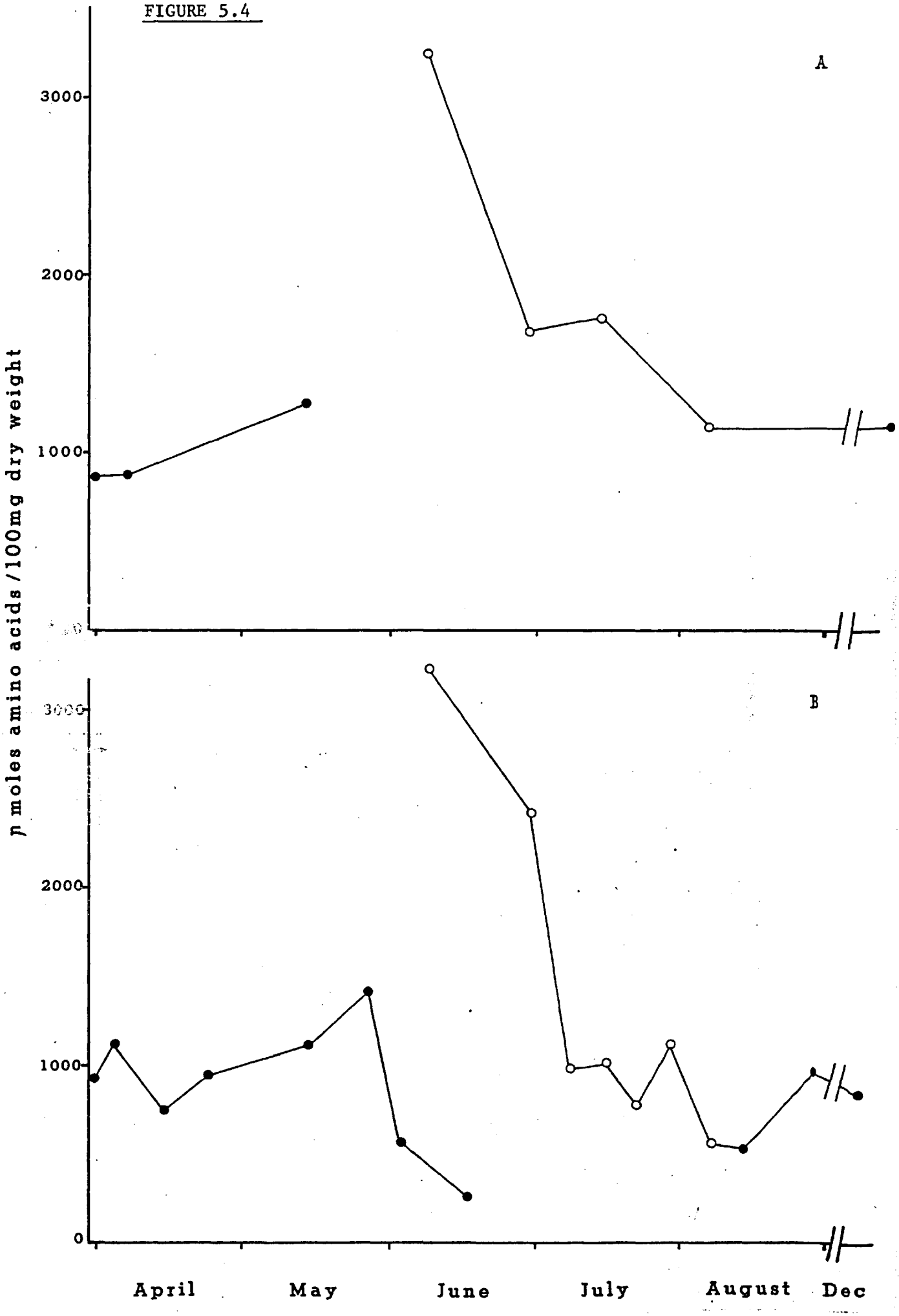

A
B
3000
2000
1000
0
n moles amino acids /100mg dry weight
April
May
June
July
August
Dec

FIGURE 5.5a Percentage changes in named amino acid levels which show variation throughout the season in Bush A

1. Aspartic acid
2. Threonine
3. Amide
4. Glutamic acid
7. Alanine
14. γ amino-butyric acid

FIGURE 5.5a

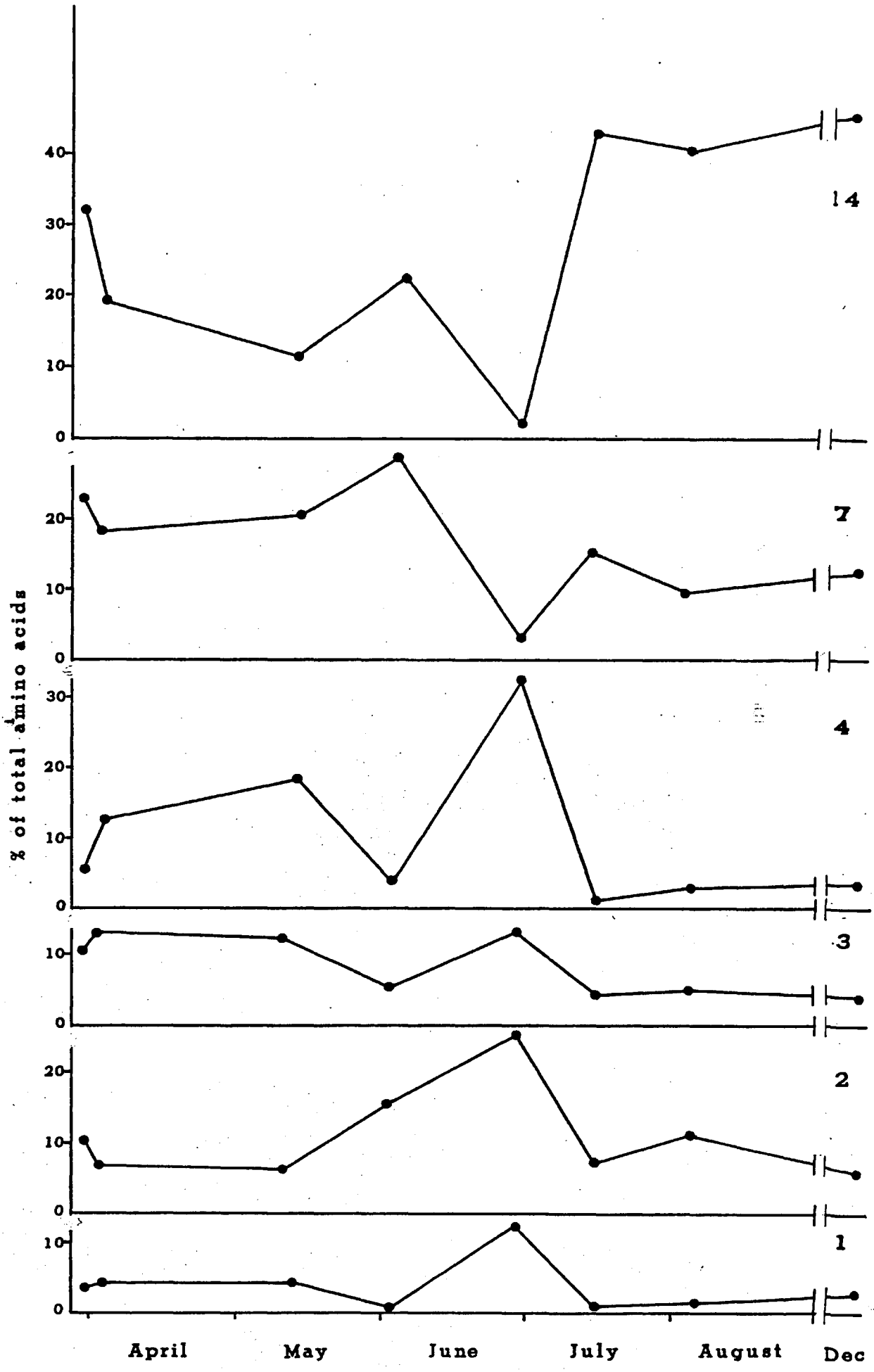
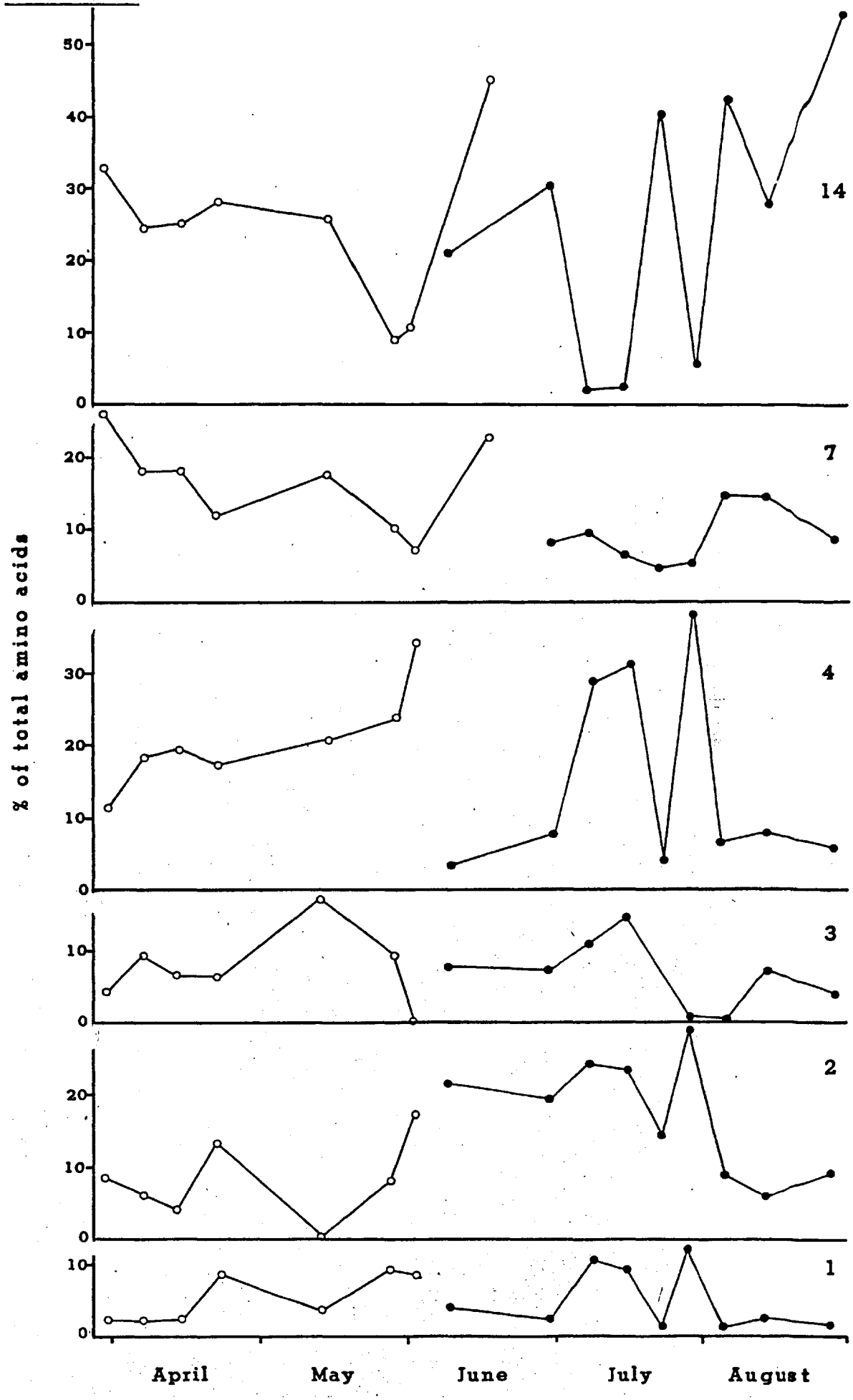

% of total amino acids
40
30
20
10
0
14
20
10
0
7
30
20
10
0
4
10
0
3
20
10
0
2
10
0
1
April
May
June
July
August
Dec

FIGURE 5.5b Percentage changes in named amino acid levels which show variation throughout the season in Bush B

1. Aspartic acid
2. Threonine
3. Amide
4. Glutamic acid
7. Alanine
14. γ amino-butyric acid

FIGURE 5.5b


% of total amino acids
50
40
30
20
10
0
14
7
4
3
2
1
April
May
June
July
August

butyric) and those for which no favourable attribute can be shown e.g. alanine. (House 1965). Glycine is included as it is not generally regarded as being related to N nutrition of a plant, (Larsen 1980).

TABLE 5.3 Index of amino acid quality.

Group I - beneficial to insect performance

Group II - adverse to insect performance.

(after Prestidge 1980)

Group I	Group II
Amide	Alanine
Threonine	Glycine
Proline	L Dopa
Aspartic acid	γ Amino butyric acid
Glutamic acid	

The seasonal differences between groups I and II on Bushes A and B for the season 1977 are shown in Fig. 5.6 a and b expressed as % of total amounts. Group I remains at lower level than II during most of the year, but as the new leaves are developing the reverse occurs and the percentage of beneficial amino acids is greater. In Bush B two peaks occur; the second may reflect the onset of flower growth, and is not seen in Bush A, which on the whole has fewer flowers.

There was no evidence that the addition of fertilisers to Bush B had any appreciable difference on the levels.

5.4 DISCUSSION

The resistance of such an 'apparent' plant (sensu Feeny 1976) as Viburnum tinus to an influx of herbivores is possible in two ways. Firstly, morphologically, by the development of thick leaves soon after initial

FIGURE 5.6a Percentage of groups I and II present during 1977 in Bush A

o - o Group I

● - ● Group II

FIGURE 5.6a

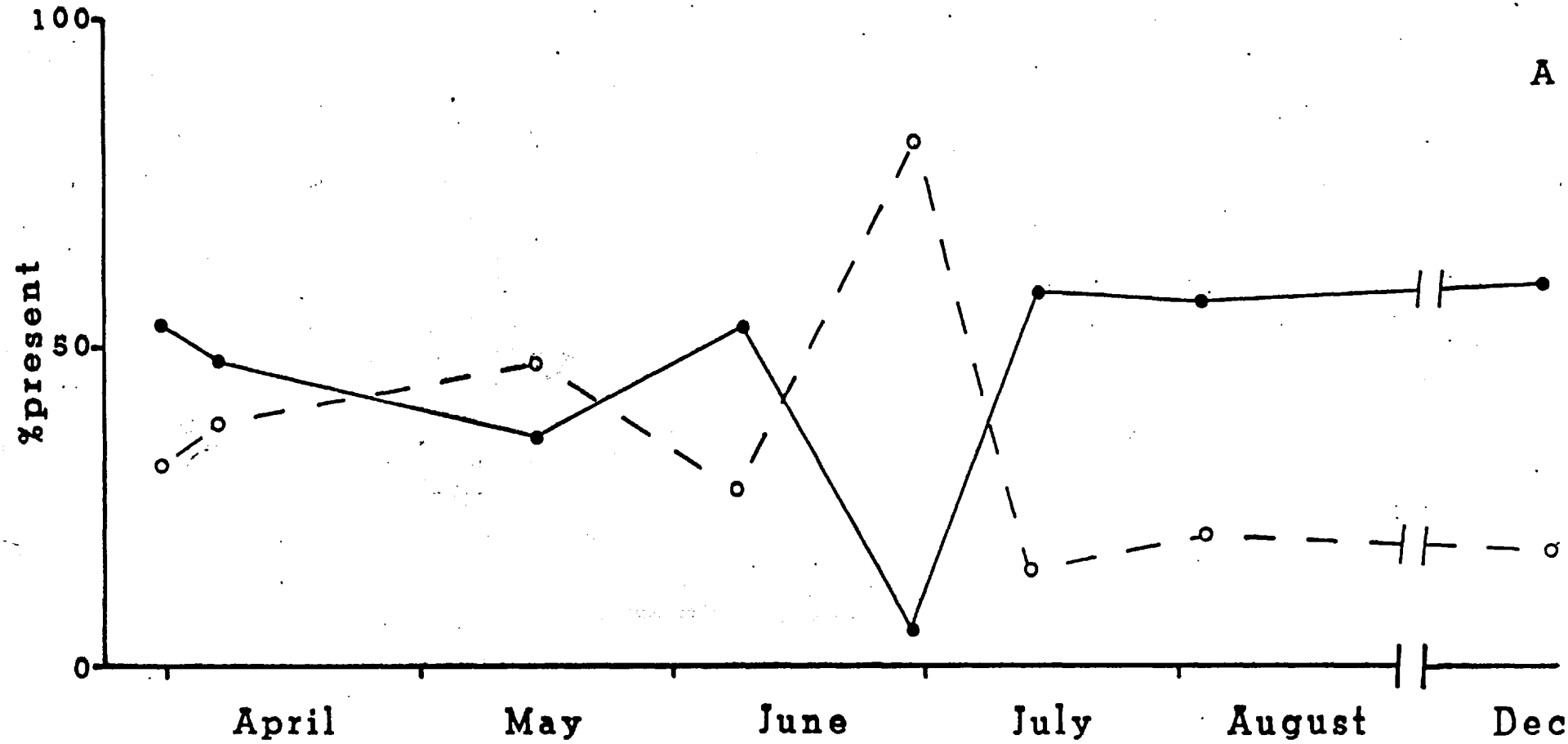
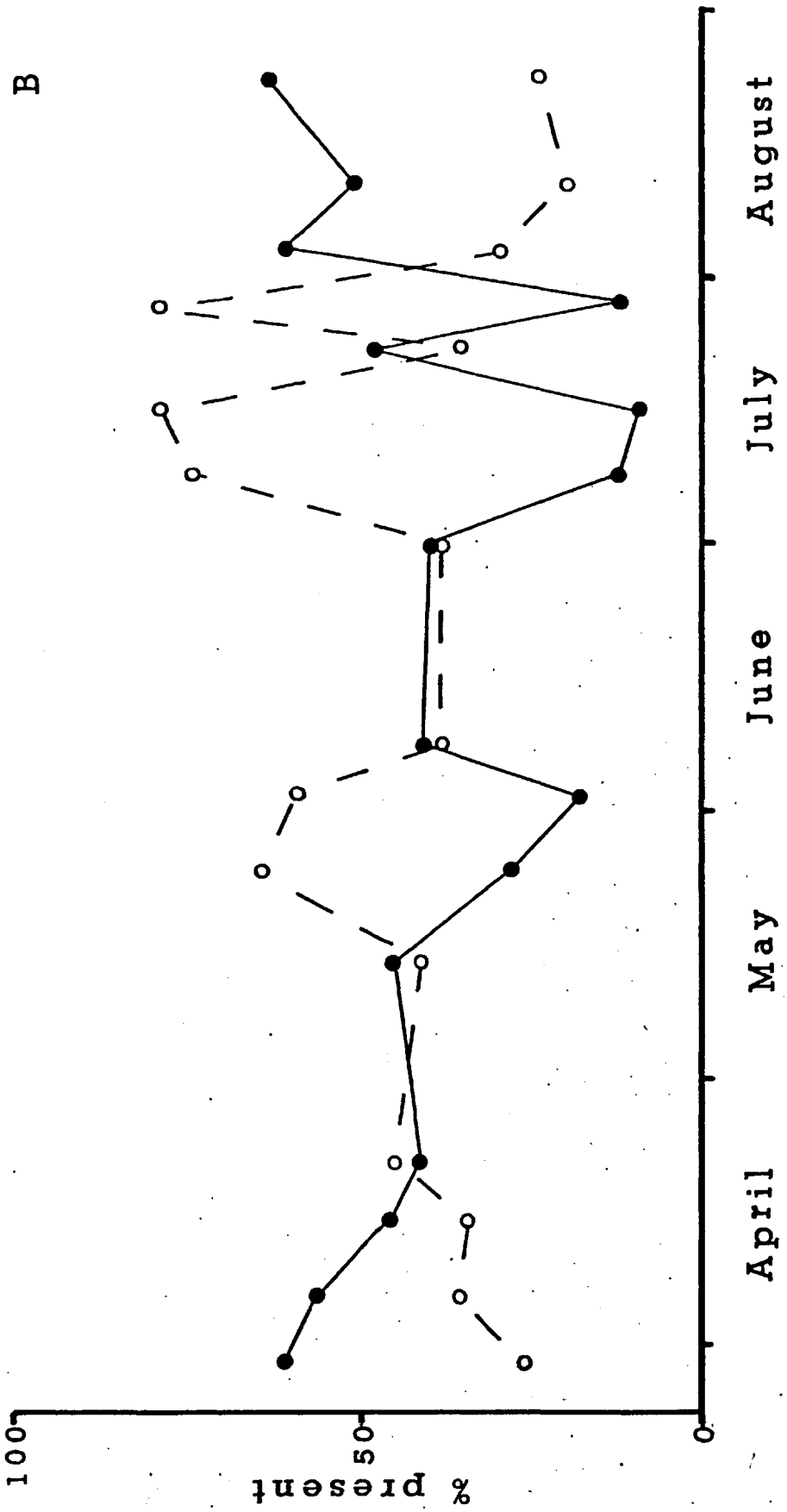


FIGURE 5.6b Percentage of groups I and II present during 1977 in Bush B

FIGURE 5.6b



growth, and the absence of chewers suggests that these leaves are unpalatable. Indeed during the whole survey no leaves damaged in this way were noticed. Secondly, by biochemical resistance, where either toxic substances are produced, amino acid levels manipulated or both. Secondary plant substances have not been measured, but the amino acid analysis seems to indicate such low levels (compared with other plant species), that only a specialist herbivore could survive.

It is interesting to speculate that the univoltine nature of Aleurotrachelus is governed by the seasonal patterns of amino acids in the host plant, and once the insect has become established, the life history mirrors the annual cycle of plant growth. This synchrony results in adult emergence, egg laying and the period of fastest growth during and immediately after the peak in nitrogen on new leaves. This is represented by a peak in absolute values and a percentage peak in numbers of beneficial amino acids (Group 1. Table 5.3). There then follows a long developmental period during which time food resources are very low.

This time corresponds to the period in which a high proportion of group II amino acids are present in Viburnum tinus. These include alanine and γ amino-butyric, which have been shown to inhibit feeding in some insects. (Chapman 1974). This long developmental period has also been found by Strong and Wang (1977) in Chelobasis perplexa (Baly.) as a means of combatting low nitrogen levels.

The nutritional advantage obtained on new leaves is short lived, and this is reflected in similar mortalities found during the larval stages of insects on both bushes A and B (see Table 7.1). The importance of food quality on oviposition has been shown by several authors (Sogawa 1971; Cheng and Pathak 1972, and Prestidge 1980) but not on nymphal

or adult survival (Hill 1976).

The importance of synchrony between host plants and insect has been well reported. Hill (1976), McNeill and Southwood (1978) and Prestidge (1980) have all shown the relationship between the number of species of phloem feeders and their abundance on grasslands, and the flushes of nitrogen in spring and autumn and at flower growth (Broodbank unpub.). This increase in numbers is caused by both increased fecundity and mobility (Waloff 1980). Additional peaks in nitrogen can be produced by cutting pastures (Andrezejawska 1965) and extended by fertilisation (Prestidge 1980). Fertiliser treatments have proved inconclusive on Viburnum and even where they have successfully raised nitrogen levels in grass (Prestidge 1980),this only occurred during the flow periods. However, it had the advantage of lengthening this period and thus reducing the importance of insect synchrony with its host plant.

The need for, and impact of, individual amino acids varies much amongst insects. Work on artificial diets has indicated the necessity of ten 'essential' amino acids; (i.e. arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine, (House 1972)). Other authors have shown the importance of the proportion of one amino acid to another, involving the grouping of various acids into families (see P. 161) van Emden (1973) Prestidge (1980). The presence during most of the year of Group II acids in Viburnum tinus would indicate that Aleurotrachelus can complete its development on very low nitrogen levels. As the proportion of essentials present is thought to contribute to the nutritive quality of the host, rather than the total amount (House, 1969), these low levels, from which most amino acids appear to be absent, are likely to be supplemented by symbionts (c.f. Dadd & Krieger 1968), which have long been recognised as allowing marginal foodstuffs to become adequate. (Richards and Brooks

1958, Brooks 1963, Griffiths and Beck 1973).

In conclusion, the low amounts of amino acids in V. tinus available to Aleurotrachelus seem to have led to the univoltine nature of the insect, and that egg laying appears to be governed by the narrow window in which the so-called "positively correlated" (Group I) amino acids become temporarily more available. The relationship of this to the population dynamics of the insect will be discussed in Chapter 6.

CHAPTER 6 - ADULT POPULATION DYNAMICS

6.1 INTRODUCTION

The preceding chapters have dealt with the effects of specific factors on the adult population and the resultant fecundity of the females. This chapter looks at the estimates of fecundity from year to year, and compares the potential number of eggs with the actual number laid. An attempt is made to discover the causes of the differences between these two estimates - potential and actual eggs, which has been categorised as k_o in Southwood and Reader (1976). k_o is broken down into its likely constituent components, and their relative importance is discussed. These include the impact of predation both by spiders and mirids, and the degree of migration over the various seasons. The number of adults affected by these three factors can be assessed and from these their subsequent impact on natality. In addition a fourth category exists which is less easy to quantify in terms of adult or egg numbers. This includes the effect of density, host plant and temperature on the fecundity of the whitefly. The relative importance of these are also discussed.

6.2 METHODS

Estimates of the number of adults on the bushes were made from the annual censuses undertaken in April. These involved a count of the larval population and their remains found on the bushes. Initially a third of bush A and all leaves on bush B were examined, but as the populations increased in size a fifth of the leaves on A and a third of those on B were counted. This represented a reasonably accurate estimate of the total larval population, and the way the various components and their remains were distributed. Additionally a survey was

made of one hundred labelled leaves throughout the year, and particularly just prior to, and after emergence. From this, the percentage emergence for any year could be obtained, which was then related to the number of living fourth instar found in April to give an estimate of adult numbers on the bushes.

The number of eggs laid in any season was obtained from egg counts on the labelled leaves and their ratio to the resulting number of second instar larvae on these leaves. This was then applied to the number of second instar larvae found on the bush at the time of the April count. The potential fecundity was then based on the maximum number of eggs laid in any year and the number of females of that year, the sex ratio being assumed to be 1 : 1.

As has already been pointed out (P. 84) the fit of the equations of Paris (1965) and Hawkes (1972) (the best fitting equations) and the steep form of the "dispersal with distance" curve suggest a tendency for aggregation around the source with only a small proportion moving far from the bush. This is supported by the flight experiments reported in Chapter 3. In addition, the population studies on other bushes (within 130m) showed dissimilar population densities which were maintained over many generations (Southwood and Reader 1976). The bush (A) around which the main studies were made is in a shrubbery and it seems likely that the habit of rapid settling by Aleurotrachelus would cause individuals within the locality to settle first on other shrubs before either leaving the vicinity or returning to the bush. From this reasoning the admittedly non -proven assumption is made that adults moving beyond 10m are lost to the population as would be emigrants. Two further assumptions are made:-

1. The effective area of the sticky traps is 1.22 sq. m, obtained

by measurement.

2. The whiteflies do not leave the bush at a height of more than 2m (P.112).

On the basis of these assumptions it was possible to estimate the numbers of adults leaving the bush in two ways. Firstly, by using the equation

$$N = \exp(a + \sqrt{b}x) \quad \text{(Hawkes 1972)} \qquad (6.1)$$

which was the best fitting curve overall. However, this equation did not provide the best fit in all years and it was therefore decided to poole the data and obtain an average slope from Hawkes' (1972) equation. This gave

$$\text{Log}_e N = 10.30 - 1.69\sqrt{x} \qquad (6.2)$$

as shown in Figure 3.7 (p.93). By doing this any distortions due to low numbers caught at greater distances from the bush would be reduced. Equation (6.2) was thus used to estimate the number of adults trapped at 10m. on 10 traps, which could then be subsequently converted to the total number passing through an annulus at 10m upto 2m. from the ground. These results are shown in Table 6.1.

The number of adults trapped by spiders was estimated by daily counts of the number of whitefly remains in the spider webs. These can also be seen in Table 6.1.

The importance of mirid predation has already been discussed in Chapter 4, and while the numbers of mirids on the bushes is known, there is no field information on the numbers of whitefly attacked. An estimate of this was therefore obtained by combining the data on the mirid population with a laboratory derived functional response, shown in Figure 6.1. To do this adult female Aleurotrachelus and C. virgula were collected from the Viburnum bushes. Individual mirids were placed in

small pill boxes containing a young Viburnum leaf in water, to which were added either 5, 10, 15, 20 or 25 whitefly, after the mirid had been starved for 5 hours. The cages were examined daily and any whitefly eaten were removed and recorded. The number of prey was then made up to the original density. All tests were carried out at 20°C for 5 days. The data were described using Holling's (1959) disc equation, namely

$$Na = \frac{a\ N\ T\ P}{1 + a\ Th\ N} \qquad (6.3)$$

where Na = total number of prey attacked

a = attack rate

N = Total number of prey

P = Prey density

Th = Handling time

T = Total time

More sophisticated models would certainly improve this fit, but this was thought unnecessary in view of the inevitable errors in extrapolating from such an experiment to the field. These estimates of numbers attacked at different densities were related to the whitefly densities on the bush for that particular year, and to the mean number of mirids found in that season for the month of June (the period of greatest whitefly abundance). These estimates are given in Table 6.1

6.3 ANALYSIS OF NATALITY

The data in Table 6.1 allows estimates of egg loss due to predation and migration, which can be expressed as k-values, that can then be related to the total mortality (k_o.) No estimates of migration were made on Bush-B. This was not thought to prohibit similar analysis, as migration was of minor importance on A, and whitefly were not observed either flying round B or settling on the adjacent bushes.

FIGURE 6.1

Numbers of whitefly attacked by mirids over a 5 day period.
(line fitted by Holling (1959) disc equation)

$a' = 0.8170$

$Th = 0.3690$

FIGURE 6.1

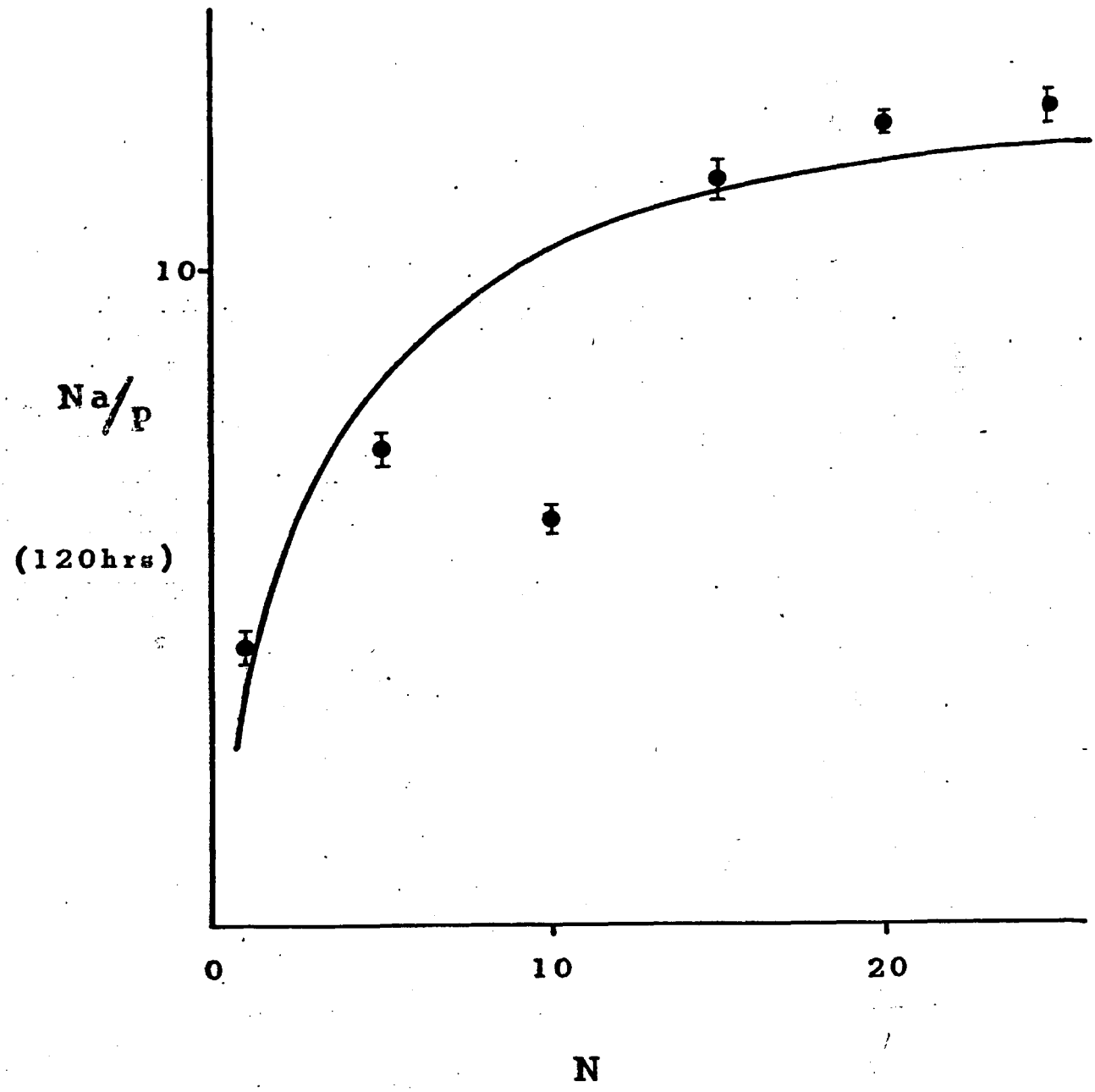


TABLE 6.1 Estimates of adult numbers on Bush A.

Year	Total Adults	No. lost by			Total Adult Loss
		Migration	Spiders	Mirids	
1963	1767				
1964	1250				
1965	2952				
1966	9688				
1967	7464				
1968	23634		443	13958.7	14401.7
1969	16322		552	9821.0	10373.0
1970	29670	1593.8	1520	12417.6	15531.4
1971	46145	3411.9	1855	6049.9	11316.8
1972	93964	14289.4	1621	4187.2	20097.6
1973	162689	27575.9	1847	56402.7	85825.6
1974	234931	31531.4	2107	33176.5	66814.9
1975	149829	21309.6	2457	40383.0	64149.6
1976	275368		3683	29468.1	33151.1
1977	293831				
1978	359252				
Estimates of adult numbers on Bush B					
1963	213				
1964	96				
1965	128				
1966	31				
1967	79				
1968	300		31	16.7	47.7
1969	624		102	253.6	355.6
1970	1367		161	423.4	584.4
1971	3716		134	1974.8	2108.8
1972	4815		101	983.7	1084.7
1973	2135		104	316.4	420.4
1974	2973		126	274.2	400.2
1975	5624		44	819.8	863.8
1976	7800		45	1368.2	1413.2
1977	10271				
1978	24205				

Values for both bushes are found in Table 6.2 and Figure 6.2.

TABLE 6.2 k - values for egg loss on Bush A

k_o - after Southwood and Reader (1976)

k_A - estimate from number of females migrating

k_B - estimate from number of females trapped by spiders

k_C - estimate from number of females attacked by mirids

k_D - estimate from total known egg loss (obtained from known adult loss - Table 6.1).

Bush A	Year	k_o	k_A	k_B	k_C	k_D
	1968	0.8981		0.0041	0.1520	0.1578*
	1969	0.5955		0.0074	0.1554	0.1661*
	1970	0.7144	0.0118	0.0113	0.1020	0.1318
	1971	0.5877	0.0164	0.0088	0.0294	0.0614
	1972	0.5756	0.0343	0.0038	0.0098	0.0491
	1973	0.6819	0.0385	0.0025	0.0827	0.1330
	1974	0.9315	0.0302	0.0020	0.0318	0.0666
	1975	0.6882	0.0346	0.0036	0.0629	0.1046
	1976	0.9117		0.0029	0.0239	0.0270*
	1977	0.7977				
	1978	1.1115				

* no migration estimate

TABLE 6.2 (Continued)

Bush B	Year	k_o	k_A	k_B	k_C	k_D
	1968	0.1723	-	0.0230	0.0123	0.0360
	1969	0.4517	-	0.0370	0.0987	0.1457
	1970	0.3595	-	0.0264	0.0731	0.1044
	1971	0.5894	-	0.0046	0.0468	0.0519
	1972	0.5986	-	0.0093	0.0205	0.0303
	1973	-	-	-	-	-
	1974	0.5964	-	0.0093	0.0205	0.0303
	1975	0.7586	-	0.0017	0.0329	0.0347
	1976	0.6972	-	0.0013	0.0399	0.0412
	1977	0.3144	-			
	1978	0.6101				

Neither separately, nor in total did the values of k_{ABC} or k_D correlate visually with the estimates of k_o (see Figure 6.2). Nor did the regression coefficients appear to make a major contribution as would be expected by a key factor (Podoler and Rodgers 1976).

If the known egg loss due to these factors contributed the major component of mortality it would be expected that k_D would make up all, or at least a considerable part of k_o; on neither bush was this the case, when the numbers of eggs lost were expressed as a percentage of the potential fecundity (Table 6.3).

On Bush A, a significantly greater percentage of eggs were lost from unknown causes than by other means ($t = 3.88$ $P<0.01$), while on Bush B the numbers accounted for was roughly similar ($t = -1.15$ ns).

FIGURE 6.2 k_o and its component values on bushes A and B.

Regression coefficients

	A	B
k_a	0.0232	
k_b	0.0127	0.0415
k_c	0.0703	0.0510
k_d	0.1349	0.0982
k_u	0.6708	0.7204

FIGURE 6.2 (Bush A)

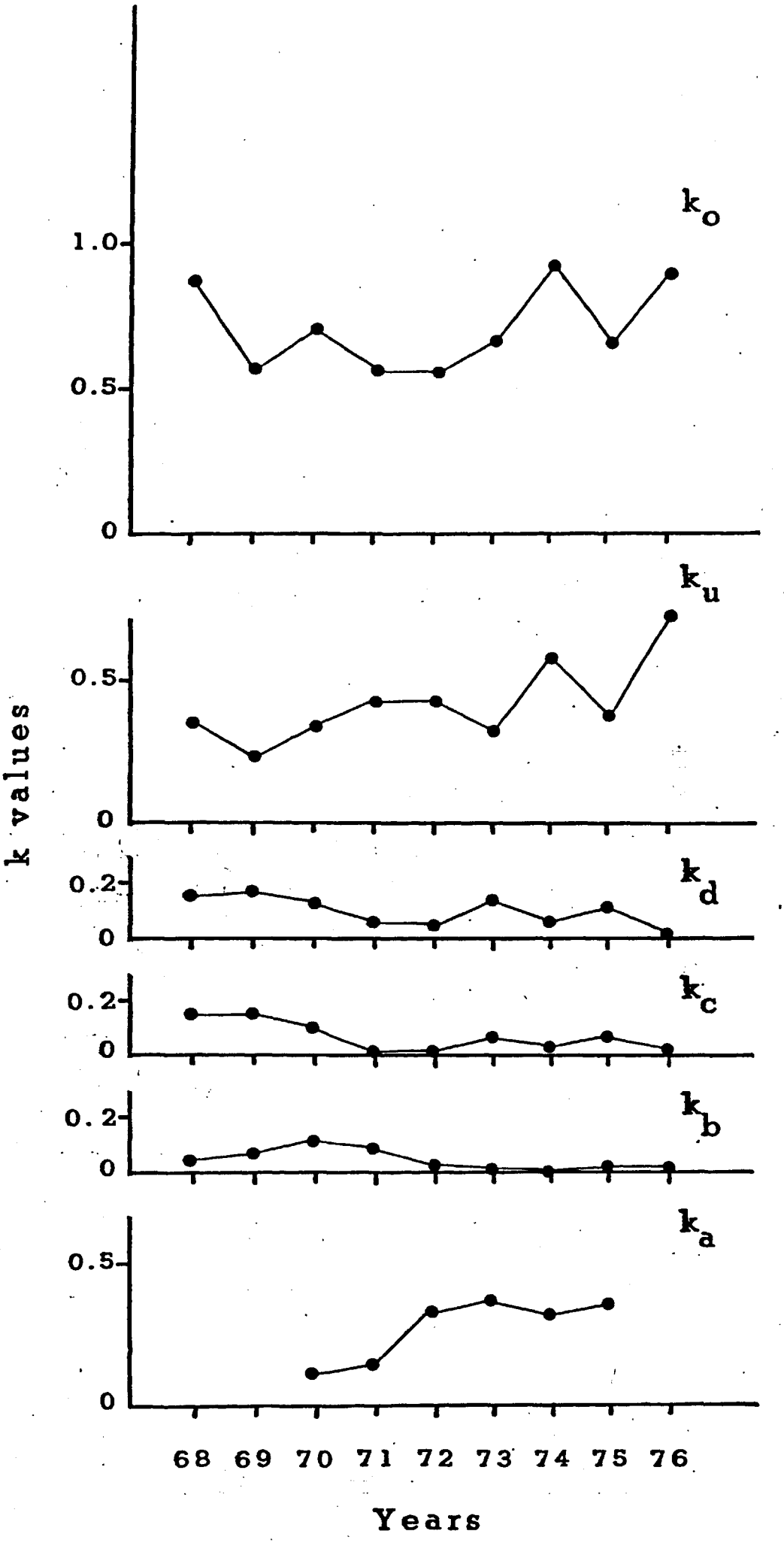


FIGURE 6.2 (Bush B)

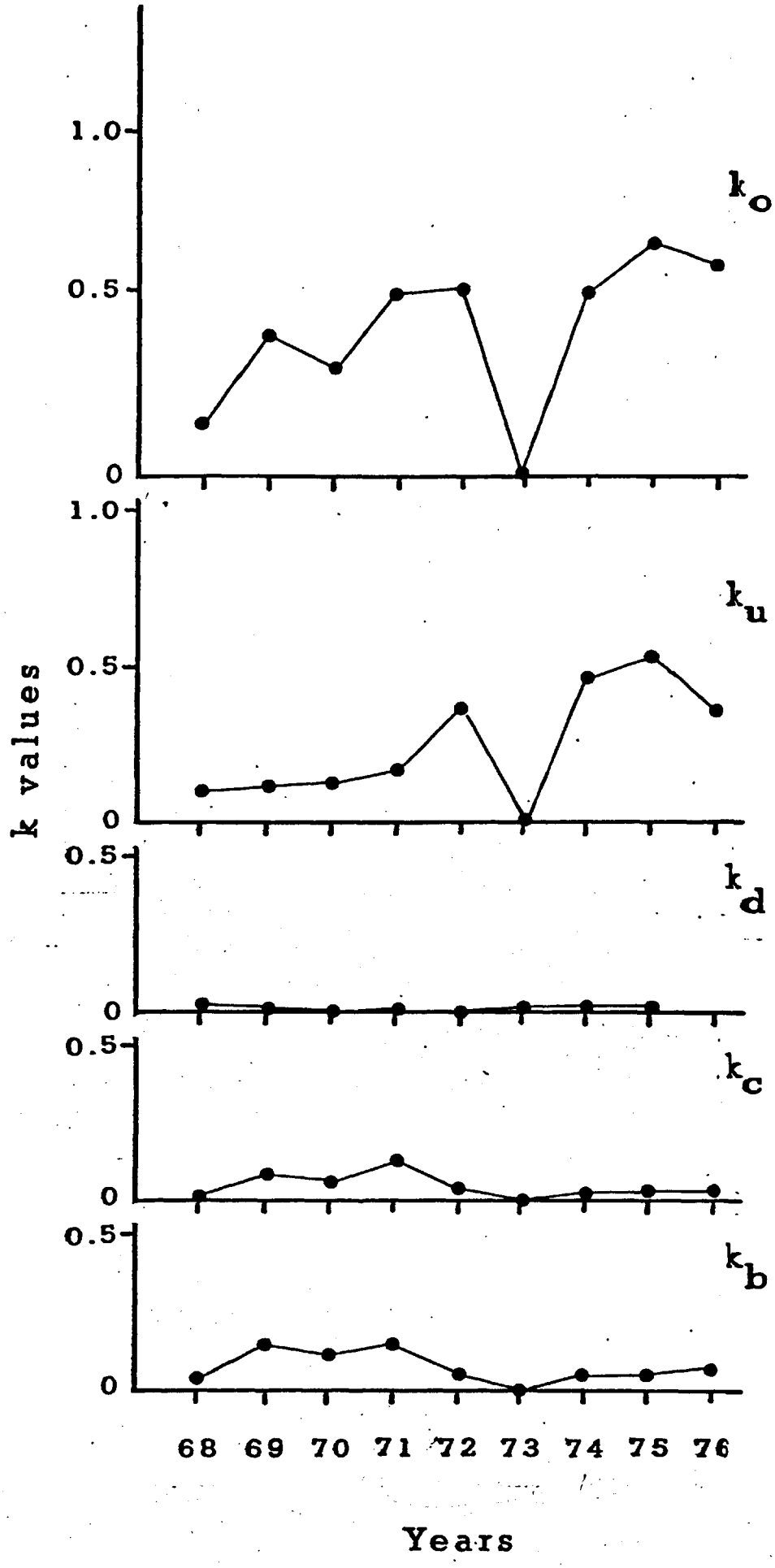


TABLE 6.3 Percentage loss of eggs by various causes on Bush A

Year	Potential Fecundity	No. eggs laid	% laid	% known loss	% unknown loss
1968	616375	77944	12.65	30.47	56.89
1969	425678	108051	25.38	31.78	42.84
1970	773794	149357	19.30	26.56	54.52
1971	1203462	314281	26.11	12.26	61.62
1972	2450581	655974	26.77	10.69	62.53
1973	4242929	882701	20.80	26.37	52.81
1974	6127001	717242	11.71	14.22	74.07
1975	3907540	801164	20.50	21.40	58.09
1976	7181597	880138	12.26	6.02	81.73
1977	7663112	1220881			
1978	9369292	724837			

Percentage loss of Bush B

	Potential Fecundity	No. eggs laid	% laid	% known loss	% unknown loss
1968	5450	3665	67.25	11.42	21.32
1969	11335	4006	35.34	40.91	23.75
1970	24832	10852	43.70	30.69	25.61
1971	67501	17376	25.74	40.74	33.52
1972	87465	22041	25.20	16.17	58.63
1973	38786	38786	-	-	-
1974	53968	13668	25.33	9.67	65.00
1975	102160	17810	17.43	11.03	71.54
1976	141687	28455	20.08	26.01	53.90

k_u is assumed to represent the unknown part of k_o, an estimate of this can be made by taking the number of eggs missing through unknown causes and using these as the mortality estimates. These values are found in Table 6.4 and in Figure 6.2, and give larger regression coefficients than the other k values (k_{ABC} and $_D$) It thus

appears that the key factor is contained in this part of k_o.

TABLE 6.4 Values of k_u from bushes A and B.

Year	A	B
1968	.3654	.1041
1969	.2429	.1178
1970	.3422	.1285
1971	.4159	.1773
1972	.4263	.3883
1973	.3262	-
1974	.5862	.4559
1975	.3777	.5458
1976	.7383	.3369

This failure to achieve the potential fecundity must thus be due to variations in fecundity rather than to the death or disappearance of adult females. The actual number of eggs laid is the result of several factors, which include density of adults, food quality - embracing synchrony with the host plant, and temperature during the egg laying period.

Because of the difficulty in quantifying these aspects in terms of adult females and thus estimating k - values, their actual values (on which the analysis would have been based) have been plotted against k_o. As k_o represents the degree of mortality in that stage, host plant quality has been plotted on an inverse scale (Figure 6.3). The correlation coefficients of host quality, whitefly density and temperature during egg laying against k_o are given in Table 6.5(a). As there may be some interaction between all the components of k_o each has also been correlated against k_u. These are given in Table 6.5(b).

FIGURE 6.3 k_o and the corresponding values for quality, density and temperature on bushes A and B.

FIGURE 6.3 (Bush A)

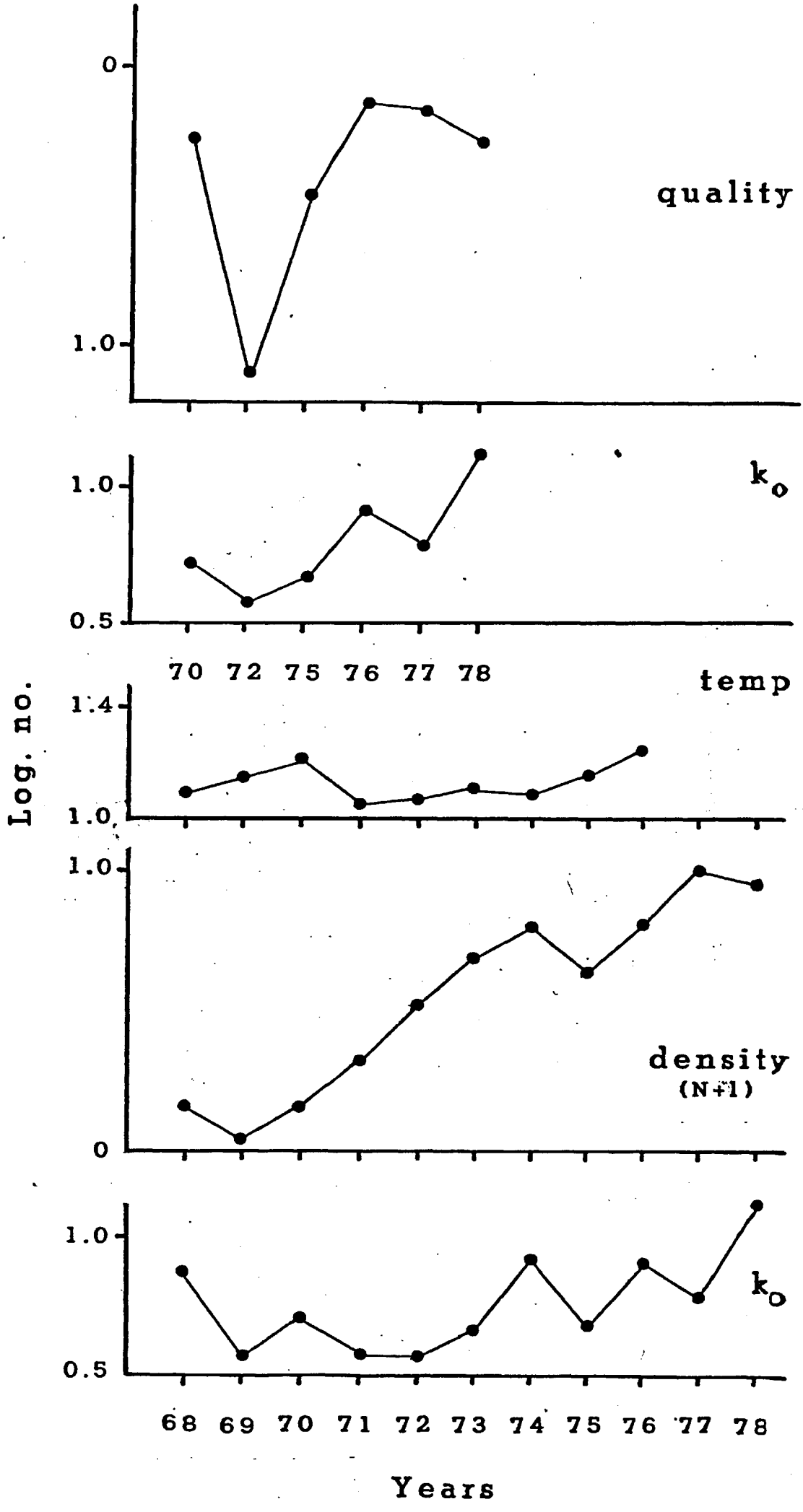


FIGURE 6.3 (Bush B)

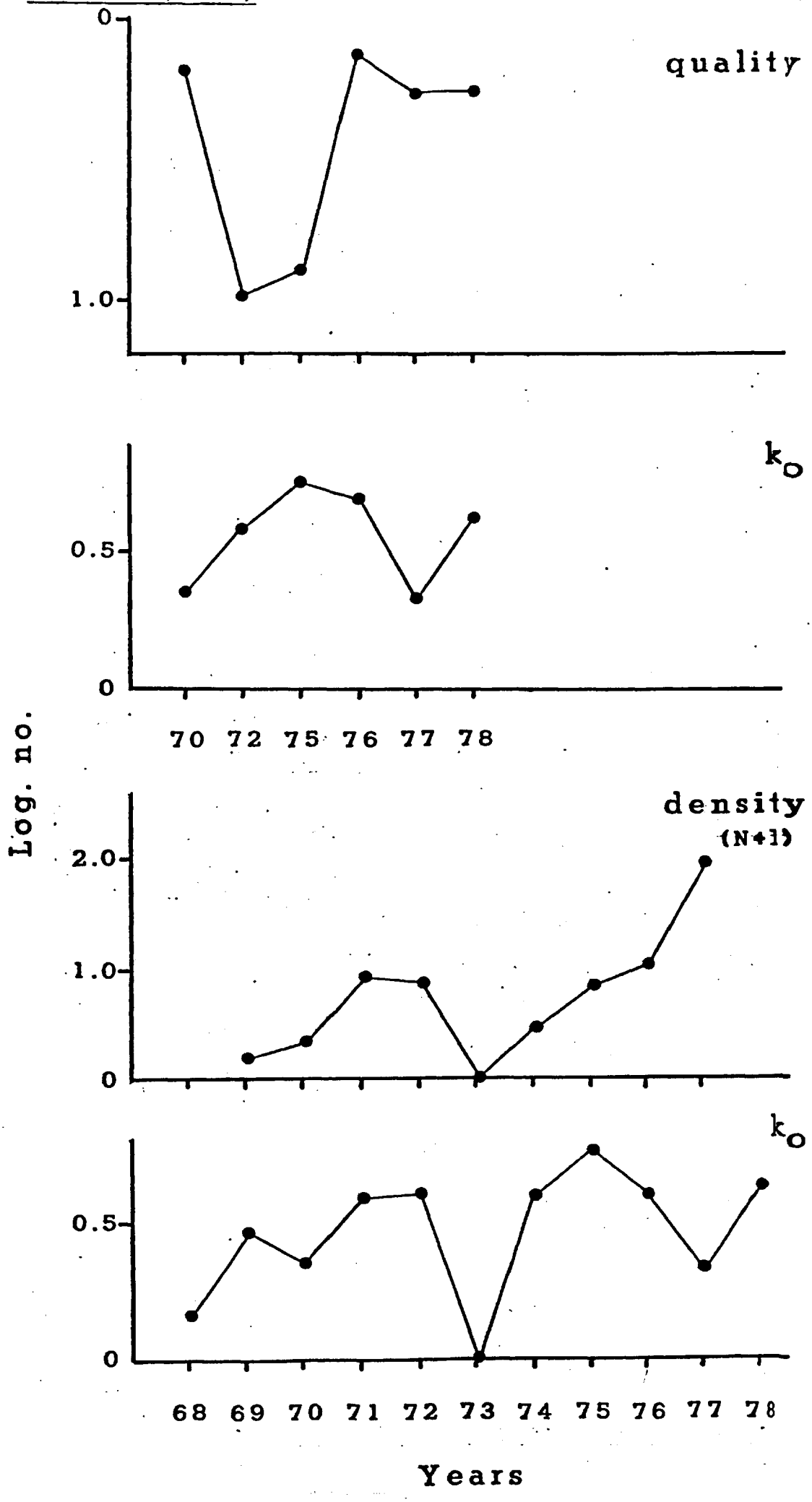


TABLE 6.5 a) Correlation coefficients of values plotted against k_o

b) Correlation coefficients of values plotted against k_u

		A		B	
a)		r	P	r	P
	quality	-0.65	ns	0.45	ns
	(quality-'78)	-0.87	<0.05	-	
	density	0.56	0.10-0.05	0.83	<0.02
	temperature	0.47	ns	0.12	ns
b)	density	0.75	<0.02	0.57	ns
	temperature	0.28	ns	0.16	ns
	quality	-0.39	ns	0.71	ns

This (Table 6.5b) increases the degree of correlation on A between mortality and density, which seems to imply that density is affecting the fecundity of the adults, rather than acting on the quantifiable components of k_o. The degree of correlation for host plant quality has declined. This may be due to the fact that fewer values were available as migration and predation were not assessed in all the same years as food quality. It still seems reasonable to assume (because of its high correlation with k_o in 5 years out of the 6 tested) that this is an important factor, and that the differences over the seasons between potential fecundity and the actual number of eggs laid are due partly to this and partly to the effects of density on the adults as the population rises.

In conclusion it appears that although predation and migration account for some of the mortality contained in k_o, they do not represent the main source of regulation at the densities found here. Mirids have the greatest impact (see Figure 6.2) and spiders are relatively

unimportant as predators due to their low numbers on the bushes. The part played by emigrating adults is also small, and this agrees both with personal observations and with the results in Chapter 3, in which few insects were found at great distances from the bush; flight appearing 'trivial' and contained within the immediate locality of the host plant. The important factors involved are the density of the adult females on the leaves and the quality of the host plant.

CHAPTER 7 - GENERAL DISCUSSION

'In studying population change biologists have long recognised three pathways of change : mortality, natality and migration' (Southwood 1975a). The significance of these on the adults of Aleurotrachelus has been investigated by key factor analysis and by field and laboratory experiments. Only in such a long term study can the key factors be identified and the relative stability of the population assessed, for although the three bushes represent three different aspects both in terms of the stability of the population and of numbers, in all cases the same key factor was found to operate (i.e. the failure of the females to lay the maximum complement of eggs (Southwood and Reader 1976)).

Larval mortality on bushes A and B (with high and intermediate populations) is a major factor in the life cycle and fluctuates annually around a similar mean value (Table 7.1). It is therefore unlikely to contribute to the different population levels observed on the two bushes. The larval mortality on Bush C is significantly higher. One reason for this is the greater importance of k_5 (the mortality of the fourth instar) on this bush, which is primarily due to loss of leaves by known causes with the resultant death of the larvae. These fluctuations in insect numbers, and the gradual decline in the size of the bush is likely to lead to the extinction of the population and the death of the bush.

Mortality of adults is one means by which the potential number of eggs laid by the female can be reduced. This increased mortality could be affected in two ways; by disease or by predators. During the years in which the survey was undertaken no evidence of disease in the population was noted, and during this time a similar pattern of adult emergence

TABLE 7.1 % survival of *A. jelinekii* from egg to adult on the three bushes

Year	A	B	C
1962/3	39.99	4.54	17.07
3/4	47.26	8.67	8.94
4/5	52.33	29.76	2.68
5/6	18.07	7.71	18.75
6/7	10.03	31.10	14.49
7/8	22.58	46.01	10.26
8/9	20.94	17.03	10.67
9/70	27.46	34.12	10.04
0/1	30.89	34.24	1.34
1/2	29.89	27.71	3.08
2/3	24.80	9.69	14.29
3/4	26.62	7.67	7.21
4/5	20.89	41.15	25.89
5/6	34.37	43.80	7.55
6/7	33.38	36.10	
$\bar{x}$	29.3	25.29	10.88
S	11.10	14.63	6.79

t for A/B 0.05 ns

t for B/C 3.36 $p<0.001$

and presence was observed. The slow growth and development found in such insects as the Viburnum whitefly imply a long period of exposure to predators (Lawton and McNeill 1979) and in the case of Aleurotrachelus to fungal attack, which covers the larvae and prevents adult emergence.

Aleurotrachelus is at the edge of its range and is the only herbivore found on the host plant in appreciable numbers. No specialist predators or parasitoids have been found, although the parasitoid of the cabbage whitefly, Encarsia tricolor, and several generalist predators are present during the year. Their impact on the larval instars will be discussed in a later publication.

Only one predator, the coniopterygid, Conwentzia psociformis, showed any numerical response to rises in adult whitefly density. No experiments were carried out on its effects on adult numbers but, at the densities found in the field, it is unlikely that its impact is significant. It probably has a greater influence on the larval instars which must present a more acceptable prey for a neuropteran larva. The importance of this and other predators may become more apparent as the population density rises, but during the period of this study it did not appear that predators were a major regulating factor.

Variations in the natality of females is the second constituent which could have influenced the key factors. No experimental evidence was found that the larval conditions produced significant effects on the number of eggs laid. There was considerable variation between years in the fecundity of females on the same bush. Additionally, more eggs in total were laid on Bush A than Bush B, regardless of the original host of the female indicating some host plant effect on

fecundity.

The third factor which appeared to influence the number of eggs laid was the density of adult whitefly. The number of eggs laid was observed to decrease with increased adult density both from experiments in the field and from the natural populations on Bush A. Bush B showed similar trends but at lower densities. No pattern was observed on Bush C. Tests with Trialeurodes indicated that reduction in egg laying was either due to the presence of eggs on the leaf or decreased oviposition space.

The influence of temperature on Aleurotrachelus is less well defined. In many whitefly species temperature affects the rate of development and hence the number of generations per year. In Aleurotrachelus the main impact of low temperature on the adult would be to lower the rate of egg laying, and hence reduce the number of eggs produced. This trend was found in laboratory experiments, but not from the field data, which raises the point of the validity of relating laboratory experiments which are performed under controlled conditions to the constantly fluctuating situation found in the field. Climate can then affect the degree of synchrony between an insect and its host plant. Hill (1976) showed that in phloem feeding Auchenorrhyncha a lengthy nymphal recruitment could enable some insects to reach adulthood at the time of high food quality. He was able to obtain an index of synchrony between the amount of adult emergence and the high leaf soluble nitrogen levels, and in the case of Dicranotropis hamata, this index of synchrony could be related to an index of fecundity.

Whiteflies on the whole favour new leaves for egg laying, but will, if conditions are crowded, lay eggs on old leaves or less suitable hosts.

Aleurotrachelus is no exception, moving from the old leaves, on which it emerges, to new ones for egg laying. The initial advantage of these new leaves is short-lived, since old leaves of Viburnum do not appear to suffer the rapid senescence which can provide limited food advantages in some crop plants (Wearing 1972).

The production of eggs must place a great drain on the nitrogen resources of a female insect, which in turn is partially reflected in the differing feeding strategies found in insects. McNeill and Southwood (1978) discuss ways in which food availability is either increased or maximised. Prestidge and McNeill (1981) point out that reproduction is more affected by the availability of nitrogen than either longevity or the rate of development. Evidence suggests (Mattson 1980, Reader and Southwood unpub) that short lived plants, from an early successional sere, have high nitrogen levels for short periods, whereas low nitrogen levels can be used as a means of defense in a long-lived 'apparent' (Feeny 1976) plant, such as Viburnum tinus. Such shrubs may be stress-adapted and contain less nitrogen than their competitive selected counter-parts (Mattson 1980). Indeed, being evergreen seems to be correlated with stress conditions and low nitrogen levels.

Specific, non-favourable amino acids can be utilised by the plant as a major source of soluble nitrogen. The large amounts of γ amino-butyric acid found in the leaves of Viburnum for a large part of the season (up to 59 % in some years) combined with the low amounts of favourable amino acids in absolute terms may well act as a herbivore deterrent Rhoades and Cates 1976), for γ amino butyric acid is known to be toxic (Bell and Janzen (1971), Rehr et al (1973)). A prohibitive amount of foliage (or phloem sap) would need to be consumed by an insect which did

not fit into the narrow window when food quality is high since even during this favourable period the nitrogen levels are low when Viburnum is compared with most other plants.

Aleurotrachelus appears to have overcome both the low nitrogen levels and any morphological or chemical defences in Viburnum tinus. Three factors probably aid this. Whitefly are known to possess quantities of symbionts which perhaps can enable inadequate diets to become nutritionally adequate. Secondly the long life history allows development to take place over a considerable period of time, providing the temperature does not fall too low. In this, it resembles the cabbage whitefly which may overwinter as a fourth instar (Iheagwam 1976). It might be expected that climate should be a limiting factor in a species at the northern edge of its range. However, only extreme winters lead to extensive mortality in the Viburnum whitefly (Southwood and Reader unpub) and even then most of this is due to damage to the plant causing leaf fall, and hence death to the sessile insect. A third aspect which has not been quantified in Aleurotrachelus but may have existed is the ability of sap feeding insects to cause sinks of nutrients in leaves (Way and Cammell (1970), Dixon and Wratten (1971)) as a means of increasing the nitrogen availability to an insect.

The third pathway of change identified by Southwood (1975a) - migration, has also been shown by Waloff (1980) to be one of the main ways in which plant feeders vary their numbers. Because of its relatively isolated position at Silwood Park it seems unlikely that the populations of Aleurotrachelus increased numerically through immigration. Additionally no evidence could be found that the flight exhibited by the Viburnum whitefly was of a type expected in a migrating insect, (i.e. it was neither prolonged nor at reasonable heights and no triggers could be found which initiated flight). The winter morph of the cabbage whitefly has a considerable rate of climb (Iheagwam 1977) and other

whiteflies have been found at various heights, for example the cotton whitefly, Bemisia tabaci, was observed at a height of twelve metres by Trehan (1944) and Glick (1939) estimated that Trialeurodes abutilonea could reach between 61 - 152 m. high. The Viburnum whitefly is better compared with the summer morph of Aleyrodes proletella both in that flight movements are confined to trivial flights or 'flits', and that they both remain in the same location for several generations (Southwood 1975b). As the population increased in size on Bush A, more insects were found to leave the bush, but this constitutes a loss to the population, rather than active dispersal, for neither the range covered nor the ability of the whitefly to find its host was sufficient to enable many insects to reach another host. No stimulus from the plant which could induce migration was found. In the green spruce aphid alate production is related both to the lowering of amino acid levels in the leaves, and also to changes in the proportions of different amino acids. (Carter and Cole 1977). It appears that Aleurotrachelus, like the less mobile leafhoppers, stabilized its environment with respect to nitrogen by closely synchronising its life cycle to the phenology of the plant (Prestidge and McNeill 1981).

Aleurotrachelus is thus an insect which seems to place little drain on the resources of its host plant. In the majority of situations the populations are preserved at very low levels, which from observations appears to be the normal occurrence, (Hickman unpub), rather than the high population found in Bush A. The habitat at Silwood remains a fairly isolated one on which this species is found, and in some ways it can be compared with the physical isolation of populations on motorways, where verges become ecological islands, which are poor in numbers of predators and parasites and which are subject to fluctuations in numbers caused by nitrogen variations (Port and Thompson 1980).

In conclusion it appears that Aleurotrachelus is an insect which has crossed the 'nutritional hurdle' (Southwood 1973) and is able to survive on an evergreen shrub with low levels of nitrogen, which places limitations on the insect in terms of food quality. These limitations restrict the fecundity of the female but when improvements occur they can be exploited causing the population to increase. Natality would thus appear to be of fundamental importance in the dynamics of this whitefly. It is the pathway through which population change occurs and will be influenced both by host plant quality and by the density of the insect itself as the population rises.

SUMMARY

1. A long term study on the Viburnum whitefly has been undertaken. This thesis examines parameters which could effect the key factor - k_o, the failure to lay the maximum complement of eggs.
2. Larval conditions did not appear to affect the fecundity of the resultant females.
3. New leaves were the preferred oviposition sites.
4. Fecundity varied annually, but appeared to fluctuate round a mean.
5. The fecundity of the female appeared to affected by the host plant.
6. The number of eggs laid decreased experimentally with density. In the natural population the number of eggs laid rose with density until a plateau had been reached, after which a fall was noted.
7. Either space for oviposition sites or the presence of eggs on the leaf appeared to be the limiting factor.
8. Fecundity was found to increase with temperature in the laboratory, but not in the field.
9. Aleurotrachelus moves from old to new leaves soon after emergence.
10. No alteration of flight patterns with climate could be established.
11. No single equation fits the density with distance data for all years, although in the majority of cases values of c of less than 2 were found, which is thought to imply an attraction between individuals.
12. Less adults were caught at heights than on traps close to the ground.
13. More males were caught at the beginning of the season, and as the population density rose, more males were found to fly.
14. Movement upto 5m. from the host bush appeared to be density dependent. However, there is no evidence that longer flights become more frequent as the population density rises.
15. Aleurotrachelus is more flight willing from a non host.

16. Younger females appear to fly longer than older ones, but there was no evidence that these had immature ovaries.
17. Whiteflies appear to vary in their host finding ability, Aleurotrachelus will land on any plant.
18. Only one predator, a coniopterygid, showed any numerical response with prey density, spiders became less effective as the population increased.
19. The amino acid concentrations varied between plants and between years. The number of eggs laid per leaf on Bushes A and B could be related to the total amino acid levels.
20. Large seasonal variations in amino acid levels exist. These result in the percentage of beneficial amino acids being high at the time of new leaf growth and egg laying.
21. The low nitrogen levels and high quantities of unfavourable amino acids could act as a defensive mechanism for Viburnum tinus.
22. A k - value analysis indicated that migration and predation are not key components of k_o. The unquantifiable aspects - density and host quality, would appear to be the governing mechanisms of the population.

ACKOWLEDGEMENTS

That this thesis has been completed is due in no small part to a number of people. Professor T.R.E. Southwood initially started the project and has been a source of help and encouragement during his time at Silwood and latterly in Oxford. I am particularly grateful to Professor M.P. Hassell, who took over as my supervisor towards the end of this project, for his help, interest and constructive criticism.

I would like to thank Dr. S. McNeill and Mr. A. Broodbank for their advice and help with the amino acid analysis; Professor J.S. Kennedy for the use of his flight chamber, and Dr. A.R. Ludlow for assistance in using it. Many people have helped with the censuses over the years, these include E. Barnard, H. Frayne, T. Kapatos, E. Mason and M. Reese. My thanks are also due to Mrs. M. Robinson for typing, and to Mrs. M. Clements for all her help in completing this thesis.

I would also like to thank my family for their constant support and encouragement, particularly my husband who has had the dubious pleasure of reading the manuscript.

REFERENCES

ADESIYUN, A.A. and SOUTHWOOD, T.R.E., (1979). Differential migration of the sexes in Oscinella frit (Diptera : Chloropidae). Entomologia Experimentalis et Applicata, 25, 59-63.

ANDREZEJAWSKA, L., (1965). Stratification and its dynamics in meadow communities of Auchenorrhyncha. Ekologia Polska, (A) 13, 685-715.

ANON., (1978). Glasshouse whitefly. Ministry of Agriculture, Fisheries and Food.

BAKER, R.R., (1978). The Evolutionary Ecology of Animal Migration. Hodder and Stoughton, London, 1012pp.

BALTENSWEILER, W., (1968). The cyclic population dynamics of the grey larch tortix, Zeiraphera griseana Hubner (= Semasia diniana Guenee) (Lepidoptera : Tortricidae). In: Insect Abundance (ed) Southwood, T.R.E. Royal Entomological Society Symposium, 4, 88-97. Blackwell Scientific Publications, Oxford.

BELL, E.A. and JANZEN, D.H., (1971). Medical and ecological considerations of L. dopa and 5 HTP in seeds. Nature, 229, 136-137.

BERNAYS, E.B., CHAPMAN, R.F., HORSEY, J. and LEATHER, E.M., (1975). The inhibitory effect of seedling grasses on feeding and survival of Acridids (Orthoptera). Bulletin of Entomological Research, 64, 413-420.

BOXTEL, W. van, WOETS, J. and LENTEREN, J.C. van, (1978). Determination of host-plant quality of egg plant (Solanum melongena L.), cucumber (Cucumis sativus L.), tomato (Lycopersicum esculentum L.) and paprika (Capsicum annuum L.) for the greenhouse whitefly (Trialeurodes vaporariorum (Westwood) (Homoptera:Aleyrodidae). Proceedings of the International Symposium on Crop Protection, Mededelingen Fac. Landbouww Rijksuniv. Gent.

BROADBENT, L., DONCASTER, J., HULL, R. and WATSON, M., (1948). Equipment used for trapping and identifying alate aphids. Proceedings of the Royal Entomological Society of London, A. 23, 57 - 58.

BROOKS, M.A., (1963). The microorganisms of healthy insects. In: Insect Pathology. An Advanced Treatise Vol. 1. (ed.) Steinhaus E.A. pp. 215-250. Academic Press, New York and London.

BURSELL, E., (1974). Environmental aspects - Temperature. In: The Physiology of Insecta Vol. 11,(ed) Rockstein M. pp. 1-84. Academic Press, New York and London.

BUTLER, C.G., (1938). On the ecology of Aleurodes brassicae Walk. (Hemiptera). Transactions of the Royal Entomological Society of London, 87, 291 - 311.

CARTER, C.I. and COLE, J., (1977). Flight regulation in the green spruce aphid (Elatobium abietinum). Annals of Applied Biology, 86, 137-151.

CHAPMAN, R.F., (1974). The chemical inhibition of feeding by phytophagous insects: a review. Bulletin of Entomological Research, 64, 339 - 363.

CHENG, C.H. and PATHAK, M.D., (1972). Resistance to Nephotettix virescens in rice varieties. Journal of Economic Entomology, 65, 1148 - 1153.

CLARK, L.R., (1963a). On the density and distribution of newly established nymphs of Cardiaspina albitextura (Psyllidea) at times of high abundance. Proceedings of the Linnean Society of New South Wales, LXXXVIII, 67 - 73.

CLARK, L.R., (1963b). The influence of population density on the number of eggs laid by ♀ of C. albitextura. Australian Journal of Zoology, 11, 190 - 201.

COOK, W.C., (1967). Life history, host plants and migrations of the Beet leafhopper in the Western United States. Technical Bulletin of the United States Department of Agriculture, 1365, 122pp.

CROMBIE, A.C., (1942). The effect of crowding upon the oviposition of grain-infesting insects. Journal of Experimental Biology, 19, 311-340.

DADD, R.H. and KRIEGER, D.L., (1968). Dietary amino-acid requirements of the aphid Myzus persicae (Sulz.). Journal of Insect Physiology, 14, 741-764.

DALMAT, H.T., (1950). Studies on the flight range of certain Simuliidae, with the use of aniline dye marker. Annals of the Entomological Society of America, 43, 537-545.

DAY, R.K., (1980).Simulation studies on the growth of a Trialeurodes vaporariorum population. unpub. Thesis for the Diploma of Imperial College.

DINGLE, H., (1965). The relation between age and flight activity in the milk weed bug Oncopeltus. Journal of Experimental Biology, 42, 269-283.

DINGLE, H., (1966). Some factors affecting flight activity in individual milkweed bugs (Oncopeltus). Journal of Experimental Biology, 44, 335-343.

DINGLE, H. and ARORA, G.K., (1973). Experimental studies of migration in bugs of the genus Dysdercus. Oecologia, 12, 119-140.

DIXON, A.F.G., (1966). The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid, Drepanosiphum platanoides Schr. (Hemiptera, Aphididae). Journal of Animal Ecology, 35, 105-112.

DIXON, A.F.G., (1969). Migration and trivial flight activity. Journal of Animal Ecology, 38, 585-606.

DIXON, A.F.G., (1976). Timing of egg hatch and viability of the sycamore aphid, Drepanosiphum platanoides (Schr.), at bud burst of sycamore, Acer pseudo-platanus L.. Journal of Animal Ecology, 45, 593-603.

DIXON, A.F.G. and WRATTON, S.D.,(1971). Laboratory studies on aggregation, size and fecundity in the black bean aphid, Aphis fabae Scop. Bulletin of Entomological Research, 61, 97-111.

DOBZHANSKY, T and WRIGHT, S., (1943). Genetics of natural populations: X. Dispersion rates in Drosophila pseudoobscura. Genetics, 28, 304-340.

DOWELL, R.V.,(1979). Host selection by the citrus blackfly Aleurocanthus woglumi (Homoptera:Aleyrodidae). Entomologia Experimentalis et Applicata, 25, 289-296.

DOWELL, R.V., HOWARD, F.W. CHERRY, R.H. and FITZPATRICK, G.E.,(1979). Field studies on the host range of the citrus blackfly Aleurocanthus woglumi (Homoptera:Aleyrodidae). Canadian Entomologist,111, 1 - 6.

DUCKETT, D.P.,(1974). Further studies of ant-aphid interaction. unpub. PhD. Thesis University of London.

DURZAN, D.J.,(1968a). Nitrogen metabolism of Picea glauca. 1. Seasonal changes in free amino acids in buds, shoot apices and leaves and the metabolism of uniformly labelled C^{14} - L - arginine by buds during the onset of dormancy. Canadian Journal of Botany, 46, 909-919.

DURZAN, D.J., (1968b). Nitrogen metabolism of Picea glauca II. Diurnal changes of free amino acids, amides, and quanidino compounds in roots, buds and leaves during the onset of dormancy of white spruce saplings. Canadian Journal of Botany, 46, 921-928.

DURZAN, D.J., (1968c). Nitrogen metabolism of Picea glauca. III Diurnal changes of amino acids, amides, protein, and chlorophyll in leaves of expanding buds. Canadian Journal of Botany, 46, 929-93 .

EL KHIDIR, E., (1963). Ecological studies on Aleyrodes brassicae with special reference to dispersal. unpublished PhD Thesis University of London.

EMBREE, D.G.,(1965). The population dynamics of the winter moth in Nova Scotia, 1954-1962. Memoirs of the Entomological Society of Canada, 46, 3 - 57.

VAN EMDEN, H.F.,(1969). The different reactions of Brevicoryne brassicae and Myzus persicae to leaf age, turgidity and soluble nitrogen in brassicas. Annals of Applied Biology, 63, 324-325.

VAN EMDEN, H.F.,(1973). Aphid-Host Plant Relationships : some recent studies. In: Perspectives in Aphid Biology (ed.) Lowe, A.D. PP. 25-43. Entomological Society of New Zealand Bulletin,2.

VAN EMDEN, H.F. and BASHFORD, M.A.,(1971). The performance of Brevicoryne brassicae and Myzus persicae in relation to plant age and leaf amino acids. Entomologia Experimentalis et Applicata, 14, 349-360.

FEENY, P., (1976). Plant Apparency and Chemical Defence. In: Recent Advances in Phytochemistry, 10, 1-40. (eds.) Wallace, J.W. and Mansell, R.L. Plenum Press, New York and London.

FREEMAN, G.H.,(1977). A model relating numbers of dispersing insects to distance and time. Journal of Applied Ecology, 14, 477-487.

GERLING, D., (1966). Biological studies on Encarsia formosa. Annals of Entomological Society of America, 59, 142-143.

GLICK, P.A., (1939). The distribution of insects, spiders and mites in the air. Technical Bulletin of United States Department of Agriculture, 673, 150pp.

GRAHAM, H.M., GLICK, P.A. and OVYE., M.T., (1967). Temperature effect on reproduction and longevity of Laboratory-reared adult pink bollworm (Lepidoptera: Gelechiidae). Annals of the Entomological Society of America, 60, 1211.

GREGORY, P.H. and READ, D.R., (1949). The spatial distribution of insect-borne plant virus diseases. Annals of Applied Biology, 36, 475-482.

GRIFFITHS, G.W. and BECK, S.D., (1973). Intracellalar symbiotes of the pea-aphid, Acyrthosiphon pisum. Journal of Insect Physiology, 19, 75-84.

HAMILTON, W.D. and MAY, R.M., (1977). Dispersal in stable habitats. Nature, 269, 578-581.

HARGREAVES, C.E.M. and LLEWELLYN, M., (1978). The ecological energetics of the willow aphid Tuberolachnus salignus: the influence of aphid aggregations. Journal of Animal Ecology, 47, 605-614.

HARGREAVES, E., (1914). The life history and habits of the green-house whitefly (Aleurodes vaporariorum Westd.). Annals of Applied Biology, 1, 303-334.

HASSELL, M.P. and SOUTHWOOD, T.R.E., (1978). Foraging strategies of insects. Annual Review of Ecology and Systematics, 9, 75-98.

HAWKES, C., (1972). The estimation of the dispersal rate of the adult cabbage root fly Erioischia brassicae (Bouche) in the presence of a brassica crop. Journal of Applied Ecology, 9, 617-632.

HILL, M.G., (1976). The population and feeding ecology of 5 species of Leafhoppers (Homoptera) on Holcus mollis L. unpub. PhD. Thesis University of London.

HODJAT, S.H., (1968). The effect of crowding on the survival rate of development, size, colour and fecundity of Dysdercus fasciatus Sign. (Hem. Pyrrhocoridae) in the laboratory. Bulletin of Entomological Research, 58, 487-504.

HOLLING, C.S., (1959). Some characteristics of simple types of predation and parasitism. Canadian Entomologist, 91, 385-398.

HOUSE, H.L., (1965). Effect of low levels of the nutrient content of a food and of nutrient inbalance on the feeding and nutrition of a phytophagous larvae (Celerio emphorbiae (Linnaeus) Lepidoptera:Sphingidae. Canadian Entomologist, 97, 62-68.

HOUSE, H.L., (1969). Effects of different proportions of nutrients in insects. Entomologia Experimentalis et Applicata, 12, 651-669.

HOUSE, H.L., (1972). Insect nutrition. In: Biology of Nutrition (ed.). T-W-Fiennes, R.N. International Encyclopaedia of Food and Nutrition, Vol. 1B. Sect. IV. pp 513-573.

HUSSEY, N.W. and GURNEY, B., (1958). Greenhouse white fly (Trialeurodes vaporariorum Westwood). Report of the Glasshouse Crops Research Institute, 1957, 134-137.

HUSSEY, N.W. and GURNEY, B., (1960). Some host plant factors affecting fecundity of white flies. Report of the Glasshouse Crops Research Institute, 1959, 99-103.

IHEAGWAM, E.U., (1976). Studies on the population dynamics, photoperiodism, and flight behaviour of the cabbage whitefly, Aleyrodes brassicae (Wlk.) Homoptera: Aleyrodidae unpub. Ph.D. Thesis University of London.

IHEAGWAM, E.U., (1977). Comparative flight performance of the seasonal morphs of the cabbage whitefly, Aleyrodes brassicae (Wlk), in the laboratory. Ecological Entomology 2, 267-271.

IHEAGWAM, E.U.,(1978). Effects of temperature on development of the immature stages of the cabbage whitefly, Aleyrodes proletella (Homoptera: Aleyrodidae). Entomologia Experimentalis et Applicata, 25, 59-63.

JOHNSON, B.,(1959). Studies on the degeneration of the flight muscles of the alate aphids. II. Histology and control of muscle breakdown. Journal of Insect Physiology, 3, 367-377.

JOHNSON, C.G.,(1969). Migration and Dispersal of Insects by flight Methuen London.763pp.

JOHNSON, C.G.,(1974). Lability of the flight system: a context for functional adaptation. In: Insect Flight (ed.) Rainey, R.C. Royal Entomological Society of London Symposium, 7, 217-234. Blackwell Scientific Publications, Oxford.

KEHAT, M. and WYNDHAM, M., (1973). The relation between food, age and flight in the Rutterglen bug, Nysius vinitor (Hemiptera: Lygaeidae). Australian Journal of Zoology,21, 427-434.

KENNEDY, J.S.,(1961). A turning point in the study of insect migration. Nature, London, 189, 785-791.

KENNEDY, J.S., (1974). Changes in responsiveness in the patterning of behavioural sequences. In: Experimental Analysis of Insect Behaviour (ed.)Barton Browne, L. pp1-6 Springer-Verlag Berlin.

KENNEDY, J.S.,(1975). Insect dispersal. In: Insects, Science and Society. (ed.) Pimentel, D. pp. 105-119. Academic Press, New York and London.

KENNEDY, J.S. and LUDLOW, A.R., (1974). Coordination of two kinds of flight activity in an aphid. Journal of Experimental Biology, 61, 173-196.

KENNEDY, J.S. and STROYAN, H.L.G., (1959). Biology of Aphids. Annual Review of Entomology, 4, 139-160.

KLOMP, H., (1968). A seventeen - year study of the abundance of the pine looper, Bupalus piniarius L. (Lepidoptera: Geometridae) In: Insect Abundance (ed.) Southwood T.R.E., Royal Entomological Society Symposium, 4, 98-108. Blackwell Scientific Publications, Oxford.

LARSEN, I., (1980). Free glycine in Italian Ryegrass exhibits a marked light dependence. Preprint of Manuscript in Preparation.

LAWSON, F.R., CHAMBERLIN, J.C. and YORK, G.T.,(1951). Dissemination of the beet leafhopper in California. Technical Bulletin of the United States Department of Agriculture,1030, 59pp.

LAWTON, J.H. and McNEILL, S., (1979). Between the devil and the deep blue sea! on the problems of being a herbivore. In: Population Dynamics (eds) Anderson, R.M., Turner, B.D. and Taylor, L.R., pp 223-244. 20th Symposium of the British Ecological Society Blackwell Scientific Publications, Oxford.

van LENTEREN, J.C., WOETS, J., van der POEL,N., van BOXTEL, S., van de MERENDONK, R., van der KAMP., NELL, H. and SEVENSTER-van de LELIE, L., (1977). Biological control of the greenhouse whitefly Trialeurodes vaporariorum by Encarsia formosa Gahan in Holland, an example of successful applied ecological research. Mededelingen Fac. Landbouww, Gent. 42, 1333 - 1342.

LEWIS, T. and TAYLOR, L.R.,(1965). Diurnal periodicity of flight by insects. Transactions of the Royal Entomological Society of London, 116, 393-479.

LLOYD, Ll.,(1921). Notes on a colour tropism of Asterochiton (Aleurodes) vaporariorum. Bulletin of Entomological Research, 12, 355-359.

MATTSON, W.J.,(1980). Herbivory and plant nitrogen. Annual Review of Ecology and Systematics,11, 119-161.

McNEILL, S., (1973). The dynamics of a population of Leptopterna dolabrata (Heteroptera: Miridae) in relation to its food resources. Journal of Animal Ecology, 42, 495-507.

McNEILL, S. and SOUTHWOOD, T.R.E., (1978). The role of nitrogen in the development of insect/plant relationships. In: Aspects of Plant and Animal Coevolution. (ed.) Harborne, J.S.,pp. 77-98. Academic Press, London, New York.

MITTLER, T.E.,(1970). Effects of dietary amino acids on the feeding rate of the aphid Myzus persicae. Entomologia Experimentalis et Applicata, 13, 432-437.

MORAN, V.C. and BUCHAN, P.R.,(1975). Oviposition by the citrus psylla, Trioza erytreae (Homoptera:Psyllidae) in relation to leaf hardness. Entomologia Experimentalis et Applicata, 18, 96-104.

MORRILL, A.W.,(1903). Notes on some Aleyrodes from Massachusetts with descriptions of new species. Massachusetts Agricultural Experimental Station, Bulletin, 1.

MORRIS, R.F., (1963). The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada, 31, 1 - 332.

MOSS, R., WATSON, A. and PARR, R., (1975). Maternal nutrition and breeding success in red grouse (Lagopus lagopus scoticus) Journal of Animal Ecology, 44, 233-244.

MOUND, L.A., (1958). Reproductive capacity of Necrobia rifpes: Studies on white flies. unpub. M.Sc. Thesis, University of London.

MOUND, L.A., (1962). Studies on the olfaction and colours sensitivity of Bemesia tabaci (Genn). (Homoptera:Aleyrodidae), Entomologia Experimentalis et Applicata, 5, 99-104.

MOUND, L.A. and HALSEY, S.H., (1978). Whitefly of the World. British Museum: Natural History, Chichester, Wiley.

NELL, H.W., SEVENSTER-van der LELIE, L.A., WOETS, J. and van LENTEREN, J.C., (1976). The parasite-host relationship between Encarsia formosa (Hymenoptera:Aphelinidae) and Trialeurodes vaporariorum (Homoptera:Aleyrodidae). II Selection of host stages for oviposition and feeding by the parasite. Zeitschift fur Angewandte Entomologie, 81, 372-376.

PARIS, O.H., (1965). The vagility of P^{32} labelled Isopods in grassland. Ecology, 46, 635-648.

PARRY, W.H., (1974). The effects of nitrogen levels in Sitka spruce needles on Elatobium abietinum (Walker) populations in north-eastern Scotland. Oecologia, 15, 305-320.

PARRY, W.H., (1976). The effect of needle age on the acceptibility of Sitka spruce needles to the aphid Elatobium abietinum (Walker). Oecologia, 23, 297-313.

PATE, J.S., (1968). Physiological aspects of inorganic and intermediate nitrogen metabolism (with special reference to the legume, Pisum arvense L.). In: Recent aspects of nitrogen metabolism in plants. (eds) Hewitt, E.J. and Cutting, C.V., pp. 219-240. Academic Press, London.

PODOLER, H.G. and ROGERS, D., (1975). A new method for the identification of key factors from life table data. Journal of Animal Ecology, 44, 85-114.

POLLARD, D.G., (1955). Feeding habit of the cotton whitefly, Bemisia tabaci Genn. (Homoptera:Aleyrodidae). Annals of Applied Biology, 43, 664-671.

POLLARD, D.G., (1971). Some observations of the mouth-parts of whiteflies, (Hem., Aleyrodidae). Entomologist's Monthly Magazine, 107, 81-88.

PORT, G.R. and THOMPSON, J.R., (1980). Outbreaks of insect herbivores on plants along motorways in the United Kingdom. Journal of Applied Ecology, 17, 649-656.

PRESTIDGE, R.A., (1980). The influence of mineral fertilization on grassland leafhopper associations. unpub. Ph.D. Thesis, University of London.

PRESTIDGE, R.A. and McNEILL, S., (1981). The importance of nitrogen in the ecology of grassland Auchenorrhyncha. In: Nitrogen as an Ecological Factor. (eds.). McNeill, S., Lee, J.A., Rorison, I.H. and Gibson, C.W.D., British Ecological Society Symposium (in press).

RAMSAY, J.A., BUTLER, C.G. and SANG, J.H., (1938). The humidity gradient at the surface of a transpiring leaf. Journal of Experimental Biology, 15, 255.

REHR, S.S., FEENY, P.P. and JANZEN, D.H., (1973). Chemical defense in central American non-ant-acacias. Journal of Animal Ecology, 42, 405-416.

RIBBANDS, C.R., (1950). Changes in behaviour of honey bees following their recovery from anaesthesia. Journal of Experimental Biology, 27, 302-310.

RICHARDS, G.A. and BROOK, S.M.A., (1958). Internal symbiosis in insects. Annual Review of Entomology, 3, 37-56.

RICHARDS, O.W. and SOUTHWOOD, T.R.E., (1968). The abundance of insects: introduction. In: Insect Abundance (ed.). Southwood, T.R.E. Royal Entomological Society of London Symposium. 4, pp 1-7. Blackwell Scientific Publications, Oxford.

RHOADES, D.F. and CATES, R.G., (1976). Towards a general theory of plant anti-herbivore chemistry. In: Recent Advances in Phytochemistry, 10, 168-213. (eds.) Wallace,J.W. and ,Mansell, R.L., Plenum Press, New York and London.

ROSE, D.J.W., (1971). The biology and dispersal of Cicadulina spp. (Cicadellidae). unpub. Ph.D. Thesis, University of London.

ROSE, D.J.W., (1972). Dispersal and quality in populations of Cicadulina species (Cicadellidae) Journal of Animal Ecology, 41, 589-609.

ROSE, D.J.W., (1973). Distances flown by Cicadulina spp. (Hem., Cicadellidae) in relation to distribution of maize streak disease in Rhodesia. Bulletin of Entomological Research, 62, 496-505.

RUSSELL, L.M., (1963). Hosts and distribution of species of Trialeurodes (Homoptera:Aleurodidae). Annals of the Entomological Society of America, 56, 149-153.

SIMPSON, J., (1954). Effects of some anaesthetics on honey bees: nitrous oxide, CO_2 ammonium nitrate smoker fumes. Bee World, 35, 149-155.

SLANSKY, F. Jr., (1974). Relationship of larval food-plants and voltinism patterns in temperate butterflies. Psyche, 81, 243-253.

SMITH, J.G., (1969a). Some effects of crop background on populations of aphids and their natural enemies on brussels sprouts. Annals of Applied Biology, 63, 326-330.

SMITH, J.G., (1969b). Effects of crop background on populations of Brassica aphids and their natural enemies. Unpub. Ph.D. Thesis University of London,

SOGAWA, K., (1971). Effects of feeding of the brown planthopper on the components in the leaf blade of rice plants. Japanese Journal of Applied Entomology and Zoology, 15, 175-179.

SOLOMON, M.G., (1973). Ecological studies of grassland leafhoppers with special reference to Psammotettix confinis (Dahlbom) (Cicadellidae, Hemiptera). Unpub. Ph.D. Thesis, University of London.

SOUTHWOOD, T.R.E., (1962). Migration of terrestrial artropods in relation to flight. Biological Reviews, 32, 171-214.

SOUTHWOOD, T.R.E., (1973). The insect/plant relationship - an evolutionary perspective. In: Insect/Plant Relationships (ed.). van Emden, H.F. Symposium Royal Entomological Society: London. 6, pp. 3-30. Blackwell Scientific Publications, Oxford.

SOUTHWOOD, T.R.E., (1975a). The dynamics of insect populations. In: Insects, Science and Society. (ed.). Pimentel, D. pp. 151-199. Academic Press, Yew York.

SOUTHWOOD, T.R.E., (1975b). The stability of the trophic milieu, its influence on the evolution of behaviour and of responsiveness to trophic signals. Colloques Internationaux du C.N.R.S. No. 265. p. 471-493.

SOUTHWOOD, T.R.E., (1977). Habitat, the templet for ecological strategies? Journal of Animal Ecology, 46, 337-365.

SOUTHWOOD, T.R.E., (1978). Ecological Methods, With Particular Reference of the Study of Insect Populations. Chapman and Hall, London 524pp.

SOUTHWOOD, T.R.E. and JEPSON, W. F. and van EMDEN, H.F., (1961). Studied on the behaviour of Oscinella frit L. (Diptera) adults of the panicle generation. Entomologia Experimentalis et Applicata, 4, 193-210.

THOMSEN, M.,(1927). Studien uber die Parthenogenese bin einigen Cocciden und Aleurodiden. Zeitschrift fur Zellforschung, 5, 1 - 116.

THORPE, W.H.,(1951). The definition of terms used in animal behaviour studies. Bulletin of Animal Behaviour, 9, 34-40.

TREHAN, K.,(1940). Studies of British Whitefly. Transactions of the Royal Entomological Society of London, 90, 575-616.

TREHAN, K.N.,(1944). Further notes on the bionomics of Bemisia gosspiperda M and L., the whitefly of cotton in the Punjab. Indian Journal of Agricultural Science, 14, 53-63.

TURNBULL, A.L., (1962). Quantitative studies of the food of Linyphia triangularis Clerck (Araneae:Linyphiidae). Canadian Entomologist, 94, 1233-1249.

VAISHAMPAYAN, A.M., KOGAN, M., WALDBAUER, G.P. and WOOLLEY, J.T.,(1975a) Spectral specific responses in the visual behaviour of the greenhouse whitefly Trialeurodes vaporariorum (Homoptera: Aleyrodidae). Entomologia Experimentalis et Applicata, 18, 344-356.

VAISHAMPAYAN, S.M., WALDBAUER, G.P. and KOGAN, M., (1975b). Visual and olfactory responses in orientation to plants by the greenhouse whitefly Trialeurodes vaporariorum (Homoptera: Aleyrodidae). Entomologia Experimentalis et Applicata, 18, 412-422.

VARLEY, G.C. and Gradwell, G.R., (1960). Key factors in population studies. Journal of Animal Ecology, 29, 399-401.

VARLEY, G.C. and GRADWELL, G.R. (1968). Population models for the winter moth. In: Insect Abundance (ed.). Southwood, T.R.E. Royal Entomological Society of London Symposium, 4, pp.132-142. Blackwell Scientific Publications, Oxford.

VARLEY, G.C., GRADWELL, G.R. and HASSELL, M.P.,(1973). Insect Population Ecology, An Analytical Approach. Blackwell Scientific Publications, Oxford. 212pp.

VERSCHOOR-van-der POEL, P.J.G. and van LENTEREN, J.C.,(1978). Host-plant selection by the greenhouse whitefly, Trialeurodes vaporariorum (Westwood) (Homoptera:Aleyrodidae). Proceedings of the International Symposium on Crop Protection. Fac. Landbouww. Rijksuniv, Gent. 43/2, 387-396.

VITARANA, S.I., (1977). Role of Encarsia formosa in the population dynamics of the greenhouse whitefly Trialeurodes vaporariorum in an enclosed environment. Unpublished M.Sc. Thesis, University of London.

WADLEY, F.M.,(1931). Ecology of Toxoptera graminus, especially as to factors affecting importance in the northern United States. Annals of the Entomological Society of America, 24, 325-395.

WALOFF, N.,(1973). Dispersal by flight of leafhoppers (Auchenorrhyncha Homoptera). Journal of Applied Ecology, 10, 705-730.

WALOFF, N., (1980). Studies on Grassland leafhoppers (Auchenorrhyncha Homoptera) and their natural enemies. Advances in Ecological Research, 11, 81-215.

WALOFF, N. and BAKKER, K., (1963). The flight activity of Miridae (Heteroptera) living on broom, Sarthamnus seoparius (L.) Journal of Animal Ecology, 32, 461-480.

WALOFF, N. and THOMPSON, P., (1980). Census data of populations of some leafhoppers (Auchenorrhyncha, Homoptera) of acidic grassland. Journal of Animal Ecology, 49, 395-416.

WATT, K.E.F., (1960). The effect of population density on fecundity in insects. Canadian Entomologist, 92, 674-695.

WAY, M.J. and CAMMELL, M., (1970). Aggregation behaviour in relation to food utilisation by aphids. In: Animal Populations in Relation to their Food Resources (ed.). Watson, A. British Ecological Society Symposium, 10, 229-246. Blackwell Scientific Publication, Oxo

WEARING, C.H., (1967). Studies on the relations of insect and host plant. II. Effects of water stress in host plants on the fecundity of Myzus persicae and Brevicoryne brassicae. Nature, 213, 1052-1053.

WEARING, C.H., (1972). Responses of Myzus persicae and Brevicoryne brassicae to leaf age and water stress in Brussels sprouts grown in pots. Entomologia Experimentalis et Applicata, 15, 61-80.

WHITE, T.C.R., (1968). An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology, 50, 905-909.

WHITE, T.C.R., (1974). A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia, 16, 279-301.

WHITE, T.C.R., (1976). Weather, food and plagues of locusts. Oecologia, 22, 119-134.

WOLFENBARGER, D.O., (1946). Dispersion of small organisms. American Midland Naturalist, 35, 1-152.

WRATTON, S.D., (1974). Aggregation in the birch aphid, Euceraphis punctipennis (Zett) in relation to food quality. Journal of Animal Ecology, 43, 191-198.

APPENDIX 2.1 Numbers of old and new leaves on the three bushes.

	A		B		C	
Year	Old	New	Old	New	Old	New
1968	13357	3334	7346	2275	3930	1228
1969	15601	4128	9842	4700	4742	1650
1970	17189	4145	13609	2689	6280	892
1971	16046	1953	13841	1512	2042	856
1972	19531	2044	19265	1607	2138	567
1973	21494	1776	18248	1292	2426	376
1974	20872	2412	22114	2643	2780	196
1975	20668	4112	23622	1662	1889	189
1976	23092	2149	23055	2372	1542	233

Appendix 3.1

The percentage of the population caught on sticky traps and the population density (Log No / new leaf) during the years 1968 - 1976.

Years	Total Population	Population Density	Percentage of the population			
			0.45m	2.50m	5.00m	7.30m
1968	23634	0.85	2.96			
1969	16322	0.60	4.99			
1970	29267	0.85	3.11	0.65	0.21	0.41
1971	46145	1.37	4.22	1.13	0.56	0.69
1972	93964	1.66	8.67	2.14	0.77	0.02
1973	162689	1.96	9.67	1.61	0.72	0.31
1974	234931	1.99	7.66	1.50	1.00	0.15
1975	149829	1.56	8.11	0.81	0.53	0.15
1976	275368	2.11		2.51	0.91	0.41

Appendix 4.1

Number of predators on Bush A.

Year	No. Spiders	No. species Predators	No. individual Predators	No. Mirids
1968	6.4	3	548.4	517.7
1969	8.9	1	606.8	606.8
1970	31.7	2	546.1	517.4
1971	28.9	1	170.9	170.9
1972	21.7	3	98.8	88.9
1973	17.3	3	1182.0	1022.9
1974	26.8	5	941.4	542.1
1975	26.2	5	1124.1	769.2
1976	31.0	6	1267.4	472.7

Appendix 4.2

Number of predators on Bush B.

Year	No. Spiders	No. species Predators	No. individual Predators	No. Mirids
1968	3.4	2	31.7	26.7
1969	16.8	1	285.9	285.9
1970	25.8	2	283.7	253.0
1971	22.0	1	419.1	419.1
1972	7.2	1	213.3	213.3
1973	14.9	3	162.3	152.0
1974	21.9	1	110.6	110.6
1975	5.2	2	197.9	197.9
1976	7.4	4	250.3	238.4

Appendix 4.3

Number of whitefly trapped by spiders and attacked by mirids on Bushes A and B.

Year	No. trapped by spiders		No. attacked by mirids	
	A	B	A	B
1968	443	31	13958.7	16.7
1969	552	102	9821.0	253.6
1970	1520	161	12417.6	423.4
1971	1855	134	6049.9	1974.8
1972	1621	101	4187.2	983.7
1973	1847	104	50402.7	316.4
1974	2107	126	33176.5	274.2
1975	2457	44	40383.0	819.8
1976	3683	45	29468.1	1368.2

Appendix 5.1

p moles of individual amino acids found in 100 mg dry weight of plant material. Amino acids numbered as in Table 5.1.

Δ indicates a sample from new leaves.

'10' indicates the 10 essential amino acids.

APPENDIX 5.1

BUSH A

Amino Acid	11.8.70$^{\Delta}$	11.8.70	6.72$^{\Delta}$	27.5.75$^{\Delta}$	2.6.75	19.6.75	19.6.75$^{\Delta}$	11.7.75$^{\Delta}$	6.8.75	6.8.75$^{\Delta}$
1	34.4	36.8	280.7	17.0	77.9	192.1	336.4	33.0	20.2	9.0
2	182.6	44.5	150.1	170.7	175.1	376.3	197.5	133.8	28.0	107.1
3	74.0	24.3	80.2	122.8	-	-	-	129.9	46.2	78.5
4	49.2	30.9	462.5	41.4	268.9	347.9	422.2	72.6	56.4	31.6
5	45.0	12.4	-	22.0	-	-	-	10.7	-	7.3
6	26.4	23.4	3.0	17.1	-	-	19.9	21.6	9.3	20.1
7	226.8	281.1	50.1	223.2	43.8	58.7	83.0	211.7	210.3	176.7
8	29.0	31.7	30.9	79.6	53.3	25.2	49.8	36.1	19.7	31.2
9	19.5	34.6	-	23.3	8.4	-	5.2	-	-	-
10	33.4	48.7	15.7	37.5	13.8	31.5	36.9	16.9	11.1	13.3
11	113.3	20.0	32.4	40.5	9.7	9.8	31.7	15.8	6.5	9.0
12	21.4	26.9	49.4	32.7	-	-	9.0	20.6	7.8	13.8
13	19.1	31.9	22.5	64.0	147.4	21.4	22.5	31.0	10.6	26.8
14	210.8	203.8	36.9	451.7	90.3	80.5	364.6	388.2	362.2	405.5
15	23.3	18.0	80.9	35.6	12.0	22.7	25.8	16.4	13.7	16.4
16	17.4	24.6	28.8	39.8	15.0	-	50.5	12.2	37.8	12.2
17			330.2			-				
u1	185.3	89.6		78.8	13.9	43.7	63.6	32.9	28.8	23.9
u2	24.5			52.7	39.8		19.8	12.7	-	23.9
u3							14.1	-	4.1	-
u4							14.1	45.4	7.9	14.0
u5										
u6										
Σ1-16	1126.3	893.8	1324.06	1418.9	915.6	1166.1	1655.3	1150.5	839.8	958.5
Σ	1336.0	983.4	1654.3	1550.4	969.3	1209.8	1767.0	1241.5	880.6	1020.3
Σ'10'	437.6	254.03	355.3	491.0	434.7	486.9	420.0	262.2	127.4	216.0
%'10'	38.85	28.42	26.83	34.60	47.47	41.75	25.37	22.79	15.17	22.54

APPENDIX 5.1

BUSH A cont.

Amino Acid	14.6.76$^{\Delta}$	29.6.76$^{\Delta}$	13.7.76$^{\Delta}$	2.8.76$^{\Delta}$	31.3.77	5.4.77	12.5.77	9.6.77$^{\Delta}$	30.6.77	14.7.77$^{\Delta}$
1	29.9	27.6	12.6	-	32.0	40.7	57.7	50.4	211.5	11.2
2	287.1	253.3	103.4	136.0	87.0	62.8	88.8	521.2	428.0	131.7
3	149.2	103.5	86.6	82.2	86.5	121.1	160.3	171.2	231.3	81.5
4	59.0	67.0	27.6	41.1	50.4	117.3	235.7	137.3	565.7	33.6
5	37.7	57.9	31.1	-	16.5	-	85.0	59.2	-	26.1
6	-	36.8	13.5	-	-	-	45.0	55.2	12.0	17.8
7	472.6	824.3	237.5	177.3	201	162.6	261.5	957.6	61.8	270.8
8	56.6	59.1	43.6	57.6	25.4	21.8	22.1	74.6	34.1	73.6
9	-	23.9	-	-	13.2	14.4	19.5	-	-	13.9
10	26.1	46.2	21.7	19.9	10.9	7.4	19.5	32.7	17.5	21.0
11	32.5	59.2	28.6	27.9	14.6	10.4	28.4	70.2	10.8	32.3
12	112.6	119.8	65.4	53.6	17.1	6.4	26.4	46.9	5.8	96.2
13	68.1	36.5	20.9	32.1	13.8	-	17.3	220.6	18.5	80.0
14	401.6	542.5	313.6	632.7	257.9	257.9	141.3	727.5	35.5	777.2
15	47.3	51.9	19.0	25.3	9.6	15.4	31.5	89.9	17.7	33.3
16	94.0	51.4	34.8	36.6	16.9	35.0	34.5	40.7	40.6	77.9
17		81.8	98.7				101.5	387.2	96.2	
u1	89.6	94.2	30.3	-	51.1	44.97	81.0	115.45	31.4	40.3
u2	41.5	49.2	14.9	-	18.2	11.83		-		
u3		14.1	7.3	7.9				19.92		
u4			5.2	7.9				29.43		
u5										
u6		32.5								
Σ1-16	1874.3	2360.9	1059.9	1322.3	852.9	873.25	1274.5	3257.6	1690.8	1778.1
Σ	2005.4	2632.7	1216.3	1338.1	927.2	930.06	1457.0	3809.6	1818.4	1818.4
Σ'10'	543.6	581.4	282.0	334.8	191.4	167.24	261.6	1050.01	565.2	447.6
%'10'	29.0	24.62	26.61	25.32	22.45	19.15	20.53	32.23	33.43	25.17

APPENDIX 5.1

BUSH A cont.

Amino Acid	4.8.77$^{\Delta}$	16.12.77	20.3.78	17.4.78	12.5.78	27.5.78	30.5.78	8.6.78$^{\Delta}$	19.6.78$^{\Delta}$
1	20.1	31.5	20.4	25.8	34.3	73.5	26.4	36.2	78.3
2	121.6	60.8	72.3	62.8	51.2	113.2	120.0	413.7	162.5
3	59.7	48.9	84.1	68.5	89.1	120.8	134.9	267.8	307.7
4	40.6	37.2	51.3	124.2	89.2	178.7	100.9	64.0	49.3
5	-	35.9	53.3	92.7	14.7	25.2	65.7	54.1	-
6	89.2	26.5	36.0	14.6	9.8	31.1	-	48.3	25.0
7	111.2	158.7	285.8	243.5	210.6	194.4	590.2	345.6	85.9
8	29.7	31.8	31.5	69.1	25.2	35.0	38.8	115.4	35.5
9	19.6	10.5	8.0	17.5	-	-	22.4	34.0	-
10	22.5	21.0	14.6	10.8	16.4	23.6	37.2	58.3	34.3
11	15.3	17.0	29.1	12.8	8.9	25.9	29.1	21.0	40.9
12	30.4	47.6	40.0	21.8	10.5	16.6	35.5	62.8	-
13	15.6	28.6	18.8	10.7	11.1	29.6	14.4	102.8	-
14	478.6	534.8	254.8	403.5	443.1	410.3	444.4	542.0	240.2
15	29.0	22.5	24.1	15.8	14.3	20.7	35.6	51.2	22.6
16	72.6	35.5	40.6	34.2	26.0	28.8	42.5	46.1	52.5
17		48.4							
u1		52.4	61.7	76.1	38.1	65.2	66.9	97.4	
u2		14.9	22.4		5.9	20.1	20.1	70.3	53.2
u3			5.2		5.6	12.5	7.5	30.8	
u4			13.5			43.9			
u5									64.0
u6									
Σ1-16	1155.7	1148.8	1064.7	1228.3	1054.4	1327.4	1741.0	2263.3	1134.7
Σ		1264.5	1167.5	1304.4	1101.0	1469.1	1835.5	2461.8	1251.9
Σ'10'	224.7	227.7	239.0	233.2	153.1	226.8	343.0	842.0	493.5
%'10'	19.42	19.82	22.45	18.99	14.52	20.85	19.70	37.20	43.49

APPENDIX 5.1

BUSH B

Amino Acid	11.8.70$^{\Delta}$	6.72$^{\Delta}$	2.6.75	18.6.75$^{\Delta}$	19.6.75	16.7.75$^{\Delta}$	14.10.75	14.6.76$^{\Delta}$	13.7.76$^{\Delta}$	31.3.77
1	27.7	193.1	40.0	147.4	146.3	12.9	36.0	-	35.4	19.6
2	66.8	202.9	45.4	105.6	144.7	-	48.7	303.7	74.7	79.3
3	31.5	108.9	61.7	228.3	50.9	142.3	64.6	86.5	27.2	38.3
4	61.8	454.2	187.8	290.8	254.1	21.9	167.8	92.7	31.5	104.4
5	57.9	-	20.0	11.7	7.5	17.9	-	33.1	21.1	-
6	40.1	-	8.0	9.6	12.8	10.9	12.2	23.4	12.3	18.4
7	240.0	81.6	112.0	43.6	52.7	32.9	129.1	715.9	156.3	242.5
8	35.1	55.0	63.5	69.4	31.5	50.1	32.5	59.2	39.0	20.8
9	48.4	-	11.2	18.6	-	-	-	-	11.9	17.4
10	44.2	26.9	16.6	17.5	17.6	27.8	9.1	39.9	13.9	15.8
11	64.0	36.3	25.4	6.2	17.6	18.3	7.9	28.9	19.9	18.8
12	26.1	60.6	4.8	18.4	8.8	-	-	46.9	47.2	9.9
13	34.6	18.8	31.8	-	25.9	-	8.6	70.4	10.1	3.0
14	134.9	13.1	222.8	56.1	110.6	546.7	247.0	439.9	190.3	304.8
15	15.4	46.6	29.8	32.0	17.9	18.4	17.8	38.9	12.7	14.3
16	75.9	30.3	21.9	19.9	30.3	24.7	17.3	21.4	23.5	9.5
17								74.9	43.8	
u1	94.6		23.6	20.6	33.9		40.3	81.5	34.5	57.0
u2					12.3	33.2	7.4	33.3		22.6
u3					11.3		7.8	21.7		24.5
u4										
u5										
u6										
Σ1-16	1004.5	1333.1	902.7	1075.1	929.0	924.8	798.6	2000.9	726.9	917.3
Σ	1099.2	1544.4	926.3	1095.6	986.5	958.0	854.3	562.4	805.1	1021.4
Σ'10'	384.4	421.7	245.6	269.2	285.5	139.3	141.9	2212.3	205.7	179.4
%'10'	38.27	31.6	27.21	25.04	30.72	15.06	17.77	28.11	28.30	19.56

APPENDIX 5.1

BUSH B cont.

Amino Acid	5.4.77	14.4.77	23.4.77	12.5.77	26.5.77	2.6.77	9.6.77$^{\Delta}$	19.6.77	30.6.77$^{\Delta}$	7.7.77$^{\Delta}$
1	25.1	18.1	87.0	40.4	130.3	50.5	132.4	11.7	62.4	102.1
2	66.9	30.8	131.9	-	112.1	101.3	698.8	-	469.9	240.1
3	102.4	50.5	59.7	190.6	130.8	-	255.1	-	171.2	105.2
4	202.5	151.1	169.5	233.8	408.7	205.4	126.8	11.1	197.4	279.0
5	-	15.1	10.0	10.2	-	-	47.5	5.2	59.2	13.3
6	165.7	11.7	16.8	17.3	146.4	-	61.1	8.4	51.3	9.0
7	202.8	141.7	124.4	196.2	142.8	41.0	566.5	59.9	200.6	90.5
8	11.6	22.4	15.6	14.9	37.2	52.6	118.8	15.5	78.8	25.2
9	19.6	15.1	-	11.2	23.8	-	-	-	31.1	-
10	12.2	9.0	8.1	17.7	25.7	12.5	69.3	2.7	68.2	23.7
11	10.9	9.2	8.1	18.7	26	9.1	92.8	4.8	53.9	8.9
12	8.1	4.4	2.9	9.1	5.2	-	41.0	-	33.5	-
13	-	9.8	9.8	16.8	19.6	15.9	193.4	-	72.4	13.8
14	268.9	197.2	270.9	299.9	130.4	65.2	700.0	118.1	733.3	20.1
15	8.2	-	15.9	19.9	39.0	20.0	80.3	13.1	75.4	8.6
16	9.7	74.3	38.7	24.1	45.6	20.5	41.1	11.6	57.5	36.1
17							132.9			
u1	62.5	27.9	35.8	70.9	63.5	19.9	144.2		72.4	19.4
u2	17.6		14.3				61.0		54.3	26.7
u3										
u4	45.1									
u5										
u6										
Σ1-16	1114.6	760.3	969.2	1120.8	1423.6	594.0	3224.9	262.1	2415.8	975.5
Σ	1239.8	788.3	1019.6	1191.7	1487.1	613.9	3563.0		2542.6	1021.6
Σ'10'	139.1	170.6	228.1	123.3	329.0	231.9	1294.5	47.7	907.2	221.4
%'10'	12.48	22.45	22.38	11.01	23.11	39.04	40.14	18.19	37.5	22.7

APPENDIX 5.1

BUSH B cont.

Amino Acid	14.7.77$^{\Delta}$	19.7.77$^{\Delta}$	26.7.77$^{\Delta}$	11.8.77	11.8.77$^{\Delta}$	4.8.77$^{\Delta}$	25.8.77$^{\Delta}$	16.12.77	14.4.78
1	96.0	9.6	136.0	12.4	12.8	6.7	16.8	-	13.6
2	247.9	113.9	319.0	25.3	33.9	54.0	92.4	66.4	46.7
3	149.9	117.5	-	17.5	36.2	1.6	42.1	37.4	26.7
4	320.8	33.2	425.9	15.1	44.8	37.8	65.8	52.5	138.8
5	-	12.5	-	9.4	28.2	16.8	23.7	33.3	-
6	-	17.8	1.2	-	9.6	21.6	17.6	30.8	-
7	67.4	38.8	60.0	110.1	73.8	83.8	84.0	157.8	166.6
8	32.71	18.2	21.8	20.3	16.9	10.5	17.1	37.6	34.6
9	-	-	10.0	8.7	-	7.6	8.4	6.8	-
10	26.3	17.8	25.0	13.9	12.0	11.8	12.3	21.0	12.2
11	18.3	17.6	11.6	26.3	8.0	11.6	9.2	19.1	7.5
12	-	11.1	4.5	6.8	18.3	28.4	-	43.4	7.8
13	-	19.6	-	-	15.0	12.7	37.1	21.0	-
14	32.9	320.0	68.3	75.9	147.8	246.9	537.7	290.0	248.5
15	15.4	10.0	10.3	14.6	8.0	7.4	12.9	16.9	-
16	14.6	19.2	14.2	11.9	49.3	15.2	18.6	28.6	44.6
17									
u1	31.5			67.14		27.8	25.47	77.8	41.7
u2	31.9	8.41		16.9		8.9			17.6
u3									
u4									
u5			33.42					31.5	
u6									
Σ1-16	1022.3	776.7	1107.8	368.1	514.6	574.4	995.5	824.3	746.6
Σ	1085.7	785.2	1141.2	452.2		611.1	1021.0	933.6	805.9
Σ'10'	355.2	216.3	124.8	120.8	143.1	130.8	207.9	217.3	145.6
%'10'	34.75	27.85	11.27	32.82	27.81	22.77	20.89	26.4	19.5

APPENDIX 5.1

BUSH B cont.

Amino Acid	17.4.78	4.5.78	12.5.78	30.5.78	8.6.78 Δ	19.6.78 Δ	19.6.78
1	18.1	24.9	37.4	21.8	26.2	50.2	215.2
2	52.9	124.8	155.6	81.0	411.7	298.4	175.3
3	46.7			133.4	243.7	123.1	240.3
4	173.9	320.4	96.0	148.5	67.6	71.8	287.3
5	17.0	-	-	41.7	57.6	24.0	-
6	15.6	79.4	174.0	19.0	41.0	40.5	-
7	207.1	110.0	165.6	257.0	308.3	198.2	37.4
8	51.8	23.0	18.7	30.2	80.3	42.7	64.8
9	-	-	-	24.3	-	-	-
10	11.6	6.9	8.8	19.6	44.0	25.3	24.8
11	10.0	7.5	9.0	25.9	45.0	26.2	15.2
12	12.5	-	9.3	17.1	45.0	69.4	-
13	-	-	7.1	19.8	124.8	93.1	-
14	232.9	298.2	391.6	350.6	512.8	444.4	136.7
15	13.9	7.0	-	33.5	38.2	23.9	12.8
16	11.4	13.6	26.2	36.2	27.9	30.5	42.0
17							
u1	84.2	71.8	51.3	69.6	105.3	52.6	22.2
u2	19.5		10.9	17.0	52.6	26.3	28.1
u3				10.3	15.5	8.7	11.1
u4					40.9	33.4	11.1
u5							
u6					31.3		
Σ1-16	875.4	1015.7	1099.3	1257.6	2074.1	1561.7	1251.8
Σ	979.1	1087.5	1150.6	1354.5	2319.8	1682.9	1324.2
Σ'10'	151.6	58.0	69.8	242.6	771.9	540.1	334.9
%'10'	17.32	5.71	6.35	19.29	37.22	34.58	26.75

APPENDIX 5.1

BUSH C

Amino Acid	11.8.70	11.8.70 Δ	6.72 Δ	28.5.75 Δ	19.6.75 Δ	19.6.75	27.5.76 Δ	14.6.76 Δ
1	30.3	9.6	276.1	190.1	326.4	178.2	28.8	25.0
2	28.7	34.8	113.8	296.9	262.0	129.1	143.0	118.3
3	26.4	21.6	109.9	-	331.1	129.1	80.4	119.3
4	23.2	16.4	478.0	465.5	854.3	371.0	59.5	53.7
5	7.0	16.9	-	-	-	-	21.3	24.2
6	21.4	12.3	5.9	16.9	-	92.0	30.6	290.9
7	142.9	109.4	41.1	18.5	34.7	21.2	63.0	25.7
8	21.8	22.2	24.2	35.1	25.2	9.8	23.4	23.0
9	8.7	8.7	-	20.0	26.4	11.7	31.1	16.1
10	18.4	21.1	11.1	28.1	19.1	11.2	40.5	19.5
11	24.4	29.1	14.9	28.2	14.0	7.9	28.6	37.8
12	6.1	12.4	32.7	4.5	-	2.7	23.5	27.9
13	11.5	11.3	14.2	61.4	56.4	21.6	40.8	298.1
14	120.6	121.6	16.4	60.8	118.3	105.2	456.2	68.9
15	12.2	9.5	72.3	20.7	100.4	11.1	70.7	177.8
16	15.0	10.7	62.8	31.2	28.4	13.4	17.1	
17			222.6					
u1	53.0	50.1	4.9	62.7	50.1	46.2	56.6	62.7
u2							45.3	33.8
u3		14.1		33.9			24.9	
u4						13.5		
u5								
u6								
Σ1-16	518.6	467.3	1273.5	1277.8	2186.6	903.4	1158.6	1326.2
Σ	571.6	531.5	1501.0	1374.3	2236.8	963.2	1285.4	1422.7
Σ'10'	140.7	147.2	313.2	521.5	531.9	215.9	395.2	477.2
%'10'	27.13	31.5	24.60	40.81	24.33	23.91	34.1	35.98

APPENDIX 5.1

BUSH C cont.

Amino Acid	25.6.76	29.6.76	28.5.78	27.6.78	27.6.78
1	7.6	9.2	158.1	13.2	20.9
2	36.3	109.1	227.6	45.0	125.8
3	29.7	143.8		47.9	120.9
4	50.1	34.8	297.9	49.5	81.1
5	23.3	37.5	-	-	-
6	67.2	20.7	15.8	-	-
7	157.8	317.6	17.3	208.2	233.5
8	35.1	50.8	26.2	26.5	27.2
9	-	-	-	25.6	28.4
10	18.1	22.9	20.6	23.2	24.8
11	25.2	38.7	17.3	22.5	24.1
12	53.4	72.2	57.0	15.8	36.8
13	23.2	28.4	-	46.8	40.0
14	764.3	492.6	29.3	364.7	376.1
15	9.7	44.6	11.8	25.9	85.3
16	169.2	44.3	22.0	48.4	25.6
17					
u1	41.4	45.2	34.5	28.4	70.2
u2	11.7	38.8	33.8	-	52.6
u3		14.1		21.7	36.8
u4				9.2	
u5					
u6					
Σ1-16	1470.2	1467.0	900.9	963.2	1125.7
Σ	1523.3	1565.2	969.2	1022.5	1285.3
Σ'10'	316.8	338.7	97.9	263.9	381.2
%'10"	21.55	23.09	10.87	27.39	33.86

APPENDIX 8

Southwood, T.R.E., Murdie,G., Yasuno, M., Tonn, R.J. and Reader, P.M. (1972). Studies on the life budget of Aedes aegypti in Wat Samphaya, Bangkok, Thailand. Bulletin of the World Health Organisation, 46, 211-226.

Southwood, T.R.E. and Reader, P.M., (1976). Population census data and key factor analysis for the Viburnum whitefly, Aleurotrachelus jelinekii (Frauenf.) on three bushes. Journal of Animal Ecology, 45, 313-325.

Southwood,T.R.E., Brown, V.K. and Reader, P.M., (1979). The relationship of plant and insect diversities. Biological Journal of the Linnean Society, 12, 327-348.

Bull. Org. mond. Santé
Bull. Wld Hlth Org. } 1972, 46, 211-226

Studies on the life budget of *Aedes aegypti* in Wat Samphaya, Bangkok, Thailand

T. R. E. SOUTHWOOD,[1] G. MURDIE,[2] M. YASUNO,[3] R. J. TONN[4] & P. M. READER[5]

For a complete understanding of the epidemiology of a vector-borne disease, a knowledge of the bionomics of the vector is needed. The development of Aedes aegypti *was studied in Wat Samphaya, Bangkok, Thailand, where work on the adult biology had been carried out the previous year (1966–67). Particular attention was given to the variation in the numbers of immature stages of the mosquito in relation to the known seasonal incidence of dengue haemorrhagic fever. Of the three types of water container in the Wat, water jars were the main source of adults, flower pot plates were less important, and the contribution of ant traps was insignificant.*

The variation in the numbers of emerging adults depended on changes in the mortality of the immature stages rather than on variations in the numbers of eggs laid. Both early and late larval instar mortalities are important, the former becoming more significant during the period March–August. The mortality between the eggs and second-instar larvae is density-dependent. There was no clear trend of association between mortality and season except for a fall in larval mortality in April–May preceding the increase in annual incidence of haemorrhagic fever, which usually occurs in June.

After reviewing the information available on mosquito ecology, a WHO Scientific Group on Mosquito Ecology (1967) reported that population data were lacking. It was suggested that life budgets (or tables) for various mosquitos should be constructed and analysed. As the WHO *Aedes* Research Unit (ARU) in Bangkok, Thailand, was already making measurements of the adult population by mark and recapture methods (Sheppard et al., 1969), it was proposed by the ARU working group for the research programme that life budget studies of the immature stages of *Aedes aegypti* should be started in Wat Samphaya, Bangkok.

These studies were designed to provide absolute measures of populations as a basis for determining the effectiveness of various control measures. They were also intended to reveal the extent of natural mortality in the various stages under different conditions, as well as variations in the oviposition level. It was hoped that these data might provide an indication of the way in which the environment could be modified to reduce the size of the mosquito population. Unfortunately, it was not possible to compare simultaneous data on the adult numbers from the mark and recapture study with those on pupal emergence. Ideally, this comparison would indicate whether the latter measure could be used to provide significant epidemiological information.

THE STUDY AREA

The work reported here was conducted at the Wat Samphaya which is situated near the Chao Phya river in Bangkok and is bounded by a slum area and by two-storey blocks of shophouses. This site was selected mainly in order to relate the life budget studies to the study of adult populations conducted there in 1966–67 (Sheppard et al., 1969).

The area of the Wat is approximately 94 by 56 m. The 31 houses each have several rooms and are

[1] Professor and Head, Department of Zoology and Applied Entomology, Imperial College, London, England.

[2] Lecturer, Department of Zoology and Applied Entomology, Imperial College.

[3] WHO *Aedes* Research Unit, Bangkok, Thailand. Present address: WHO Research Unit on Genetic Control of Mosquitos, Delhi, India.

[4] WHO *Aedes* Research Unit, Bangkok. Present address: East Africa *Aedes* Research Unit, Dar es Salaam, Tanzania.

[5] Assistant Experimental Officer, Department of Zoology and Applied Entomology, Imperial College.

occupied by about 100 priests and some schoolchildren. The major breeding containers for *Ae. aegypti* are about 100 water jars, 50 ant traps, and 50 flower pot plates, all of which can be regarded as good habitats for the larvae. There are very few other miscellaneous receptacles suitable as potential habitats. In the Wat, as in Bangkok as a whole, *Ae. aegypti* was the only mosquito breeding in the great majority of water containers.

METHODS

All water jars, ant traps, flower pot plates, and rooms in the study area were numbered. To estimate the numbers of larvae and pupae in the area, random samples of 10 water jars, 1 ant trap (later 5 ant traps), and 1 flower pot plate (later 5 flower pot plates) were sampled 3 or 4 times each week. All immature stages of mosquito in the water jars were sampled by means of a plankton net, and larvae in ant traps and flower pot plates were extracted with a pipette. After they had been counted, the larvae were replaced in the containers. The first- and second-instar larvae were not distinguished. Pupae were taken to the field laboratory in the study area and placed in plastic emergence cages measuring 10 by 12 by 17 cm.

To estimate total production, 10 water jars, 20 ant traps, and 20 flower pot plates were placed beside randomly chosen receptacles of each kind. These experimental receptacles were left uncovered for 48 hours for oviposition by mosquitos. After this exposure, eggs laid in each water container were counted repeatedly by 2–4 persons and then each container was flooded after another 48 hours of incubation. The number of eggs hatching was determined by extracting all newly hatched larvae each day, usually over a period of 10 days. Experimental containers for oviposition were moved to newly chosen sites in each experimental period. The mean number of eggs per container of each type multiplied by the number of containers of that type filled with water gave an indication of the total number of eggs laid in the Wat.

To obtain data on the development pattern of each immature stage, four series of containers of each type were used. The first-instar larvae hatching in one day, usually the morning after each experimental oviposition container was flooded, were transferred to a second series of containers. A total of 30 cement water jars was placed under the floor of a house to provide conditions similar to those offered by non-experimental water jars. Similarly, 60 ceramic ant traps and 60 earthenware flower pot plates were placed on the floor of a room in the Wat. Aged water taken from non-experimental containers of each type was used for rearing larvae in the experimental containers. After the initial oviposition period the access of further mosquitos to the experimental containers was prevented by the use of mesh covers.

When the introduced larvae reached the third instar, they were transferred to the third series of containers and fourth-instar larvae were transferred to the fourth set. Pupae were transferred to emergence cages similar to those described above. The numbers of larvae and pupae transferred, and of emerged adults, were recorded daily until almost all larvae became adults. When few eggs hatched, first-instar larvae reared in the laboratory from mosquitos caught at the Wat were introduced into the containers to provide the data sought.

DEVELOPMENTAL VARIABLES

A knowledge of the average time and time range occupied by each developmental stage is fundamental to the construction and analysis of a life budget. Although laboratory data have sometimes been used, they are unsatisfactory, as the present study clearly shows. Data from Christophers (1960) have been compared with the mean development times observed in the experimental containers (Table 1). These estimates were based on the time taken for half the population to moult to the next stage; this was determined arithmetically because graphs showed that the fall-off was not suitable for probit

Table 1. Mean development times (days) of various immature stages of *Ae. aegypti* in different containers in the Wat Samphaya during November–August 1967–68, compared with laboratory measurements made at 28°C (Christophers' data)

Container	Egg (after flooding)	Larval instar			Pupa	Total days from egg to adult
		I+II	III	IV		
water jar	1.45	5.20	3.21	6.51	2.20	18.57
ant trap	2.59	4.57	4.16	6.84	1.95	20.11
flower pot plate	2.88	3.98	3.32	5.49	1.28	16.95
Christophers' (1960) data	3.10	2.90	0.84	1.00	2.00	9.84

analysis, nor was it possible to make the calculation from successive peaks.

One approach to the construction of a life budget proposed here (see below) requires information on the pattern of development, the percentage of a cohort entering each stage on each day of the total range of development time. In *Ae. aegypti* the eggs may hatch over a very long period, and the stimulus for hatching is apparently flooding (Christophers, 1960). In the present study, therefore, development time was calculated from the day of flooding. Occasionally some eggs would hatch before artificial flooding occurred, especially in the flower pot plates since these containers could be inundated by rain. The mean hatching patterns in each type of container are shown in Table 2.

METHODS FOR THE CONSTRUCTION OF A LIFE BUDGET

Most methods of population analysis involving the construction of life budgets are designed to be used for species that have discrete generations, yet the majority of insect species, particularly in the tropics, have overlapping generations or, like *Ae. aegypti*, breed continuously. Hughes (1963) devised a method for aphids that depended on the estimate of the rate of reproduction and its projection; this method is not entirely appropriate for *Ae. aegypti* studies, particularly as it is possible to measure natality (= oviposition in *Aedes*) in the field. Two simpler methods are therefore being used.

Daily populations on a time-specific basis

In this method daily values are calculated for the unique events, e.g., oviposition, hatching, and emergence, while the populations of the various developmental stages are expressed as numbers per median day. This is done by dividing an absolute estimate of the total population by the development time in days; the same approach is used in the graphical method to determine the total population of a stage of a discrete generation (Southwood, 1966). This concept assumes a steady mortality rate *within* each stage, and a constant level of recruitment over a period extending back in time to the date when the oldest pupa was recruited.

In view of the fairly steady level over several weeks of the female population in the Wat, indicated by the mark and recapture experiments (Sheppard et al., 1969), the use of this method seems justified. At any time when the population is increasing or decreasing rapidly, it will, respectively, over- and underestimate mortality, and its value is thus limited.

The life budgets calculated on this basis are given in Tables 3–5 and presented graphically in Fig. 4 and 5. As the maximum potential natality was not calculated, a modification of the method of Varley & Gradwell (1960), in which only mortality was considered, was used for analysis. However, the role of natality can be investigated separately (p. 221). The actual population numbers are converted to logarithms and the various mortalities are expressed as the differences between the logarithms of the populations under consideration. These are, of course, equivalent to the ratio of one population to the other and are termed k values (Varley & Gradwell, 1960; Southwood, 1966). Because variations in actual numbers between the different occasions could be due to sampling errors, emphasis in the following discussion is placed on the comparison of these population ratios expressing mortality.

The expected daily population on an age-specific basis

The basis of this method is the determination of the number of individuals that would be expected in the field if there were no mortality during development, the starting-point being the number of eggs laid each day. If it is assumed that every individual has a constant and identical rate of development and that the third instar, for example, lasts 3 days and is achieved on the tenth day after oviposition, then the total number of third-instar larvae expected on a given day (n) would be the sum of the eggs laid on days n–9, n–10, and n–11. In fact, the development rate is not constant, but falls within a range (Table 2); therefore, the number of individuals of any stage on a given day will be the sum of contributions from oviposition on many days (see Fig. 1). Although the addition of the various components is theoretically straightforward, in practice they are so numerous that the summation must be done by computer. A computer programme was therefore devised.[1]

The expected numbers can be calculated by means of this programme and the total mortality occurring between the egg and each developmental stage is found by subtracting the actual numbers from the expected numbers. The use of this method in this study assumes the following particular conditions:

(1) the daily number of eggs laid in any type of container in the Wat is fully represented by the monthly sample;

[1] An account of the computer programme has been deposited in the WHO Library, and copies may be obtained on request from Chief Librarian, World Health Organization, 1211 Geneva 27, Switzerland.

Table 2. The development pattern of *Ae. aegypti* in different containers in the Wat Samphaya (percentage of the population moulting on given day)

Container	Moult	Day after flooding													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
water jars	egg–I	38.97	16.01	9.16	6.63	4.5	2.03	1.39	0.93	0.41	0.16	0.08	0.06	—[a]	
	II–III		1.03	10.97	14.74	14.65	13.23	11.49	13.71	5.77	4.6	3.8	1.83	2.26	1.56
	III–IV				1.87	3.22	11.26	14.82	12.02	6.6	12.98	7.45	5.95	4.87	3.71
	IV–pupa						1.16	1.56	2.52	1.93	5.2	5.43	4.74	8.44	4.71
	pupa–adult								0.76	2.09	2.25	1.63	4.31	6.05	6.01
ant traps	egg–I	49.69	11.77	9.03	1.98	1.52	2.79	1.14	0.16	0.37	0.49	—	0.33	—[b]	
	II–III		8.85	10.72	15.43	14.01	9.94	12.63	10.47	5.23	5.46	3.15	1.91	1.06	0.78
	III–IV				2.57	5.9	9.56	9.61	9.98	6.67	5.72	12.68	5.72	8.92	2.12
	IV–pupa						1.14	—	—	0.31	1.45	5.09	3.34	23.61	13.55
	pupa–adult										0.33	—	0.66	8.40	2.63
flower pot plates	egg–I	33.96	23.77	16.09	3.04	1.12	0.47	0.11	0.43	—[c]					
	II–III		8.64	14.07	21.85	15.86	13.71	8.85	7.41	3.13	2.27	1.78	0.66	0.29	0.84
	III–IV			0.17	6.34	10.60	16.0	13.51	10.32	8.46	6.21	7.65	3.09	3.29	2.89
	IV–pupa						1.36	3.07	7.61	12.6	7.55	6.85	6.86	4.42	6.04
	pupa–adult							0.22	2.08	3.88	8.59	11.88	9.26	7.93	3.54

Container	Moult	Day after flooding													
		15	16	17	18	19	20	21	22	23	24	25	26	27	28
water jars	egg–I														
	II–III	—	0.18	0.18											
	III–IV	3.39	4.02	2.92	1.94	0.76	0.31	1.31	0.26	0.24	—	—	0.04	—	0.04
	IV–pupa	9.07	7.6	6.76	8.32	4.70	4.08	5.34	4.09	3.8	3.55	1.59	1.3	1.33	1.95
	pupa–adult	9.65	4.94	10.07	5.24	5.83	7.38	3.87	4.7	6.08	3.99	4.35	3.21	2.38	1.33
ant traps	egg–I														
	II–III	—	—	0.38											
	III–IV	3.56	1.79	2.0	1.63	1.6	2.53	5.31	0.67	0.36	—	0.39	0.21	—	0.51
	IV–pupa	5.51	3.61	2.48	1.52	1.45	3.03	3.03	7.06	3.33	2.40	6.87	3.85	1.52	1.58
	pupa–adult	23.99	15.93	6.22	2.27	5.16	1.47	2.29	1.58	4.85	5.9	5.48	1.91	5.15	0.33
flower pot plates	egg–I														
	II–III	—	—	0.31	0.17	—	—	0.09							
	III–IV	1.3	2.2	1.86	0.81	0.58	0.25	2.27	0.83	0.44	0.38	0.10	0.21	0.29	
	IV–pupa	4.01	6.61	5.45	3.87	2.61	3.78	1.59	1.5	2.04	1.28	2.24	2.5	0.99	1.5
	pupa-adult	6.55	5.86	6.3	5.69	5.15	2.24	2.97	2.25	0.91	1.56	0.81	2.04	2.76	2.08

Container	Moult	Day after flooding													
		29	30	31	32	33	34	35	36	37	38	39	40	41	42–45
water jars	egg–I														
	II–III														
	III–IV														
	IV-pupa	—	—	0.31	0.33	—	0.21								
	pupa–adult	0.99	1.7	0.24	—	0.34	0.36	0.24							
ant traps	egg–I														
	II–III														
	III–IV														
	IV–pupa	0.45	—	2.5	—	0.45	—	0.45	—	—	—	—	—	—	0.45
	pupa–adult	—	5.46												
flower pot plates	egg–I														
	II–III														
	III–IV														
	IV–pupa	1.41	0.28	0.28	0.46	0.09	0.29	0.17	0.09	0.5	—	—	—	—	0.09
	pupa–adult	2.17	1.66	—	0.52	0.68	0.1	0.1	0.19	0.1	0.1				

[a] 19.69 % hatched before flooding. [b] 20.73 % hatched before flooding. [c] 21.9 % hatched before flooding.

Table 3. Life budget and *K* values in water jars from October to December 1967 and from February to August 1968

Stage	Number	Log	*k*	Number	Log	*k*
	October 1967			November 1967		
eggs	6898	3.83885	1.19906	6503	3.81311	1.23219
I + II	436.3	2.63979	0.11604	380.9	2.58092	0.02825
III	333.8	2.52375	0.13281	357.0	2.55267	0.25600
IV	245.9	2.39094	0.03301	197.9	2.29667	0.52362
pupae	228.0	2.35793		59.3	1.77305	
			K = 1.48092			*K* = 2.04006
	December 1967			February 1968		
eggs	4025	3.60477	1.12333	3499	3.54407	1.26487
I + II	302.8	2.48144	0.03119	190.2	2.27920	$\bar{1}$.94274
III	281.6	2.45025	0.18308	216.8	2.33646	0.39545
IV	184.6	2.26717	0.84229	87.3	1.94101	0.23259
pupae	26.6	1.42488		51.1	1.70842	
			K = 2.17989			*K* = 1.83565
	March 1968			April 1968		
eggs	4141	3.61710	1.03164	2554	3.40722	0.43548
I + II	384.7	2.58546	0.46753	936.7	2.97174	0.44411
III	131.2	2.11793	0.25520	336.8	2.52763	0.43072
IV	72.9	1.86273	0.27727	125.0	2.09691	0.01234
pupae	38.5	1.58546		121.5	2.08457	
			K = 2.03164			*K* = 1.32265
	June 1968			July 1968		
eggs	4044	3.60681	1.19840	7280	3.86213	1.51383
I + II	256.1	2.40841	0.18517	222.9	2.34830	0.06727
III	167.2	2.22324	0.71945	190.9	2.28103	0.47013
IV	31.9	1.50379	0.28107	64.7	1.81090	0.46455
pupae	16.7	1.22272		22.2	1.34635	
			K = 2.38409			*K* = 2.51578
	August 1968					
eggs	3646	3.56229	0.97234			
I + II	388.9	2.58995	0.17465			
III	260.2	2.41530	0.30437			
IV	129.1	2.11093	0.65003			
pupae	28.9	1.46090				
			K = 2.10139			

Table 4. Life budget and K values in ant traps from October to December 1967 and from February to August 1968

Stage	Number	Log	*k*	Number	Log	*k*
	October 1967			November 1967		
eggs	92.2	1.96473	$\bar{1}$.73148	90.0	1.95424	$\bar{1}$.62996
I + II	171.1	2.23325	0.88107	71.3	2.32428	0.85299
III	22.5	1.35218	0.35654	29.6	1.47129	0.34096
IV	9.9	0.99564		13.5	1.13033	
pupae	0	0		0	0	
	December 1967			February 1968		
eggs	114.75	2.06070	$\bar{1}$.86703	149.9	2.17609	0.29471
I + II	156.2	2.19367	0.28145	76.1	1.88138	0.33731
III	81.7	1.91222	0.00805	35.0	1.54407	0.27690
IV	80.2	1.90417	1.26072	18.5	1.26717	0.86923
pupae	4.4	0.64345		2.5	0.39794	
			K = 1.41725			K = 1.77815
	March 1968			April 1968		
eggs	302.7	2.48144	0.50555	107.5	2.03141	0.17832
I + II	94.6	1.97589	0.28836	71.3	1.85309	0.32289
III	48.7	1.68753	0.09424	33.9	1.53020	0.38719
IV	39.2	1.59329	1.76078	13.9	1.14301	0.76280
pupae	0.68	$\bar{1}$.83251		2.4	0.38021	
			K = 2.64893			K = 1.65120
	June 1968			July 1968		
eggs	85.7	1.93298	0.15338	60.7	1.78319	0.06802
I + II	60.2	1.77960	0.25716	51.9	1.71517	0.08678
III	33.3	1.52244	0.63035	42.5	1.62839	0.44370
IV	7.8	0.89209		15.3	1.18469	0.12399
pupae	0	0		11.5	1.06070	
						K = 0.72249
	August 1968					
eggs	11.02	1.04217	$\bar{2}$.74506			
I + II	198.2	2.29711	0.58869			
III	51.1	1.70842	0.54705			
IV	14.5	1.16137	0.98528			
pupae	1.5	0.17609				
			K = 0.86608			

Table 5. Life budget and *K* values in flower pot plates from October 1967 to December 1967 and from February 1968 to August 1968

Stage	Number	Log	*k*	Number	Log	*k*
	October 1967			November 1967		
eggs	38.7	1.58771	$\bar{1}$.56240	90.0	1.95424	$\bar{1}$.82391
I + II	105.6	2.02531	$\bar{1}$.66928	134.6	2.13033	1.01974
III	226.5	2.35603	0.24882	12.9	1.11059	$\bar{1}$.50421
IV	127.9	2.10721	0.61306	40.4	1.60638	0.42169
pupae	31.2	1.49415		15.3	1.18469	
			K = 0.09356			*K* = 0.76955
	December 1967			February 1968		
eggs	31.5	1.49831	$\bar{1}$.89734	90.45	1.95641	0.25140
I + II	39.9	1.60097	0.68716	50.7	1.70501	1.32480
III	8.2	0.91381	$\bar{1}$.69897	2.4	0.38021	$\bar{1}$.47712
IV	16.4	1.21484	$\bar{1}$.36727	8.0	0.90309	$\bar{1}$.79929
pupae	70.4	1.84757		12.7	1.10380	
			K = 1.65074			*K* = 0.85261
	March 1968			April 1968		
eggs	638.2	2.80496	0.97694	95.6	1.98046	$\bar{1}$.98570
I + II	67.3	1.82802	0.67573	98.8	1.99476	0.13144
III	14.2	1.15229	$\bar{1}$.99092	73.0	1.86332	0.32803
IV	14.5	1.16137	1.11998	34.3	1.53529	0.04253
pupae	1.1	0.04139		31.1	1.49276	
			K = 2.76357			*K* = 0.48770
	June 1968			July 1968		
eggs	46.2	1.66464	$\bar{1}$.84575	76.1	1.88138	0.68437
I + II	65.9	1.81889	0.41577	15.7	1.19701	0.32311
III	25.3	1.40312	0.38609	7.5	0.87390	0.14881
IV	10.4	1.01703	$\bar{1}$.61220	5.3	0.72509	$\bar{1}$.92369
pupae	25.4	1.40483		6.3	0.80140	
			K = 0.25981			*K* = 1.07998
	August 1968					
eggs	226.1	2.35430	0.53541			
I + II	65.9	1.81889	0.53109			
III	19.4	1.28780	0.03495			
IV	17.9	1.25285	$\bar{1}$.89415			
pupae	22.8	1.35870				
			K = 0.99560			

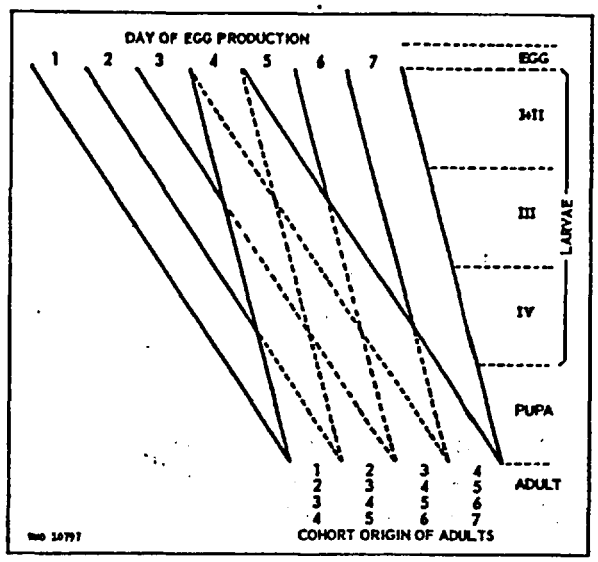


Fig. 1. The contribution of a single egg cohort, produced at day 4, to a mixed population of overlapping generations. The lines of different slope represent the fastest and slowest developers and the age extremes of the numbers of a single cohort.

(2) the development times observed monthly in the experimental containers are true of the natural populations for the whole of that month;

(3) the containers in the Wat dry out or are emptied, cleaned, and refilled with water at random.

Unfortunately, these conditions are not completely satisfied. The monthly egg counts cannot be accepted with full confidence as representing daily oviposition in the Wat. An alternative approach would be to interpolate between monthly counts to obtain daily estimates, but this was considered inappropriate in the present study. However, by using the stable age proportions (Table 6) of each instar, based on the geometric mean development times implicit in the method, we can obtain a second series of time-specific estimates of mortality to compare with those of method 1.

Comparison of mortality in water jars revealed by the two methods

The expected numbers of larvae arising from method 2 were calculated from the mean monthly counts of first- plus second-instar larvae and the expected proportion of pupae to first- plus second-instar larvae for each month (Table 6). The differences between $\log_{10}$ numbers of expected and observed pupae gives an estimate of cumulative mortality (Table 7). The values, compared month by month, are of the same order of magnitude (Spearman's rank correlation $r_s = 0.95$; $P < 0.01$) but it is realized that these two methods are not completely independent since they are based on the same num-

Table 6. Expected proportions of the populations in the various stages when a stable age distribution has been reached; computed from the developmental pattern for water jars

Experiment	Date	Stage			
		I + II larvae	III larvae	IV larvae	Pupae
1	29 Oct. 1967	0.352	0.456	0.119	0.072
2	18 Nov. 1967	0.338	0.298	0.220	0.143
3	23 Dec. 1967	0.269	0.236	0.350	0.144
4	19 Feb. 1968	0.399	0.214	0.301	0.085
5	27 March 1968	0.257	0.162	0.466	0.115
6	29 April 1968	0.355	0.196	0.290	0.159
7	9 June 1968	0.240	0.197	0.450	0.113
8	13 July 1968	0.290	0.143	0.447	0.170
9	19 Aug. 1968	0.247	0.122	0.549	0.083

Table 7. Comparison of mortality between larval stage II and pupae expressed as difference between log populations, i.e., $k_2 + k_3 + k_4$.

Experiment	Date	Mortality	
		Method 1	Method 2
1	29 Oct. 1967	0.2818	—[a]
2	18 Nov. 1967	0.8079	0.8074
3	23 Dec. 1967	1.0566	1.1583
4	19 Feb. 1968	0.5708	0.2722
5	27 March 1968	1.0000	1.0244
6	29 April 1968	0.8872	0.9288
7	9 June 1968	1.1857	1.2332
8	13 July 1968	1.0020	1.0916
9	19 Aug. 1968	1.1291	1.0287

[a] Calculated mortality less than 0.

ber of early stage larvae. No clear indication of which method is the more appropriate is available at this stage. However, method 2 is based on a complete set of developmental information for each month, while method 1 utilizes 50% development times averaged over all the monthly experiments. This seems to favour method 2, but to use the method in this form, egg counts would have to be included. This would necessitate the use of 50% development times for the egg stage, and since the mortality estimates (Table 7) are so similar, it was considered that the use of a mixed model would not be justified. Therefore, estimates in the rest of this report are derived by method 1.

SURVIVAL UNDER DIFFERENT CONDITIONS

Gross comparisons of the numbers of the different stages in the various containers are made in Fig. 2 and 3. These numbers are not absolute populations since they have not been corrected to allow for the different development times of the stages. They do show, however, that with a few exceptions there is a considerable fall-off in gross numbers between the egg and pupal stages; survival in ant traps appears to be less than in the other types of container.

When absolute population values from the life budget (Tables 3–5) are used (Fig. 4 and 5), it can be

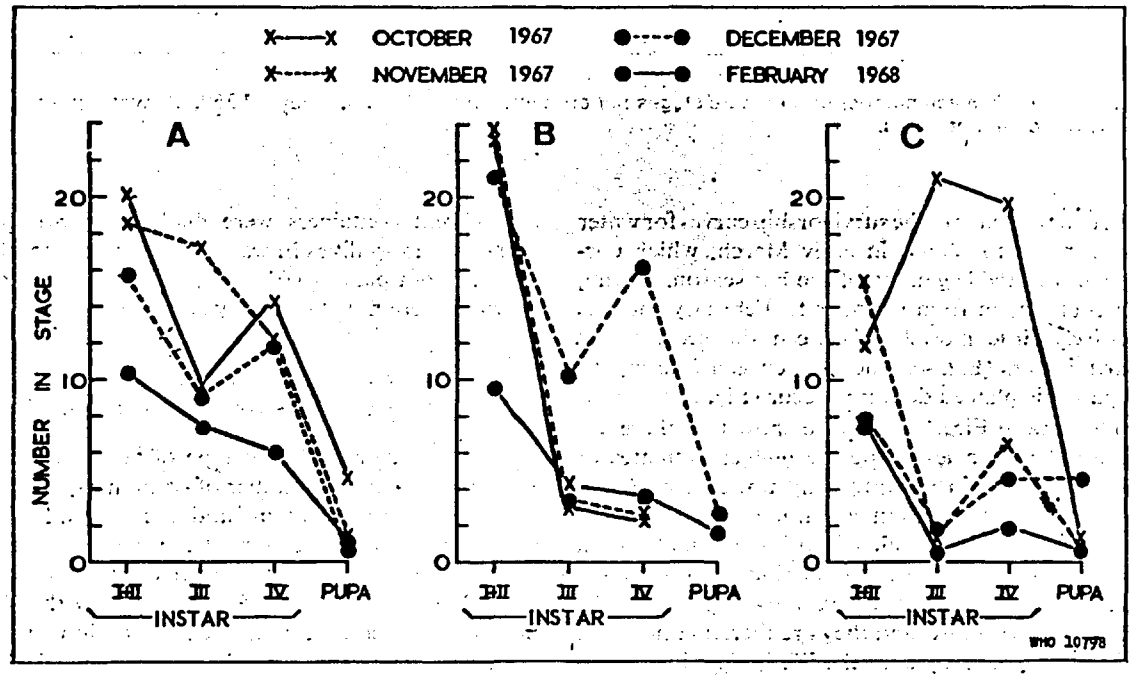


Fig. 2. Monthly mean number of immature stages per container in the Wat Samphaya, 1967–68. A, water jar; B, ant traps; C, flower pot plates.

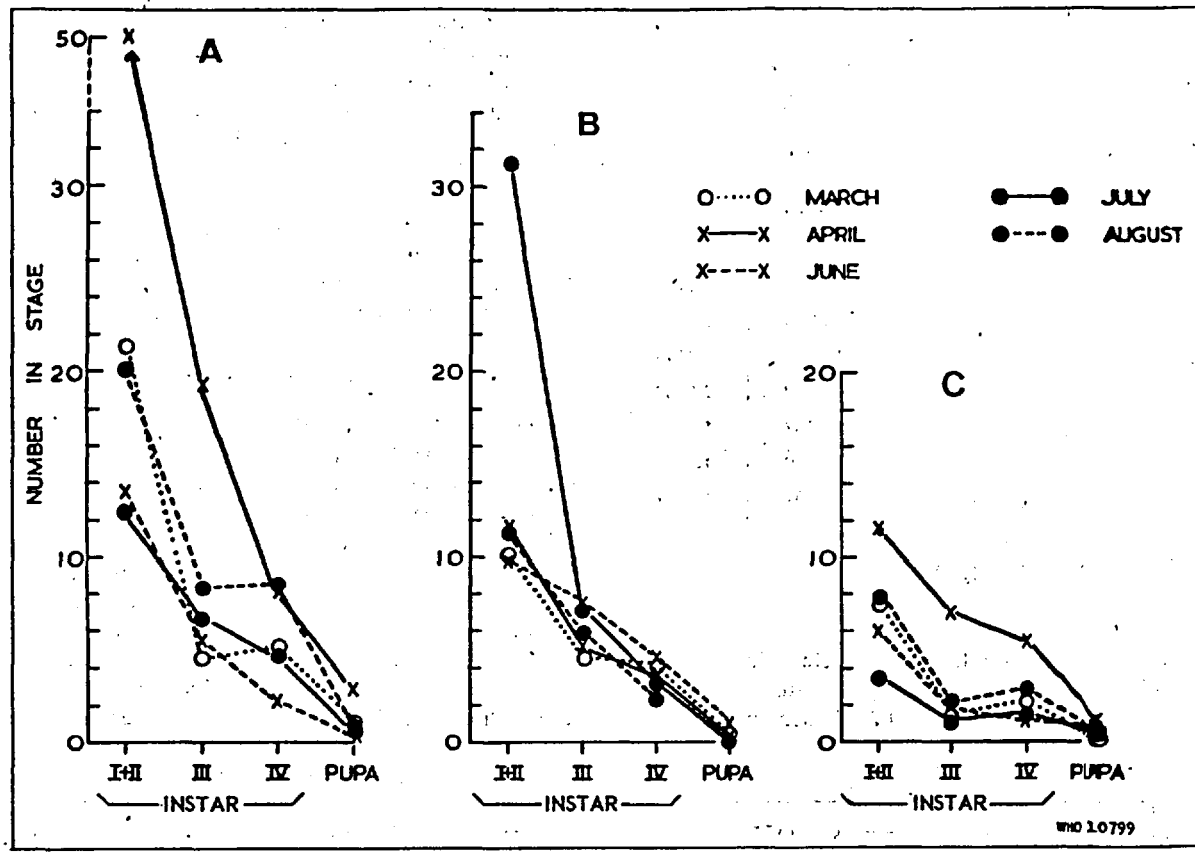


Fig. 3. Monthly mean number of immature stages per container in the Wat Samphaya, 1968. A, water jars; B, ant traps; C, flower pot plates.

seen that the shape of the survivorship curves for water jars appears to change in early March, which corresponds to the beginning of the hot season. During the cool season from October to February there is relatively little mortality between the second and fourth instars (Fig. 4), whereas between March and August this plateau does not occur (Fig. 5).

The data in Fig. 4 and 5 also show that there are more inconsistencies in the life budget estimates of the populations in ant traps and flower pot plates. The sources of variation are not obvious but are probably more the result of unstable conditions in the containers than of errors arising from the small number of samples. Clearly, these data must be interpreted with care, and they are therefore not used in the detailed analysis of the life budget in the following sections.

Gross comparisons between mean total mortalities in different containers were made using Student's *t* test. The mortalities in water jars were greater than in flower pot plates ($0.01 > P > 0.002$); other comparisons were not statistically significant.

CONTRIBUTION OF DIFFERENT TYPES OF CONTAINER TO THE POPULATIONS OF ADULTS IN THE WAT

The importance of each type of container in the Wat depends on the number of containers, the number of eggs laid in them, and the survival of the immature stages. The sum of the mean number of pupae for each type of container over the 9 experimental periods (Tables 3–5) multiplied by the mean percentage emergence gives the contribution made by each type (Table 8). This shows that water jars are the main source of the adult population and that the contribution of ant traps is quite insignificant.

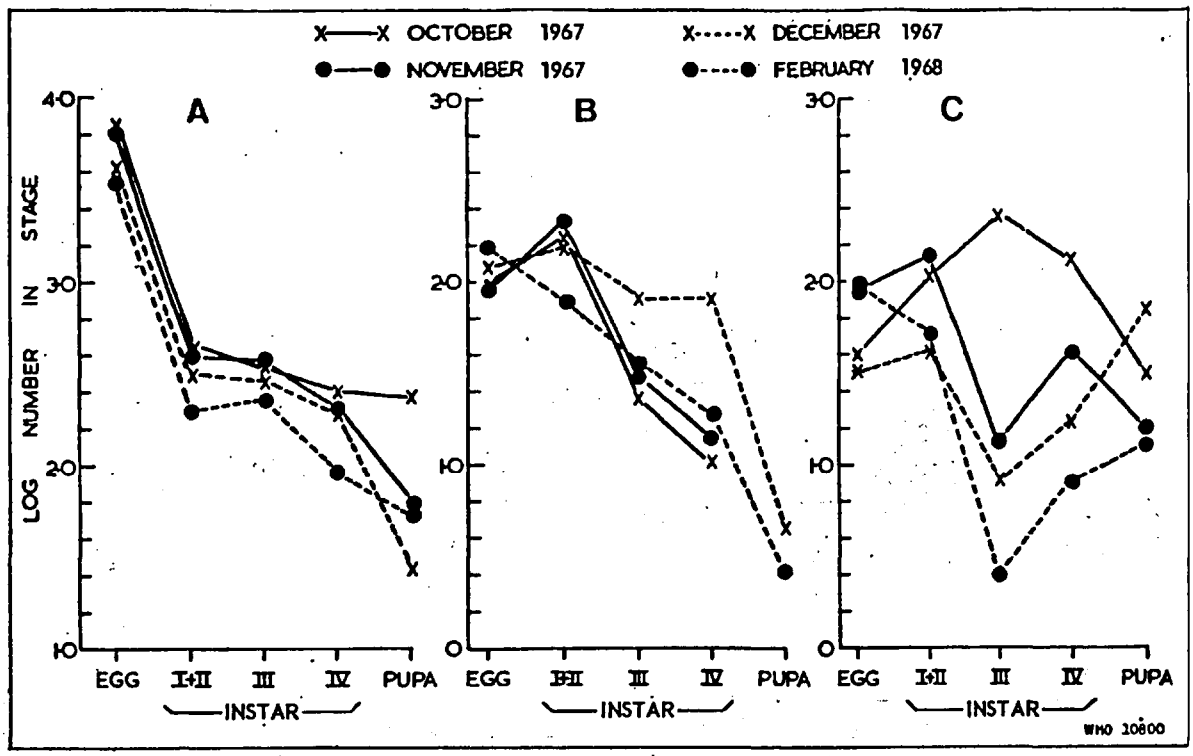


Fig. 4. Monthly survivorship curves for the immature stages, based on total numbers corrected for development time, 1967–68. A, water jars; B, ant traps; C, flower pot plates.

THE RELATIVE ROLES OF NATALITY AND MORTALITY

A method for comparing the relative importance of natality (the number of eggs laid) and mortality is described by Southwood (1967). This can be applied to the data from the three types of container given in Tables 3–5, i.e., for the months of November–August. This is done in Fig. 6, which clearly shows that the variations in the numbers of emerging adults are related to variations in mortality rather than natality.

RECOGNITION OF THE KEY MORTALITY FACTORS

From Fig. 7 it can be seen that in ant traps and from October to February in water jars the variation in total mortality (K) from egg to pupa is due mostly to variations in k_4, i.e., the death of larvae between the fourth instar and pupation. From March onwards there is an interesting increase in the role of k_1 for water jars, i.e., deaths between eggs and second-instar larvae, which account for the largest proportion of total mortality. The change in the key factor coincides with the beginning of the hot season and the change in survivorship curves noted earlier (p. 219).

Unfortunately, only 12 of the 27 sets of life table data gave complete budgets (Tables 3–5). This is largely because none of the information for flower pot plates is acceptable, and no pupae developed in the ant traps in November, December, and July. A source of error in oviposition estimates could have been the use of clean experimental ant traps and flower pot plates to facilitate counting. Possibly they were less attractive as oviposition sites and led to eggs laid in non-experimental containers being underestimated.

The mortality factors k_1 and k_4 were analysed for density dependence by plotting each against the log density of the stage on which they acted (Fig. 8). Clearly k_1 is density-dependent, the mortality rate increasing with density; this could result from competition between young larvae. The regression of k_1 on density with a slope greater than 1.0 indicates overcompensating mortality and hence an increase

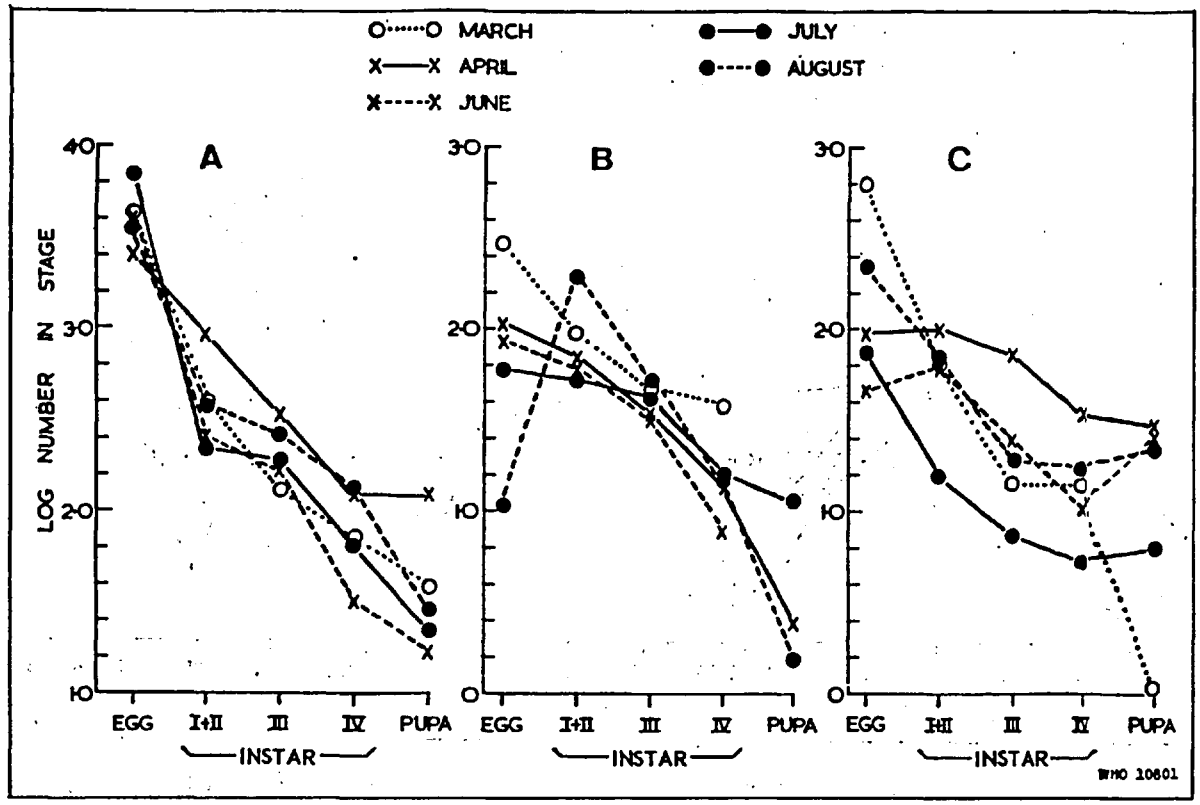


Fig. 5. Monthly survivorship curves for the immature stages, based on total numbers corrected for development times, 1968. A, water jars; B, ant traps; C, flower pot plates.

in the magnitude of the fluctuations in population size. Factor k_4 acts independently of density but is an important component of the total, K (p. 221).

Table 8. Comparison of contributions of the various types of container to the adult population emerging in the Wat Samphaya during the nine experimental periods

	Water jars	Ant traps	Flower pot plates
total daily mean pupae	65.87	2.56	24.03
mean percentage emergence	83.25	84.07	83.55
total mean daily emergence	54.84	2.15	20.08
percentage of emerging adults	71.2	2.8	26.0

COMPARISON OF SEASONAL TRENDS IN MORTALITY AND ADULT NUMBERS

Sheppard et al. (1969) have given an account of fluctuations in the numbers of adults in the Wat determined by mark, release, and recapture during the period in 1966–67 immediately preceding the present study. Their work revealed certain fluctuations and, in particular, a rise between April and July which they believed to be real. Their population estimates (Table 8 of Sheppard et al.) are plotted together with total mortality (K, on an inverse scale) against data by month in Fig. 9. It will be seen that although the data refer to successive years there is evidence of correspondence between peaks and troughs with the mortality curve slightly in advance.

This appears to give independent support to the view that the population rise in April is a real phenomenon. It is particularly noteworthy that the present study suggests that the fall in mortality levels

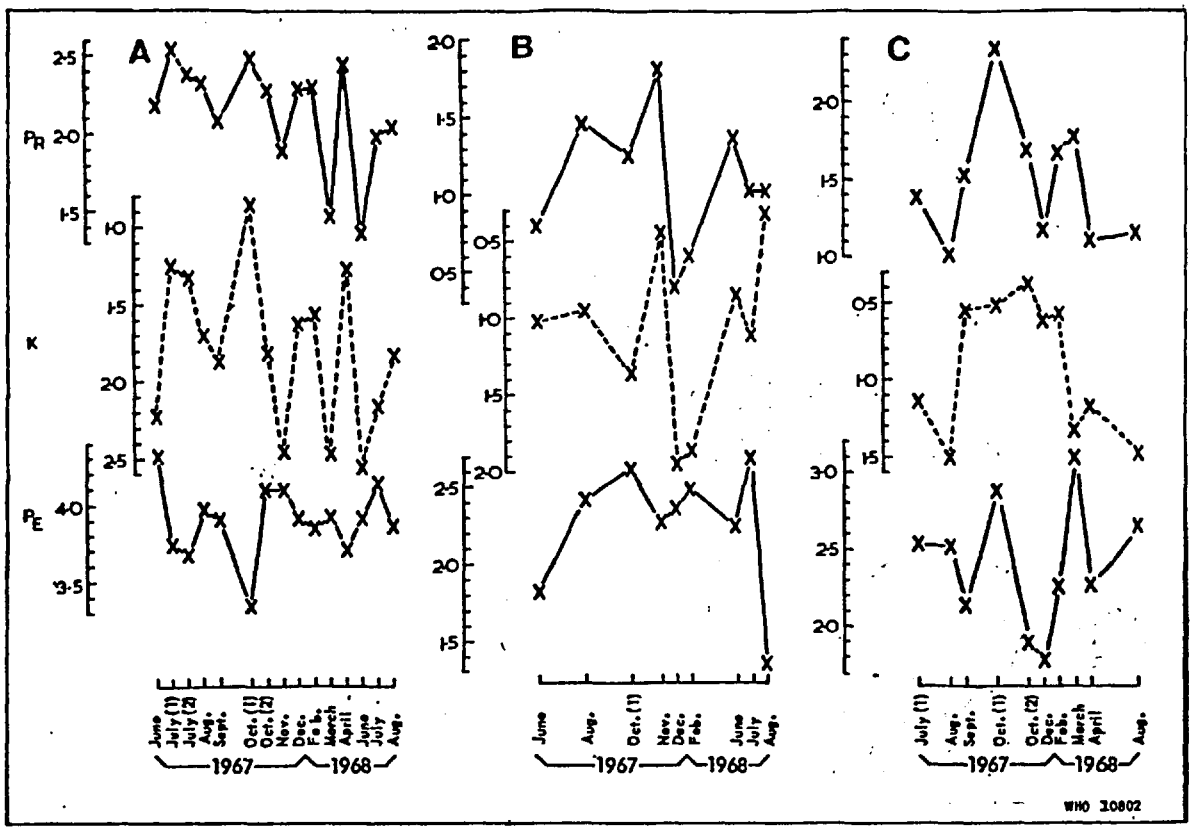


Fig. 6. Comparison of the importance of natality (P_E) and mortality (K) in determining the number of adults (P_R) in the Wat Samphaya, 1967–68. A, water jars; B, ant traps; C, flower pot plates.

is associated with a change in the importance of early larval mortality, which supplemented late larval mortality at the onset of hotter weather.

DISCUSSION AND CONCLUSIONS

Fluctuations in the number of adult mosquitos emerging in the Wat are, on the evidence given here, determined by the mortality of immature stages, rather than by changes in the number of eggs laid. The most significant mortalities occur during the early (first and second) and last (fourth) larval instars. Many larvae seem to spend an excessively long period in the last instar and then fail to develop further. The mortality in the first instar is probably density-dependent. It seems, therefore, that in the absence of predators and disease both these mortalities could arise from competition effects, presumably resulting from food shortage. This point requires further study.

From the beginning of the hot season in March, the survival of the early instars becomes more significant in the dynamics of the population and this leads to a rise in the numbers of adults emerging. It is possible that this gives independent support to, and an explanation of, the rise in adult numbers between April and July suggested by the mark and recapture studies of Sheppard et al. (1969). Whether the fall in larval mortality in April–May is the trigger for a chain of events that leads to the rise in incidence of dengue in June (*Wkly. Epidem. Rec.*, 1970) will depend not only on the establishment of the relationships suggested above, but also on the influence of the initially larger mosquito population on the biting rate, on the proportion of infected mosquitos in the population, and on the survival of adult mosquitos.

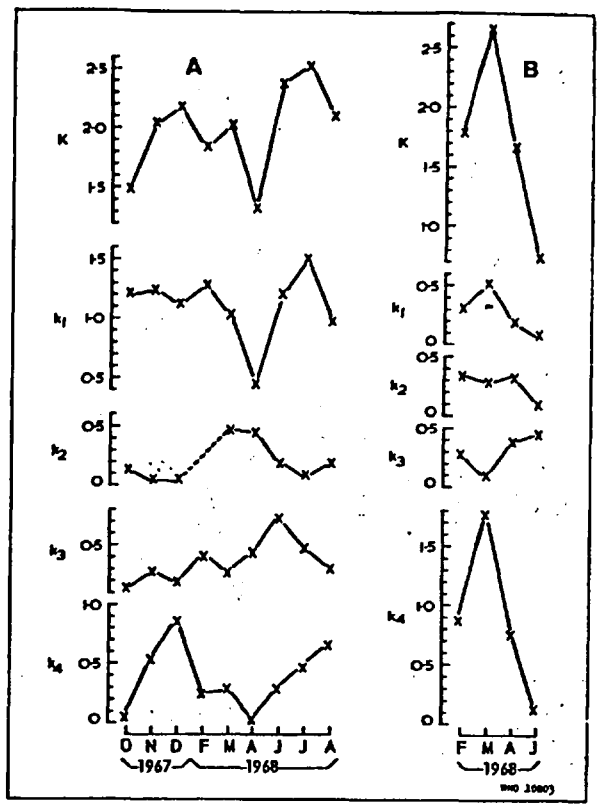


Fig. 7. Comparison of changes in various component mortalities (k_1-k_4) with changes in total mortality (K). A, water jars; B, ant traps.

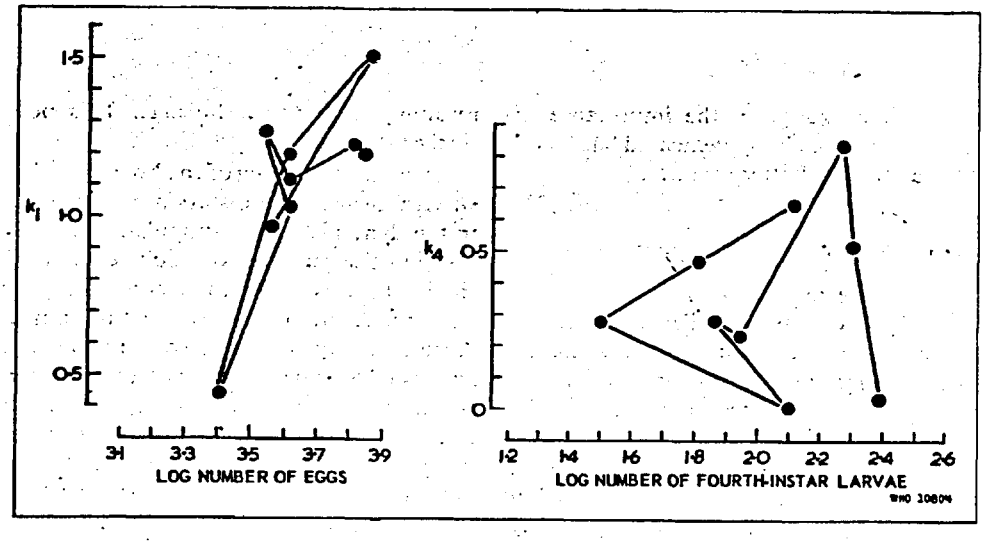


Fig. 8. Relationship between mortality and the population density at the start of the age interval in which it operates. k_1 = Mortality from egg to second-instar larvae on numbers of eggs. k_4 = Mortality from fourth-instar larvae to pupae on numbers of fourth-instar larvae.

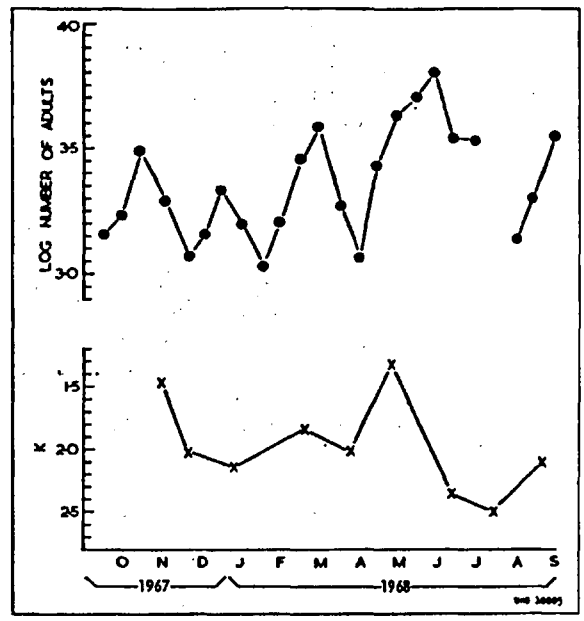


Fig 9. Comparison of the population trends in adults during 1967–68 (from mark, release, recapture studies), and of seasonal variations in total development mortality in water jars (*K* being plotted inversely) during 1967–68.

RÉSUMÉ

ÉTUDES SUR LE BUDGET VITAL D'*AEDES AEGYPTI* À WAT SAMPHAYA, BANGKOK (THAÏLANDE)

Pour bien comprendre l'épidémiologie d'une maladie transmise par un vecteur, il est indispensable de disposer d'informations sur la dynamique de population de ce dernier. Les études menées sur *Aedes aegypti* à Wat Samphaya (Bangkok) en 1967/68 ont porté en particulier sur les variations numériques des stades immatures ainsi que sur leurs relations avec les données antérieures concernant les populations d'adultes et les fluctuations saisonnières de l'incidence du syndrome dengue/fièvre hémorragique.

On a estimé le nombre d'œufs, de larves et de nymphes d'*Aedes* présents dans les trois types de récipients les plus courants (jarres, pièges à fourmis, soucoupes placées sous les pots de fleurs) grâce à des sondages pratiqués 3 à 4 fois par semaine. Le nombre d'œufs pondus a été évalué à l'aide d'ovipièges et les aspects du développement de chaque stade immature ont été étudiés en se basant sur l'évolution de larves d'âge connu. On a constaté que la durée d'évolution des différents stades était plus longue dans le milieu naturel qu'au laboratoire, en raison probablement d'un apport insuffisant de nourriture.

Deux méthodes permettent d'établir le budget vital d'une population d'insectes caractérisée par un chevauchement des générations successives. La première consiste à calculer les effectifs quotidiens de chaque stade en divisant le chiffre estimé de la population globale par la durée d'évolution en jours. Dans la seconde, on évalue les effectifs quotidiens de chaque stade d'après le nombre d'œufs pondus chaque jour et le rythme de développement, la mortalité étant considérée comme nulle.

Les jarres représentent le principal lieu de production d'*Aedes* adultes à Wat Samphaya. Dans les pièges à fourmis et les soucoupes, les taux de survie subissent des variations considérables, dues sans doute à l'instabilité des conditions de milieu (notamment la quantité d'eau disponible) dans ce genre de récipients. La mortalité globale d'*Aedes* est significativement moins élevée dans les soucoupes que dans les jarres.

Dans les jarres, les variations de la mortalité contribuent davantage aux fluctuations du nombre total des éclosions imaginales que les variations du nombre d'œufs pondus. D'octobre 1967 à février 1968, le facteur déterminant l'aspect de la courbe de mortalité globale a été la mortalité des larves entre le 4e stade et la nymphose (k_4), mais à partir de mars 1968 la mortalité des insectes entre le stade de l'œuf et le 2e stade larvaire (k_1) a été en majeure partie responsable de la mortalité globale. L'importance de k_1 est fonction de la densité de l'effectif au stade sur lequel il agit. Il semble qu'en l'absence d'infection larvaire et d'intervention de prédateurs la mortalité des larves durant les 1er et 4e stades soit influencée par la concurrence entre individus, probablement due au manque de nourriture.

A une mortalité accrue parmi les larves aux premiers stades, constatée en mars, succède, par un phénomène de compensation, une baisse de la mortalité larvaire globale en avril-mai. Cela pourrait expliquer l'augmentation du nombre d'*Aedes* adultes d'avril à juillet. Il reste à établir s'il existe un lien entre ces variations de la mortalité larvaire et la fréquence plus élevée de la dengue/fièvre hémorragique en juin et à étudier l'influence de l'augmentation du nombre et du taux de survie des vecteurs sur l'intensité de la transmission de la maladie.

REFERENCES

Christophers, S. R. (1960) Aedes aegypti *L., the yellow fever mosquito*, Cambridge University Press

Hughes, R. D. (1963) *J. anim. Ecol.*, 32, 393-424

Sheppard, P. M., Macdonald, W. W., Tonn, R. J. & Grab, B. (1969) *J. anim. Ecol.*, 38, 361-702

Southwood, T. R. E. (1966) *Ecological methods*, London, Methuen

Southwood, T. R. E. (1967) *J. anim. Ecol.*, 36, 519-529

Varley, G. C. & Gradwell, G. R. (1960) *J. anim. Ecol.*, 29, 399-401

WHO Scientific Group on Mosquito Ecology (1967) *Wld Hlth Org. techn. Rep. Ser.*, No. 368

Wkly Epidem. Rec., 1970, 45, 201-208

PRINTED IN SWITZERLAND

POPULATION CENSUS DATA AND KEY FACTOR ANALYSIS FOR THE VIBURNUM WHITEFLY, *ALEUROTRACHELUS JELINEKII* (FRAUENF.), ON THREE BUSHES

BY T. R. E. SOUTHWOOD AND P. M. READER

Department of Zoology and Applied Entomology, Imperial College, London

INTRODUCTION

Long-term studies of field populations are essential for the understanding of animal population dynamics. Before embarking on the present study it was decided to select an animal where sampling problems would be reduced. As the later larval stages of the viburnum whitefly, *Aleurotrachelus jelinekii* (Frauenfeld), are sedentary and easily visible and their habitat is totally accessible, it was apparent that complete population censuses, limited in accuracy only by human fallibility, would be possible. Besides this methodological attraction the species has two features of intrinsic ecological interest and one further technical advantage.

Firstly, although the most favoured host plant, *Viburnum tinus* L., an ornamental evergreen, and the whitefly are not native to Britain, their presence here may be considered as the northwards extension of their southern European range. Thus the role of climatically determined mortality and other 'edge of range' effects might be revealed (Richards 1961; Huffaker & Messenger 1964; Richards & Southwood 1968). Secondly, in the particular local situation at Silwood Park it was noted that three apparently similar-sized bushes of laurustinus (*V. tinus*) harboured populations of the whitefly of very different magnitudes (Fig. 1). An investigation might indicate the types of factor and interactions that determine the levels around which a population fluctuates.

Lastly, the invertebrate community of *V. tinus* in southern Britain is very simple, so that predators could be associated with the whitefly without elaborate testing; a considerable technical advantage.

In this paper an account is given of the changes in size of the insect's populations and the habitats and of the analysis of these data by key factor methods. Subsequent papers will consider the various components of the population processes; notably predation and other causes of mortality and the roles of migration, of crowding and of nutritive status of the host plant in the different populations.

BIONOMICS OF ALEUROTRACHELUS JELINEKII

The natural distribution of *A. jelinekii* is essentially Mediterranean, being recorded from France (as far north as Normandy), Spain, Yugoslavia, Turkey (Mound 1962) and the Crimea (Korobitzin 1967). Its principal host in Britain is *Viburnum tinus*, although it occurs, on some other *Viburnum* spp. and on *Arbutus* spp. The first adults have always been observed during the last week of May or the first week of June. Their level of migration is relatively low (P. M. Reader & T. R. E. Southwood, unpublished). Females live slightly longer than males; the population of adults reaches a peak about one to two

weeks after the first emergence, but occasional individuals may be found until mid-August. Adults rest mostly on the underside of the leaves of the host plant: females lay their eggs, in the manner typical of whiteflies, in a vaguely circular arrangement around the resting site, which itself becomes slightly covered in wax. Up to thirty eggs may be present in such a cluster.

The eggs are sausage shaped, initially pale, becoming brown some hours after laying: they are figured by Mound (1962) and illustrated in colour by Southwood (1968). Hatching occurs about four weeks after laying; the empty egg cases remain attached, often for more than a year, providing a useful, but potentially confusing, population index.

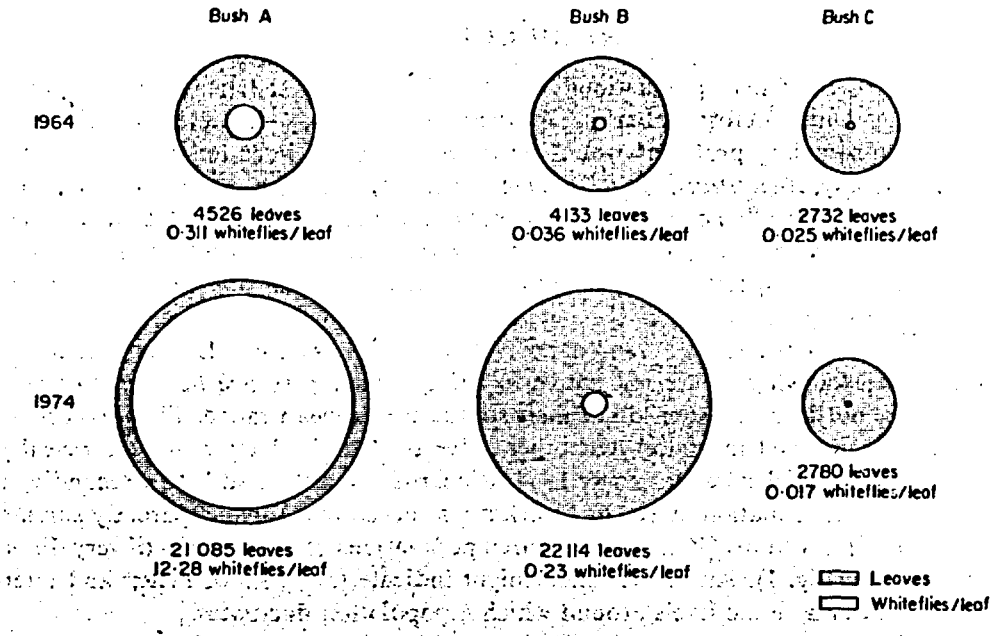


FIG. 1. Comparison of the relative sizes in 1964 and 1974 of the three habitats (bushes of *Viburnum tinus*), and the whitefly populations on them.

The first stage larvae are greenish, flattened (length 0·3 mm) and along with the adults are the only mobile stage. They move over the leaf under-surface for one to two days before they settle, moulting to second instar in two to three weeks. The remainder of the larval life is spent in the position where this stage settles.

The second, third and fourth instars are all black, with white floculent waxy extrusions. They are described by Mound (1962) and Korobitsin (1967) and illustrated in colour by Southwood (1968). The earliest fourth instar larvae appear in late September and most individuals have entered this stage by November. This instar, which is about 1 mm in length, remains on the leaves until the following spring when the adults emerge. Unlike truly temperate whiteflies that often overwinter in an apparently diapause condition on fallen leaves (or as adults), *Aleurotrachelus jelinekii* larvae are merely quiescent, probably feeding intermittently throughout the winter and definitely resuming feeding in the spring. Thus any whitefly larva on a leaf that falls off the bush during the winter months perishes because its food supply fails.

THE HOST PLANT

Viburnum tinus is an evergreen shrub that has white flowers in the spring. The new leaves appear in May and become full sized in about six to eight weeks. During the present study it was found that over 90% of leaves normally survived into the second season and a smaller percentage through to the third and later years. Adults mostly congregate on the young leaves, but a proportion (about 20%) of eggs are laid on the older leaves (which will still have some of the previous season's empty egg cases) and larvae may actually develop on leaves in their second season. Some leaves fall off every winter; prolonged and severe frosts (as in 1962–3), kill many leaves and grey squirrels (*Sciurus carolinerisis* Gmelin) also remove leaves.

THE STUDY SITE

The study was commenced on three bushes of *Viburnum tinus*, each about 5 ft in height. At that time these were the only *V. tinus* in the grounds of Imperial College Field Station, Silwood Park. There were also two strawberry trees, *Arbutus unedo* L. that harboured very small populations of *Aleurotrachelus jelinekii*. These therefore represented the complete *A. jelinekii* populations in the area. The bushes were as follows.

Bush A. On the extreme western side of the Silwood front lawn, surrounded by other evergreen bushes (*Choysia, Mahonia, Cupressus*) and shaded by a clump of cedars (*Cedrus*).

Bush B. On the east side of the Silwood front lawn surrounded by other evergreen shrubs (*Buxus, Rhododendron*) and partially shaded by coniferous and deciduous trees. 130 m from bush A.

Bush C. In a woodland site over 250 m due south of the bush A surrounded by *R. ponticum* L. and *Prunus laurocerasus* L. and shaded by beech (*Fagus*) and other deciduous trees.

METHODS OF ESTIMATING ABSOLUTE POPULATIONS

Each April every leaf on the bushes was examined (but from 1966 only every third leaf on bushes A and B, and in 1974 every fifth leaf on bush A). The following were recorded: the numbers of larvae in the second, third and fourth instars, subdivided into those alive, dead (unknown cause: they are entirely black and flat), dead (due to a predator: a hole torn in the case) and fallen off (where a 'ring' only remains on the leaf). Note was also taken of any dead first instar, some of which remained as empty exoskeletons on the leaf. This direct 'April count' was the 'fix' for the absolute population for that season and provided estimates (of the numbers entering the second, third and fourth instars and the survival of the latter during the winter) that are essentially free of sampling errors, other than those due to human fallibility.

A number (eighty new, twenty old) of leaves were labelled, normally in August and the fate of the cohorts on these determined by examination every two months. Initially, in 1963–4 they were examined more frequently, but it was found that mortality of the leaves and the larvae on them was unduly high; presumably from the effects of continually twisting the petiole. The proportions of fourth instar larvae dying from fungus, parasitism and other causes and the number of adults emerging and the number of eggs originally laid were determined from these leaves. The total number of eggs laid were estimated by taking the ratio of eggs to numbers entering the second instar on labelled leaves and

applying this ratio to the total entering the second instar (measured at the April count). The examination of the proportion of empty to total egg cases on labelled leaves provides an estimate of the numbers of first instar larvae hatching.

Originally it was believed that a count of the empty egg cases would provide an estimate of eggs laid, but now it is known that leaves may survive for several years and at least a proportion of the egg cases remain attached. Thus the estimates for eggs laid in 1962, published by Southwood (1968), were too high. (As virtually all the leaves fell off the bush following the severe frosts of 1962–3, estimates for the next year did not suffer from this problem). Accordingly, for 1962–3, estimates were based on the proportions of living fourth instar larvae to eggs on surviving leaves. (In essence this is the same as the method used for other years). This estimate of the egg population (i.e. 59 200) was tolerably close to one (63 500) based on an alternative method considering the all years' averages: 14% of total leaves are aged under one year and these have about 80% of the eggs laid on them.

THE GROWTH OF THE BUSHES AND THE WHITEFLY POPULATIONS

In 1962 the bushes were all approximately the same size. The severe winter of 1962-3 destroyed the great majority of the leaves on the bushes A and B; the bush C in its sheltered position was less severely affected. By 1964 bushes A and B had 'recovered' so far as leaf number was concerned and overtaken bush C (Fig. 1) although during that season the latter bush grew nearly 4000 new leaves (Fig. 2). Eleven seasons later bushes A and B were still about the same size as each other, with over five times the 1964 number of leaves. The number of whiteflies on both bushes had also increased over these eleven seasons: about 170-fold on bush A, some 40-fold on bush B (Table 1). In contrast, neither the leaf number nor the whitefly population of bush C in 1974 were significantly different from their values in 1964.

The numbers of leaves on the bushes over the years is shown in Fig. 2 and a number of 'disturbances' may be noted. In 1963 and 1964, leaf number of bushes A and B increased greatly as they recovered from the 'frost-defoliation' of 1962–3. In the autumn of 1965 much of the shelter (*Rhododendron ponticum* L.) to the north of bush B was removed and the increased wind was probably responsible for the loss of leaves that winter. After two years the bush recovered and is now about the same size as bush A. Whilst bushes A and B are not now in close spatial competition with other shrubs, bush C abuts large rhododendrons. In 1966 and 1967 numbers of leaves (about 600 and 1390 respectively) were bitten off bush C by grey squirrels. During the following two years the bush almost regained its former size, but a heavy squirrel attack in the winter of 1970–1 (nearly 1900 leaves were recovered near the bush), once more reduced the number of leaves on the bush to about 2000. Meanwhile, the surrounding rhododendrons and laurel flourished and clearly now compete severely with the bush; some branches have died. In conclusion,

(a) bush A has suffered one major disturbance (the 1962–3 frost)
(b) bush B has been disturbed twice (the frost, the 1966–7 exposure)
(c) bush C has been disturbed four times (the frost and grey squirrels); most recently it appears to be suffering from competition from surrounding bushes.

Turning now to the relationship of these habitat and environmental variations with the whitefly population. A consideration of Fig. 1 might lead to the supposition that bush C represents a 'steady state'. In terms of the whitefly population growth index (N_{t+1}/N_t) the reverse is true. A comparison of the indices of growth for leaf numbers and whitefly populations is shown in Fig. 3. The following observations are noteworthy.

(i) After defoliation by frost in 1962–3, there was, on bushes A and B, a high rate of new leaf production for two years, the whitefly population on bush A, however, commenced rapid growth only in the second year and did not 'recover' (reach its previous level) until the third season (1965–6).

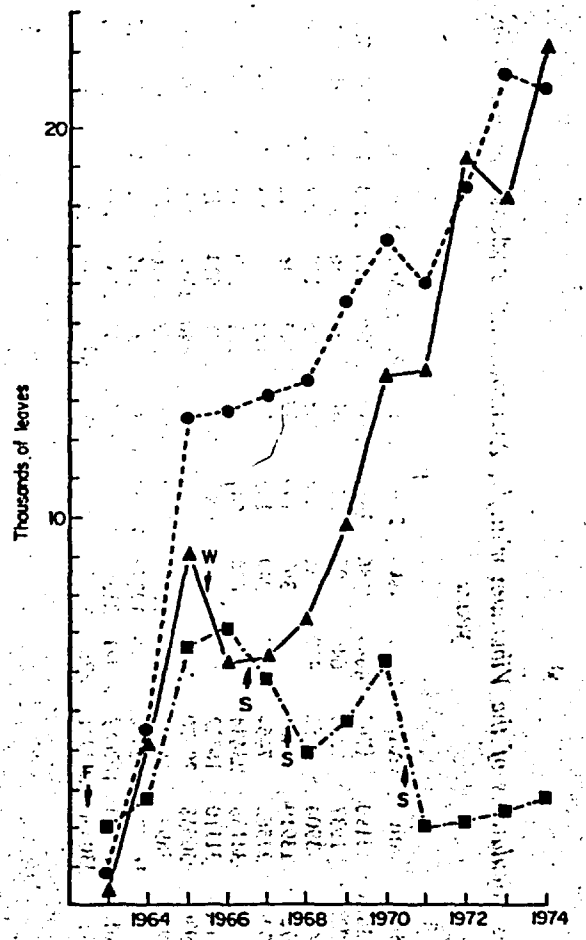


FIG. 2. The changes in the number of leaves on the three bushes of *Viburnum tinus* over twelve seasons. The known causes of overwinter defoliation are marked: F, frost; W, wind exposure (Bush B); S, grey squirrels (Bush C). ●, Bush A; ▲, Bush B; ■, Bush C.

(ii) After the wind-exposure defoliation of bush B in 1965–6, leaf production and whitefly population growth remained depressed for two years. The 'recovery' of the bush in 1967–8 was accompanied by a very large increase in the whitefly population.

(iii) The season 1968–9 was relatively poor for whitefly population growth on all three bushes, but thereafter on bushes A and B the population grew at a fairly steady rate.

(iv) The rates of change of leaf and whitefly numbers on bush C have fluctuated considerably over the whole period, largely due to the action of grey squirrels. The 'steady state' of this bush suggested by Fig. 1 is due to the balance between increases in some years and decreases in others, rather than any subtly governed mechanism. This is

Table 1. *The life budgets of three populations of the Viburnum whitefly,* Aleurotrachelus jelenkii *Fraunfeld over twelve years*

	A						B						C					
Season	Eggs	1st	2nd	3rd	4th	Ad.	Eggs	1st	2nd	3rd	4th	Ad.	Eggs	1st	2nd	3rd	4th	Ad.
1962–3	59200	58383	28404	23676	13190	1767	4689	4586	2658	1590	708	213	1160	729	708	677	597	198
1963–4	4099	4025	2816	2261	1937	1250	646	603	202	201	168	56	526	519	191	178	146	47
1964–5	7460	7423	4393	4361	3904	2952	430	421	208	208	195	128	299	292	155	150	115	8
1965–6	77002	72074	17680	17218	13919	9688	402	393	199	197	144	31	32	31	14	14	9	6
1966–7	74443	72805	29323	29241	27562	7464	254	249	137	137	134	79	69	67	36	35	25	10
1967–8	104675	102372	35062	34938	34136	23634	652	638	587	587	582	300	78	76	28	28	28	8
1968–9	77944	77172	35741	34906	31110	16322	3665	3585	1061	1054	1021	624	75	73	29	28	27	8
1969–70	108051	104918	77012	59300	50658	29670	4006	3918	2961	2784	2640	1367	269	263	109	108	97	27
1970–1	149357	146818	102809	89683	78943	46145	10852	10765	8447	7079	6209	3716	967	946	369	367	348	13
1971–2	314281	304224	210840	183163	164027	93964	17376	17249	14754	13585	12236	4815	422	413	159	157	152	13
1972–3	655974	645347	403015	366154	300583	162689	22041	21556	12904	10411	6957	2135	133	130	55	54	48	19
1973–4	882701	869372	452962	387179	330390	234931	38786	38274	10028	8438	6756	2973	208	203	86	86	75	15

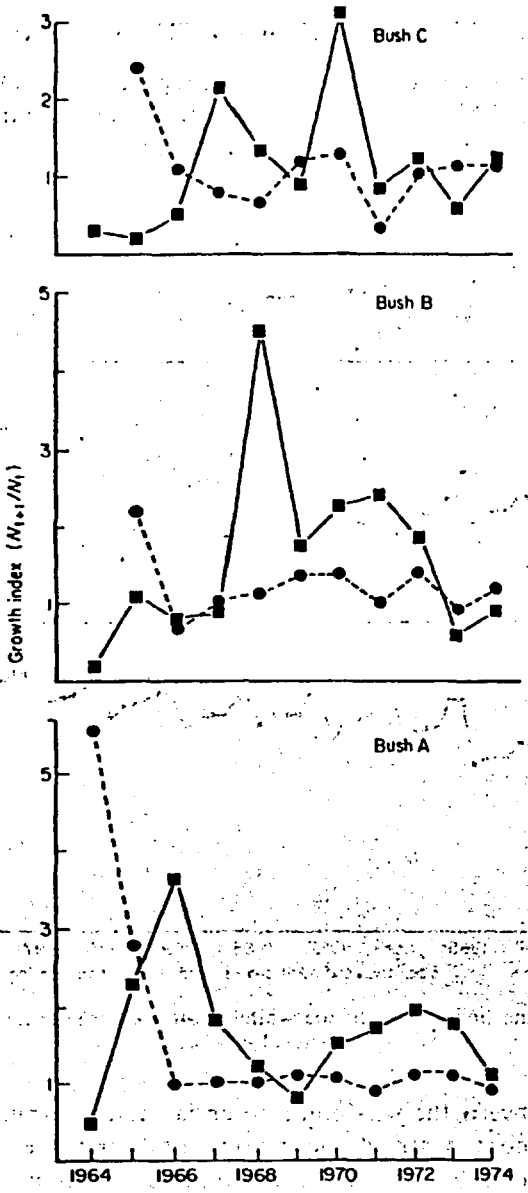


FIG. 3. The growth indices (N_{t+1}/N_t) for the whitefly population and for the total leaf number on the three bushes. ■, Whitefly; ●, leaves.

clearly shown by the comparison of the variances of the leaf and the whitefly population growth indices of bushes C and A for the period 1967–74 (n = 8):

	Leaf number growth index		Whitefly population growth index	
	Mean	Variance	Mean	Variance
Bush C	0·96	0·11	1·44	0·66
Bush A	1·07	0·006	1·52	0·16

THE LIFE BUDGETS AND THEIR ANALYSIS

A total of thirty-six basic life budgets have been prepared for the three populations over twelve seasons (Fig. 4; Table 1). These have been analysed using the method of Varley & Gradwell (1960) and the following k-values calculated:

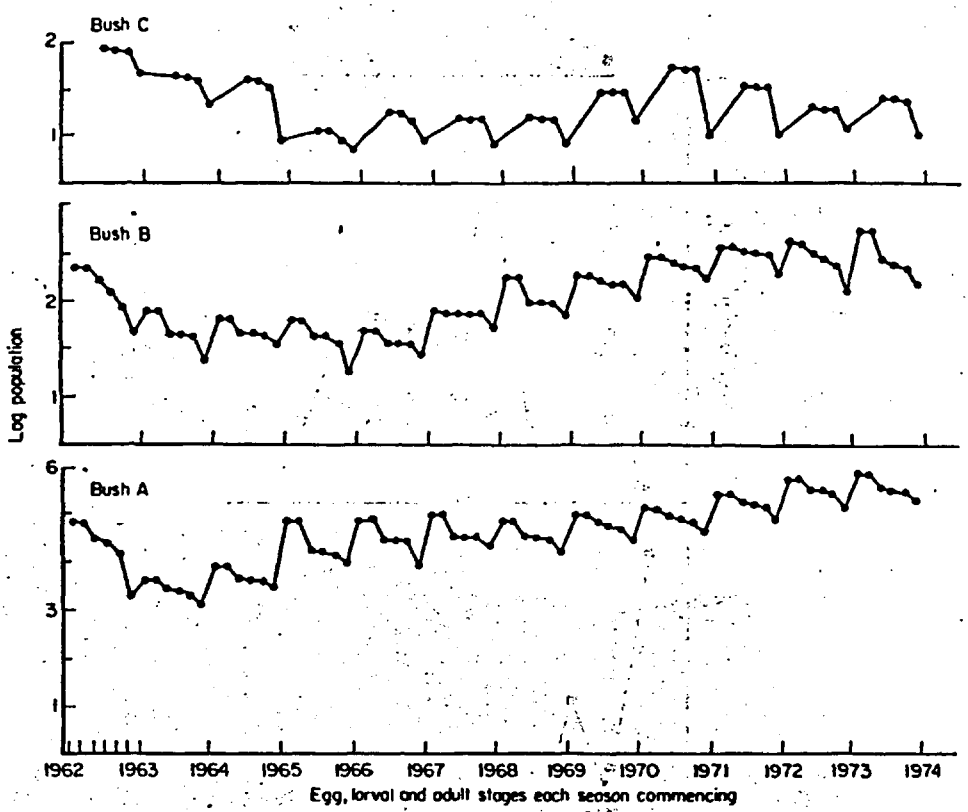


FIG. 4. The absolute populations of the whitefly, *Aleurotrachelus jelinekii*, on the three bushes, 1962–74.

k_0—the difference between the maximum potential natality (number of adult females emerging × maximum observed mean fecundity) and the number of eggs laid, includes effects of adult mortality, migration and variations in fecundity;
k_1—mortality due to egg infertility and predation (insignificant, if any);
k_2—mortality of first instar larvae;
k_3—mortality of second instar larvae;
k_4—mortality of third instar larvae;
k_5—mortality of fourth instar larvae.

Because of sampling problems, reliable egg and first instar estimates are not available for bush C; here $k_0+k_1+k_2 = k_{0-2}$.

Total generation mortality (K)

It can be seen from Fig. 5 that the extent of the variation in this is different in the three populations. The means and variances, in parenthesis, for K ($n = 12$) are bush A, 1·56

(0·03) bush B, 1·64 (0·18) and bush C, 1·59 (0·45). This supports the analysis based on population growth indices that bush C was in reality the least stable and bush A the most.

The key factor

The key-factor, i.e. the 'mortality' whose variation makes the greatest contribution to the changes in total generation mortality (K), can be often recognized by visual correlation (Fig. 5), but a more precise evaluation was obtained by calculating the regression of each k on K (Podoler & Rogers 1975). The values of the regression coefficient for each k-value on each bush are given in Table 2.

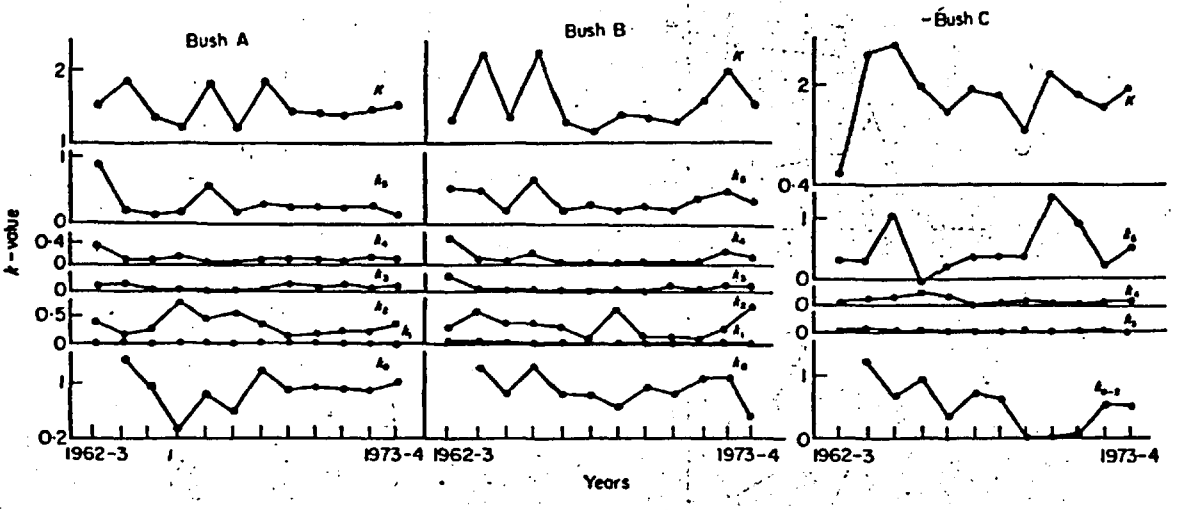


FIG. 5. Key factor analysis for the three populations of the whitefly, *Aleurotrachelus jelinekii*, over twelve seasons.

Table 2. *Regression coefficients for various k-values on K for the three bushes (A, B and C)*

	A	B	C
k_0	0·77	0·41	
k_1	0·01	0·01	0·55
k_2	0·07	0·15	
k_3	0·04	0·03	0·02
k_4	0·00	0·07	0·03
k_5	0·19	0·27	0·32

It is apparent that, in spite of the many other differences between the bushes, the same key-factor, k_0, operates in the three populations. This factor is compounded by:

(a) adult mortality prior to or during reproduction; predation by spiders was the main mortality recognized in this category;
(b) adult emigration from the bush;
(c) variations in the number of eggs laid by females.

Direct assessments have been made of these processes and the evidence will be presented in a later paper.

Regulation

The extent to which any factor is regulating (density dependent) can be determined by

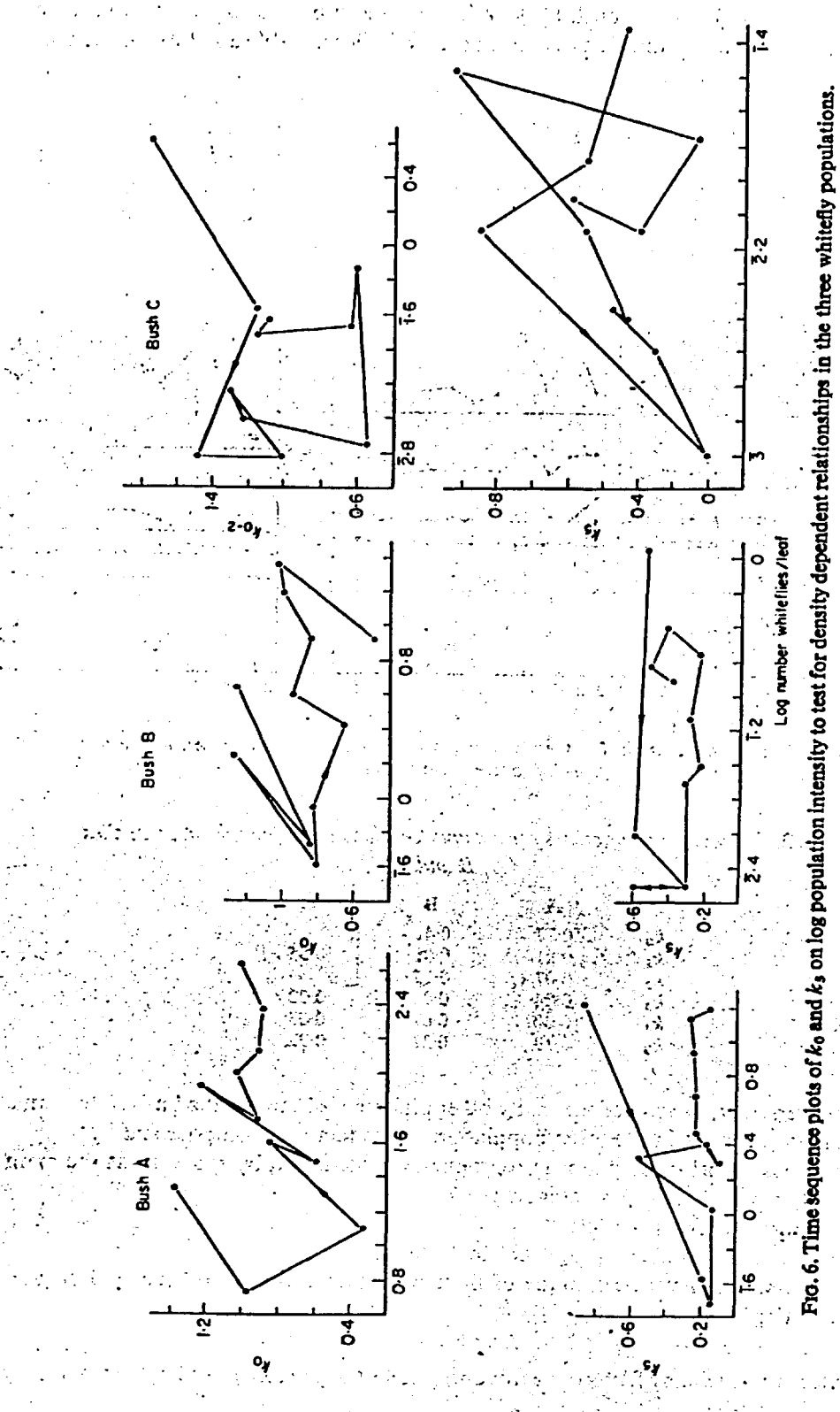


FIG. 6. Time sequence plots of k_0 and k_3 on log population intensity to test for density dependent relationships in the three whitefly populations.

calculating the regression of k on the density of the numbers entering the stage. Population density is frequently taken as absolute population in the habitat, but with the increasing size of bushes A and B this is not a true measure of density. The most meaningful measure is numbers per leaf, i.e. a measure of population intensity. Tests for density dependence were therefore carried out expressing the density of the numbers entering the stage as numbers per leaf, the leaf number being the following April count. (Thus k_0–k_3 all relate to the same leaf number.) Time sequence plots were prepared to test for delayed density dependence (Fig. 6).

Neither graphical nor numerical analysis suggested any density dependence in any of the k-values other than k_0. As may be seen from Fig. 6 there appears to be a relationship between k_0 and population intensity (numbers/leaf) during certain years. Indeed for bush A, the regression of k_0 on population intensity is significant for years 4–12 ($b = 0{\cdot}39$) and 4–8 ($b = 1{\cdot}10$). This significance is not reliable, because the two terms are not independent and the further test (see Southwood 1966, p. 303) of the significance of the departure of the regression of initial on final numbers (and vice versa) from unity, did not confirm density dependent action by k_0. Furthermore, the thirty-three point plot of k_0 values, for both bushes A and B with (or without) the addition of k_{0-2} values for bush C, on population density showed no relationship.

One would therefore conclude from this census data, analysed by the conventional methods, that density dependent regulation appears to be absent in these populations. The extent to which this conclusion is only partly correct will be shown in a subsequent paper on the analysis of particular population processes (as opposed to the age specific survivals discussed here).

DISCUSSION

The results presented in this paper may be considered from the aspects of change and stability in the population. The major change with time is in the population levels which, as the habitats were changing in size, are best expressed in terms of population intensity (numbers/leaf). Taking the numbers of fourth instars per leaf on bush C in 1964 (Fig. 1) as unity, the relative intensities were approximately:

	A	B	C
1964	12	1·5	1
1974	491	9	0·7

The stability of the population level of bush C is more apparent than real. The population was small, the total number of adults ranging (1964–74) from 6 to 47, and thus relatively small changes in absolute numbers cause large proportional changes. Indeed when the indices of population growth (N_{t+1}/N_t) are compared it is found that for both leaf number (habitat size) and whitefly population the variance of these is greater for bush C than for bush A. On analysis bush C is found to represent the most unstable condition: a small population in an apparently unfavourable habitat, where the availability of the food resource fluctuated.

Steady growth in numbers was exhibited by the population on bush A, although it took three seasons to settle down after the disturbance (perturbation) caused by the severe frost of 1962–3. Bush B exhibited an intermediate condition with two major perturbations in the environment and again the whitefly population showed a recovery period of two to three generations. The key factor was k_0: hence year to year variations in population growth are likely to be due to changes in natality and/or adult survival.

The basic population dynamics thus seem similar on the three bushes. But whereas bush C exhibits a strongly perturbed situation, one with a high stochastic element; bush A, after an initial climatically induced disturbance, behaved more like a deterministic simulation. These observations appear to mirror simulations of theoretical models with different levels of 'noise' described by Southwood (1975).

The failure to detect regulation in the relatively sparse populations on bushes B and C is perhaps not surprising. There is no evidence that density dependent mechanisms operate in every generation in all populations (Richards & Southwood 1968). However, on bush A the whitefly population has grown at a faster rate than the habitat and by 1974 its population intensity was about seven hundred times that on bush C. It might be supposed (and will be shown in a later paper) that, at least in recent years, some weak regulatory factors would operate in this population and our failure to detect them is due to methodological difficulties. As sampling conditions could seldom be better in insect populations in the field, this has wide implications for the analysis of field data.

ACKNOWLEDGMENTS

We are most grateful to various colleagues who have helped us with counting, calculating and other technical tasks at various times since 1962, namely Mesdames E. Barnard, M. Candey, H. Frayne, T. Kapatos, C. Lunn and J. Sinclair, and Drs W. Milne and C. Seymour.

SUMMARY

(1) A census of three populations of the viburnum whitefly, *Aleurotrachelus jelinekii*, has revealed very different trends over thirteen seasons (1962–74), although the habitats (the host bushes) were originally of similar size and are exposed to the same general climatic influences. In 1964 the bush with the highest population (bush A) had twelve times the population intensity (numbers/leaf) of the bush with the lowest density (bush C); by 1974 the difference in population intensity was over seven hundred fold (Fig. 1).

(2) The same key factor (k_0) operated in all three populations and population growth was markedly depressed on all bushes in 1968–9.

(3) The population (bush C) that was apparently most stable in the level of its absolute numbers, in fact showed the greatest generation to generation change (expressed either as N_{t+1}/N_t or K). This variation was a reflection of disturbances in the habitat (perturbations) due, in this instance, to the effects of other animals (grey squirrels) and of climate.

(4) The other two populations showed less evidence of perturbations. In these the causes of initial fluctuations were climate (bush A) and climate and the removal of adjacent shrubs (bush B). The populations took more than one season to 'recover' from a major disturbance (e.g. when, on bush A, only 6% of the population survived in 1962-3, it was not until 1965–6 that the initial egg population had been exceeded). Therefore, it may be concluded that climatic disturbances had a powerful, but occasional, effect in these 'edge of range' populations.

(5) The regulation of the population by density dependent mechanisms could not be detected from the census data.

REFERENCES

Huffaker, C. B. & Messenger, P. S. (1964). The concept of significance of natural control. *Biological Control of Insect Pests and Weeds* (Ed. by P. De Bach), pp. 74–117. Chapman & Hall, London.

Korobitzin, V. G. (1967). To the cognition of Aleroids (Homoptera, Aleyrodoidea) of the Crimea (In Russian). *Trudy gos. nikit. bot Sada*, 39, 305–65.

Mound, L. A. (1962). *Aleurotrachelus jelinekii* (Frauen) (Hem. Aleyrodidae) in Southern England. *Entomologists' mon. Mag.* 97, 196–7.

Podoler, H. G. & Rogers, D. (1975). A new method for the identification of key factors from life table data. *J. Anim. Ecol.* 44, 85–114.

Richards, O. W. (1961). The theoretical and practical study of natural insect populations. *A. Rev. Ent.* 6, 147–62.

Richards, O. W. & Southwood, T. R. E. (1968). The abundance of insects: Introduction. *Insect Abundance* (Ed. by T. R. E. Southwood), pp. 1–7. Blackwell Scientific Publications, Oxford.

Southwood, T. R. E. (1966). *Ecological Methods, with Particular Reference to the Study of Insects*. Methuen, London.

Southwood, T. R. E. (1968). The abundance of animals. *Inaug. Lect. Imp. Coll. Sci. Technol.* 8, 1–16.

Southwood, T. R. E. (1975). The dynamics of insect populations. *Insects, Science and Society* (Ed. by D. Pimentel), pp. 151–99. Academic Press, New York.

Varley, G. C. & Gradwell, G. R. (1960). Key factors in population studies. *J. Anim. Ecol.* 29, 399–401.

(*Received* 16 *May* 1975)

Biological Journal of the Linnean Society, 12: 327–348. With 11 figures

December 1979

The relationships of plant and insect diversities in succession

T. R. E. SOUTHWOOD, V. K. BROWN AND P. M. READER

Department of Zoology and Applied Entomology, Imperial College, London

Accepted for publication April 1979

The basic features of an intensive study on the various stages of a secondary succession, from fallow field to birch woodland, are described. The α–β diversities of the green plants, and two orders of insects, Heteroptera and adult Coleoptera, are described. For the vegetation, in addition to taxonomic diversity, structural diversity, with both spatial and architectural components, was recognized. It was found that up to a successional age of 16 months, the taxonomic diversities of plants and insects rose; thereafter the diversity of the plant species declined far more than the insect species diversity. It was concluded that in the later successional stages the maintenance of a high level of taxonomic diversity of these orders of insects is correlated with the rising structural diversity of the green plants, which virtually compensates for their falling taxonomic diversity. The larger fungi appear to show a similar trend to the insects.

KEY WORDS: – succession – taxonomic diversity – structural diversity – green plants – Coleoptera – Heteroptera.

CONTENTS

Introduction 327
The expression of diversity 328
The sites 328
Methods 330
Sampling 330
Recording and analysis 331
Results and discussion 332
Taxonomic diversity of the vegetation 332
Structural diversity of the vegetation 335
Taxonomic diversity of the Heteroptera and Coleoptera 336
Comparison of plant and insect diversities 340
Summary and conclusions 344
Acknowledgements 344
References 344

INTRODUCTION

"Many structural and functional attributes of the community change during its successional development" (Ricklefs, 1973). Indeed one of us has suggested that succession provides one of the cardinal axes of the habitat templet within which the ecological strategies of community components (plants and animals) may be organized (Southwood, 1977a). Succession may be viewed as a process

0024–4066/79/080327–22/$02.00/0

© 1979 The Linnean Society of London

that follows a disturbance or disaster (Harper, 1977); its characteristic feature is that, as the patch of habitat in question moves through the successional processes there is an increase in durational stability, the length of time it remains in a particular condition (humus level, dominant plant, etc.). Thus the favourableness of habitats that are early in the successional sequence will vary greatly in space; highly favourable habitats will arise in new locations, a feature termed by Baker (1978) the "ontogeny of habitat development".

However, in spite of Ricklefs (1973) general statement, quoted above, he goes on to state (correctly we believe) that "the complexity of community organization along a successional gradient has never been measured". It seems that although various components have often been assessed over a portion of a successional gradient, a holistic study has not been made. Such a study is necessary to test the predictions that arise from many, often firmly established, generalizations with regard to properties such as productivity, diversity, trophic links or concepts, such as apparency (Feeny, 1976; Southwood, 1977b) and r and K selection (MacArthur, 1960; Pianka, 1970) and their relation to succession.

The present paper is the first of a series that will describe an intensive study on the characters and attributes of the macro-organisms of a typical secondary succession in southern Britain. It relates the taxonomic diversity of two groups of insects, Coleoptera and Heteroptera, to the taxonomic and structural diversity of plants in a succession.

The expression of diversity

A general association between plant and animal diversity has long been recognized. However, a number of different properties contribute to diversity. That most usually considered is the number of different species and its relation to number of individuals, we refer to this as taxonomic diversity. However, structure is also important; the relevance of plant structure to the diversity of birds has often been demonstrated (MacArthur & MacArthur, 1961; Karr, 1968; Recher, 1969; James, 1971) whilst Lawton (1978) has recently stressed the probable role of plant architecture in relation to insect diversity. The shape or form of an animal is a comparable character (Van Valen, 1965; Findley, 1973). We believe that for vegetation it is useful to distinguish two components of structural diversity: spatial diversity, the distribution of plant structures in space above ground level and architectural diversity, the distribution of different types of plant structure (Table 1).

An important study on the relationships of insect and plant diversities is that of Murdoch, Evans & Peterson (1972) who investigated these in three "Old Field" sites, using leafhoppers (Homoptera: Auchenorrhyncha). They confirmed the general correlation between plant and animal diversity, but because the structural (spatial) and taxonomic diversity of their plants were in all cases positively correlated, they were unable to resolve the influence of these variables on the taxonomic diversity of the insects.

The sites

The Imperial College Field Station at Silwood Park, Ascot, Berkshire, consists of 93 ha (230 acres) and is a mosaic of vegetational types, principally arable

Table 1. Plant architecture—types of structure

Dead wood over 10 cm dia.	Flower buds
Dead wood over 2 cm dia., under 10 cm	Open flowers
Dead wood under 2 cm dia.	Dead flowers (not covered by next item—e.g. old catkins)
Bark on dead wood over 10 cm dia.	Ripening/ripe fruits (seeds)
Bark on dead wood 2–10 cm dia.	Old fruiting structures
Bark on dead wood under 2 cm dia.	Dead leaves
Bark on living wood over 10 cm dia.	Dead stems
Bark on living wood 2–10 cm dia.	Mosses—epiphytes
Bark on living wood under 2 cm dia.	Mosses—on soil surface
Green stems	Liverworts—epiphytes
Leaves of monocotyledons	Liverworts—on soil surface
Petioles	Lichens & algae—epiphytes
Leaf surface—upper (if distinct)	Lichens & algae—on soil surface
Leaf surface—lower	Fungal fruiting bodies—on vegetation
Leaf buds/scales	Fungal fruiting bodies—on soil surface
Flowering stems	

crops, grassland and woodland. Our study sites, selected to represent various ages in the secondary succession, were typical of types represented in several localities in Silwood Park and were within 250 m of each other. We therefore consider that there is no great spatial barrier to colonization of any of these sites by the same organisms. Each site is on slightly raised ground, of area 405 m^2, and is part of a larger region of similar vegetation. In 1977 all three sites were fenced with wire-netting to exclude rabbits, this was only partly successful, so that each site continued to be lightly grazed by young rabbits. The three sites were:

Young field

This site is part of a long-standing arable area; it was treated with weed-killer to destroy perennial weeds, shallow ploughed, harrowed and lightly rolled in mid-March. This field was six weeks old at the time of the first sample. The young field, so prepared in 1977, was left undisturbed in 1978 providing information for the second year of a secondary succession. A new young field was established in March 1978 in a similar situation.

Old field

In 1971 the soil excavated for the construction of a substantial building (the 'Nuclear Reactor Centre') was covered with top soil (from the site) and left undisturbed apart from fairly severe rabbit grazing in 1975–6. This was thus a six year old site in 1977, at the start of the project.

Woodland

This site was a small section of a large birch-dominated woodland with an occasional large oak (*Quercus robur*) and beech (*Fagus sylvatica*). Typically for the acid gravels, on which the sites occur, birch (*Betula pendula* and *B. pubescens*) dominated the secondary growth, after selective felling in 1947.

The equivalent successional age of this site is uncertain, for it was woodland prior to 1947 when Imperial College acquired Silwood Park. However, there are other sites at Silwood where a similar vegetation has developed but, on which the birch trees are much older. These were regularly grazed by cattle until the First World War, thereafter grazing was discontinued and the trees developed naturally. Thus we consider that the age of our woodland site is around 60 years.

However, birch may not be the climax to the sere (Tansley 1939). We recognized that the low taxonomic diversity of the vegetation of this late successional stage, would allow for the separate consideration of the different aspects of diversity.

METHODS

Sampling

Sampling plan

A stratified sampling programme was followed in order to reduce systematic errors and to speed and simplify the sampling process. Each site was divided into 45 squares, 3 × 3 m, arranged in a 9 × 5 pattern. The actual samples were then taken within these squares as described below. In the Woodland site a scaffold and board 'cat walk', 7 m long, was erected diagonally across the plot; the platform level was at 6 m. Five complete samples were taken throughout the year at times that were judged to reflect biological seasons, namely: January, early May, early June, early July and mid/late September. Additional vegetational samples were taken in late July and late August in 1977.

Vegetation

Sampling pins were the principal method used; they were marked at intervals of 25, 25, 50 and successive 100's mm from soil level. Generally a 550 mm long pin was adequate, but in tall vegetation a 1 m pin was required. In the woodland site a 10 m pole of bamboo rods was used, it was divided into ten sections and held on a 1 m high stake (i.e. it sampled up to 11 m). Additionally in the woodland site, a helium-filled weather balloon buoyed on string marked in metres was used and the 1 m sampling pin was placed through the vegetation around the 'tree-top cat walk'. The total number of samples taken is shown in Tables 2 and 3, usually five samples were taken from each square by throwing the sampling pin haphazardly, from each corner and centrally. In the woodland site ground cover was sampled in this manner. For the trees the tall pole was placed within each square in a position determined by throwing a sampling pin. The data from the balloon and 'cat walk' methods were used to correct the pole surveys; the former with regard to vegetation over 11 m above ground level and the latter for the details of plant architecture in the canopy. Inevitably these estimates for the tree canopy were less accurate than those for the field layer, but the mean number of touches in 1978, namely 16.5, compared reasonably with the 17.5 estimated in 1977. We are not concerned with percentage cover, but as the sampling pins were 4 mm in diameter the number of touches would slightly overestimate this feature.

Fruiting bodies of the larger fungi were sampled by counting those present in nine randomly selected squares in each site in October 1977.

Macro-invertebrates

On field layer vegetation these were sampled with a D-vac suction apparatus. One sample was taken from approximately the centre of each 3 × 3 m square: to simplify sorting and other procedures five samples (i.e. from one line of squares) were combined in the field (taken successively without emptying the bag). Thus there were nine main samples from each site on each occasion, each of five

subsamples, and representing the fauna from 0.47 m². The D-vac apparatus was held in position for 1 min, after it was removed the spot was carefully searched by eye and any invertebrates still present collected: Mollusca, Isopoda and large Coleoptera were amongst those commonly found. In the Woodland the leaf litter was covered with a piece of 35 mm mesh wire-netting. This restricted the number of fallen leaves entering the suction apparatus and prevented clogging of the bag. The bracken, when fully grown, was sampled separately. The arboreal fauna was sampled with a specially designed beating bag; it was found that the bag prevented the escape of the active insects more effectively than the traditional tray. Ten 'bagfulls' were sampled from the lower canopy, one of these from the oak tree, that constituted about 10% of the canopy, and ten from the upper (i.e. from the 'tree-top cat walk') on each sampling occasion. This method was calibrated in relation to the ground surface area i.e. to the D-vac samples by two approaches: (i) visual estimates by four different persons of the number of bagfulls per area of canopy, (ii) 'knockdown' sampling with a Hudson ULV-Bak-Pak mistblower and 1% pyrethrin insecticide of an area (16 m²) of comparable canopy near the study site. The visual estimates gave a mean 4.17 bagfulls/m², the knockdown based on Heteroptera an estimate of 4.55 bagfulls/m²; thus it was concluded that 20 'bagfulls' were more or less equivalent to 45 D-vac samples (i.e. 4.2 m²).

There are 55 living tree trunks on the site and the fauna of these was sampled by collecting visually with a pooter from ground level to 2 m on five trunks, i.e. equivalent to 10 m of trunk. Allowing for an efficiency of about 75% and 15 m of trunk and major branches (too large for the bag samples) we consider that these catches represented about 1% of the superficial bark fauna on the site. They were therefore added to the beating and D-vac samples to give an estimate of the total macro-invertebrates from a column of vegetation in the woodland arising from 4.2 m² of ground surface (i.e. about 1% of the site). Soil samples were taken from each site and extracted in Berlese-Tullgren funnels and the avifauna recorded during simultaneous observations: data from these methods are not used in this paper so further discussion is omitted.

Recording and analysis

Taxonomic diversity

A measure of taxonomic diversity of the vegetation, comparable to that normally used for a fauna, was obtained by regarding one or more touches of a sampling pin by a species as an "individual". The total individuals for that plant species was thus the number of sampling pins it touched. The concept of the individual, used in this way, is inappropriate for trees that may constitute the canopy over a large area, but it can be used as a measure of the taxonomic diversity in some hundreds of vertical columns of vegetation, each of diameter 4 mm. The insect taxonomic diversity was assessed in the usual way by identifying all individuals in a sample to species.

Spatial diversity

The number of touches by a piece of vegetation (any species or any part) was recorded within each height division of the sampling pins (or poles, these

corrected for their greater diameter). These data therefore show how plant structures are distributed vertically in space, the height divisions may be regarded as categories (analogous to species in taxonomic diversity) and the structures to individuals. A similar approach was adopted by Murdoch *et al.* (1972); they referred to it as foliage height diversity, however, we concerned ourselves with parts of the plant other than foliage.

Architectural complexity

Lawton (1978) states "there are more ways of making a living on a bush than on a bluebell" and growth form of the vegetation is indeed likely to be an influence on the richness of the associated fauna (Strong & Levin, 1979). We therefore sought to record the diversity of types of plant structures: the different categories into which plant structures were separated according to their architecture are listed in Table 1. As will be seen these were defined largely on botanical grounds but cognisance was taken of the way different animals will utilize plant parts, e.g. on a leaf of a dicotyledon the upper and lower surfaces provide different habitats, as do living and dead wood, the space between the bark and the wood is another 'microhabitat' only found on dead wood. In animals form is an analogous variable; studies have been made on vertebrates (e.g. Karr & James, 1974), but not on invertebrates. A morphometric analysis of the form in some of the insect groups found in this survey has been undertaken by one of us and will be reported elsewhere (Brown, in preparation).

RESULTS AND DISCUSSION

Taxonomic diversity of the vegetation

β-diversity gradient

Changes in diversity with time occur in all three sites; in the Old Field and Woodland sites these changes are mostly seasonal for there has been little change in β-diversity during the first two seasons. This is evidenced by the high value of the Sørensens Index of Similarity ($I_s = 2J/A + B$, where J = species present in both samples; A and B = species present in samples A and B respectively (Table 2)). In the Young Field the seasonal changes are confounded and essentially dominated by the changes in basic species composition: the extent to which the Young Field moves very quickly along a β-diversity gradient is shown by the relatively low (0.64) Index of Similarity between the first and second years in the same site. The taxonomic composition of the Young Field in its second year is only marginally closer to that in its first year, than it is to the Old Field ($I_s = 0.64$ cf. $I_s = 0.53$). That this is a successional change along a β-diversity gradient and not simply a seasonal effect is shown by the higher value of the index (0.74) between the two Young Fields in their first season, although they represent different sites and different seasons.

Further evidence of the change in composition of the Young Field over the first 18 months of succession is provided by the species gain (colonization) and loss (extinction) curves (Fig. 1). It must be noted that whilst actual colonization will occur *before* the species is recorded in the samples, actual extinction is likely to occur *after* the species is last recorded; therefore the time gap indicated in Fig. 1 is an underestimate. The rapid accumulation of species in the first season occurred

Table 2. Indices of Similarity (I_s) between the flora (green plants) recorded in the different sites between May and October in two seasons

Total sampling points	Comparison	Index
2970	Woodland 1977 v Woodland 1978 (same site)	0.87
2250	Old Field 1977 v Old Field 1978 (same site)	0.87
2900	Young Field 1977 v New Young Field 1978 (same age, different site)	0.74
2675	Young Field 1977 v Young Field 1978 (same site, different age)	0.64
2075	Young Field 1978 v Old Field 1978 (different age and sites)	0.53
3105	Young Field 1977 v Old Field 1977 (different age and sites)	0.45
2300	New Young Field 1978 v Old Field 1978 (different age and sites)	0.28

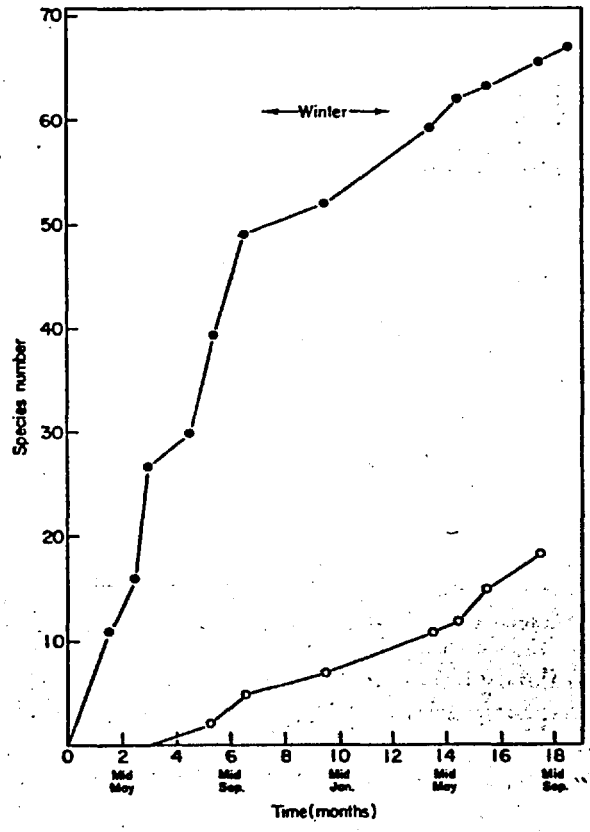


Figure 1. Plant species gain and loss rates in Young Field vegetation over two years. ●, Colonization; O, extinction.

in two main 'waves', those that appeared before the fourth month and flowered during the first season and those that grew in the late summer and autumn. Undoubtedly the dry spell in the middle of the summer of 1977 accentuated this, but even so the 11 species of 'primary colonizers' do seem to constitute a community of 'ruderals': of the seven dicotyledons in this group, six were 'extinct' (so far as sampling was concerned) within 18 months, though at one time they were all very abundant. In the new Young Field in 1978 the same

seven* species were recorded after six weeks, along with one further species, *Tripleurospermum inodorum* that was not recorded until the twelfth week of 1977.

The β-diversity relationships of the different sites in the various parts of the growing season are shown by the Indices of Similarity displayed in the Trellis diagram (Appendix 1), these are most easily appreciated by reference to the dendrogram (Fig. 2) which shows:–

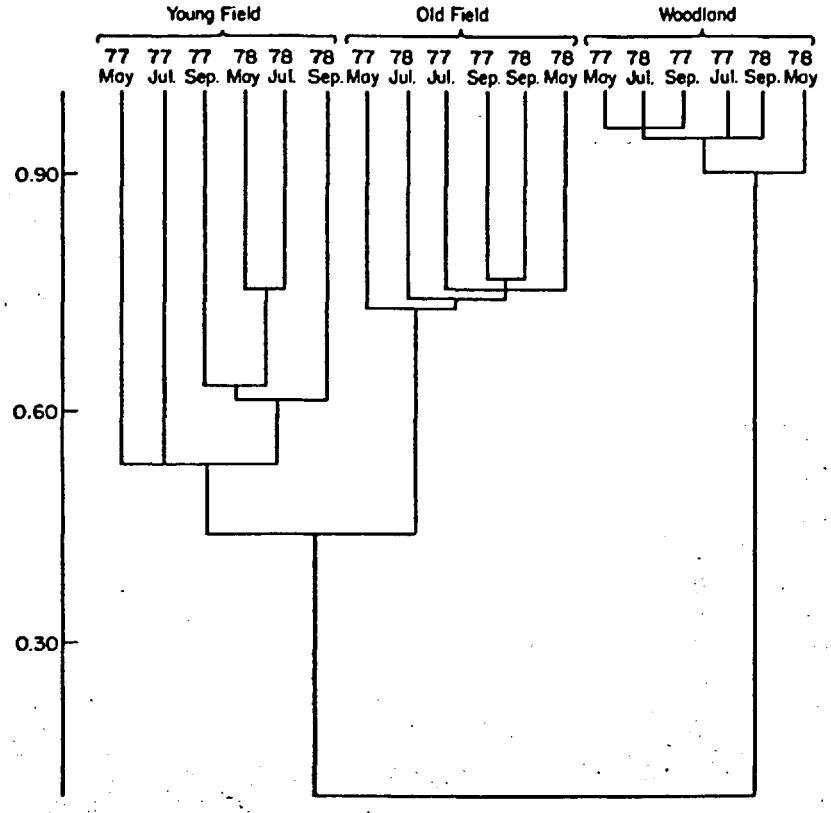


Figure 2. Dendrogram of taxonomic similarity of vegetation in three sites over two years.

(i) The close similarity between the samples from the Woodland site at three times in each of two years (in May 1978 the bracken (*Pteridium aquilinum*) croziers had not risen above the leaf litter).

(ii) The similarity, but not at quite such a high level, between the Old Field samples.

(iii) The relatively low similarity between the six Young Field samples in the two seasons. Two groups of samples can be recognized, those two from the first three months of the succession and the remainder. This supports the view, derived from Fig. 1 and associated data, that there are really two communities: ruderals and early successionals in the Young Field.

Thus we can conclude that whereas β-diversity changes in the Woodland and Old Field sites are insignificant (over two years) and reflect seasonal changes, those in the Young Field are a reflection of an underlying change in the structure

* *Capsella bursa-pastoris, Chenopodium album, Polygonum aviculare, Senecio vulgaris, Spergularia media, Stellaria media* and *Veronica persica.*

of the community of green plants. Very approximately one can recognize four "communities": the ruderals, the early successionals (both in Young Field), the mid-successionals (Old Field) and the late successionals (Woodland). The distances these are apart on a β-diversity gradient may be estimated by calculating $1-I_s$ for each comparison. These are shown in the upper part of Fig. 3, the I_s values are those for the whole season, i.e. for a cluster of points and not for each sampling occasion (as cited in Appendix 1).

α-diversity

This describes the segregation of units into categories, here of records of individuals into species. There are a number of indices, one of the most useful is Williams' α, although the Berger-Parker dominance index (d) is both useful and simple to calculate (May, 1976; Taylor, Kempton & Woiwood, 1976; Southwood, 1978). In this study, Williams' α has been employed and was calculated by a maximum likelihood method. Indices for the vegetation samples are given in Appendix 2.

It will be observed that the taxonomic diversity of the green plants varies with the successional age of the site at the date of sampling; if α is plotted against age in months on a logarithmic scale then a slightly skewed normal curve is described (Fig. 3, bottom). It is interesting that the β-diversity distances between the groups of samples seem to correspond proportionally to the successional age differences on a logarithmic scale (Fig. 3, top). This suggests that in this sere the species turnover rate is linear with regard to time expressed as log successional age.

The α-diversity of a sample is well expressed by the dominance diversity curves; the steeper the slope the less equitable the distribution of individuals between species. When such plots are examined for different samples (Fig. 4) it is seen that as diversity rises so the equitability increases; likewise once diversity falls (after the age of about 16 months in these spring initiated secondary successions) then equitability falls; there is thus one set of 'rising' curves representing the ruderal and early successional stages and another set of 'falling' curves from early to late successional stages (Fig. 4). These changes in form with age, from an apparently geometric series to an approach towards MacArthur's broken-stick model and then back again, have implications regarding the underlying processes: we intend to explore these in a later paper.

The taxonomic diversity of the green plants (mosses, ferns and flowering plants) therefore rises and then falls through succession. The diversity of the fungi, as represented by their fruiting bodies, continues to rise (Appendix 2).

Structural diversity of the vegetation

As indicated above this has two components, spatial and architectural and these have been separated.

Spatial diversity

This is a measure of the distribution of plant structures (of any type or species) in the vertical plane. Profiles for the three sites show how the level of maximal density is at ground level in the ruderals; in the mid-successionals stratification is beginning, whilst in the late successionals the canopy is well formed (Fig. 5). The woodland canopy is clearly multilayered (Horn, 1971). Lawton (1978, fig. 7.10)

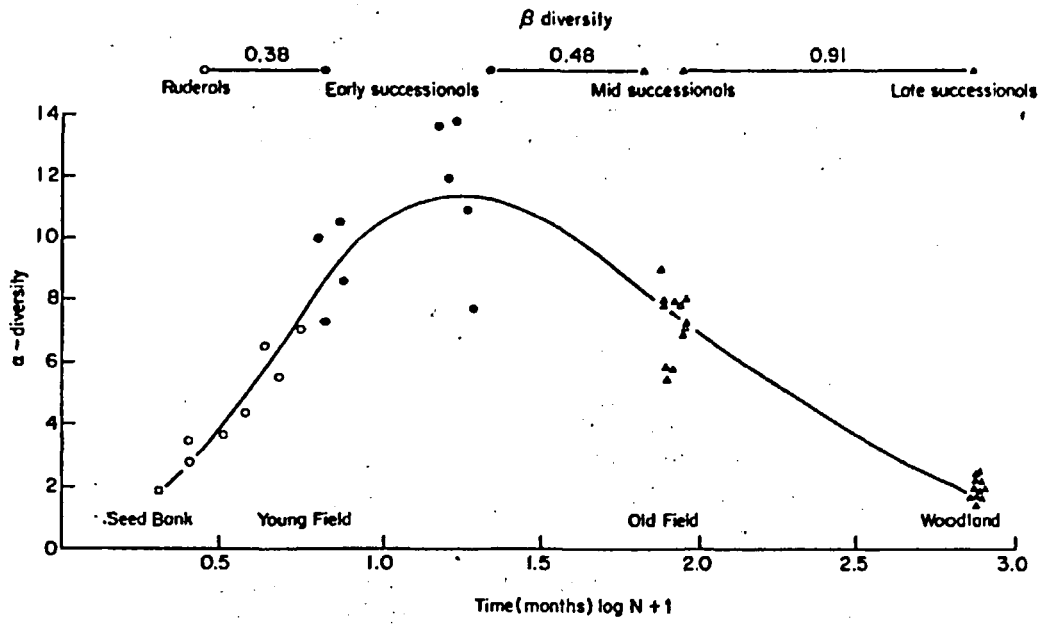


Figure 5. Taxonomic diversity of the green plants in the study areas. (Top) The distances between the different groups of samples in terms of β-diversity (values for $1-I_3$). (Bottom) The α-diversity (as Williams' α) for sites plotted against log successional age. □, Seed Bank; ○, Young Field; ●, Young Field after one year; △, Old Field; ▲, Woodland.

has postulated how structural diversity will change with season; our data (Fig. 6) tend to support his suggestions with maximal diversity in mid-summer; however, with woody branches and trunks the spatial diversity of the woodland site was high even in early spring. The scale adopted (12 height categories in the first metre and then each metre thereafter) clearly reduced the categories in arboreal vegetation; this is, however, still the most diverse. Moreover, it is true that changes in microclimate that will affect the associated fauna occur over much smaller height differences in the first metre above ground, than thereafter.

Architectural diversity

The types of plant structure, listed in Table 1, were utilized as the categories. Architectural complexity also increases through successional stages, although not as markedly as spatial complexity (Table 3). The Old Field is dominated by monocotyledons and this may be reflected in its low architectural diversity.

Taxonomic diversity of Heteroptera and Coleoptera

Both these groups contain phytophagous, predatory and fungivorous species, although no fungivorous Heteroptera were found. In a later study we intend to investigate diversity patterns in different trophic groups, but here we are concerned simply with the relationship of insect diversity to plant diversity.

β-diversity

The Indices of Similarity between the insects sampled in the period May-October from the different sites show the same trends as those for the vegetation

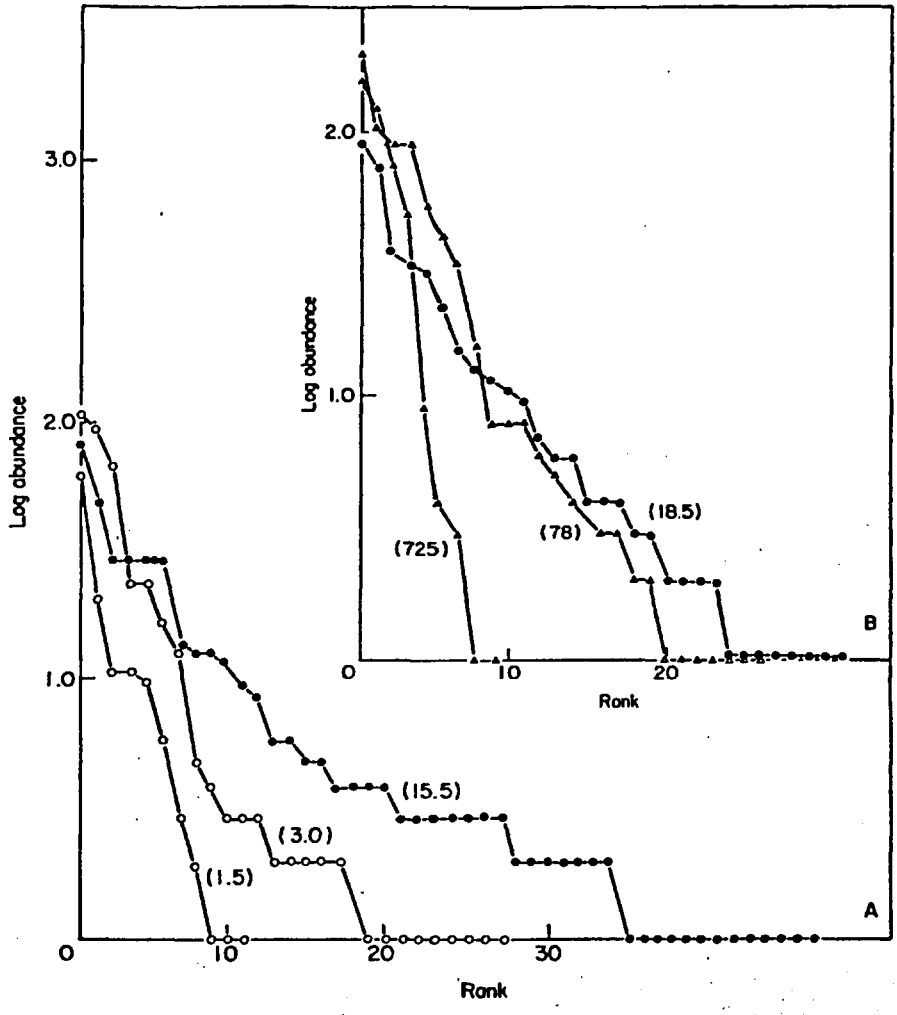


Figure 4. Dominance diversity curves for six samples of green plants from sites of different successional age (age in months in parenthesis). A. 'Rising' set with increasing diversity (and equitability) for the first 16 months of succession. B. 'Falling' set with decreasing diversity from 16 months of succession. ○, Young Field (age 1.5 months); ●, Young Field (age 15.5 months); ●, Young Field (age 18.5 months); △, Old Field (age 77 months); ▲, Woodland (age 725 months).

(compare Table 4 with Table 2). Namely, the relative consistency of the insect fauna in the Woodland and Old Field sites in successive years, and between those in the Young Fields of up to six months in successional age in successive years, although these are different sites. However, the similarity between sites of different successional age (even the Young Field in the same site in successive years) is low. The indices also show the closer resemblance of the Young Field after one year to the Old Field than to the New Young Field ($I_S = 0.40, 0.34$ cf. 0.26, 0.21 for Heteroptera and Coleoptera respectively). It will be noted that the indices for the insect fauna are lower than those for the plants, we believe this is largely a reflection of the greater mobility and species richness of the insects. The Coleoptera, where there are many predatory and saprophagous species show the trends less clearly and have lower indices than the Heteroptera.

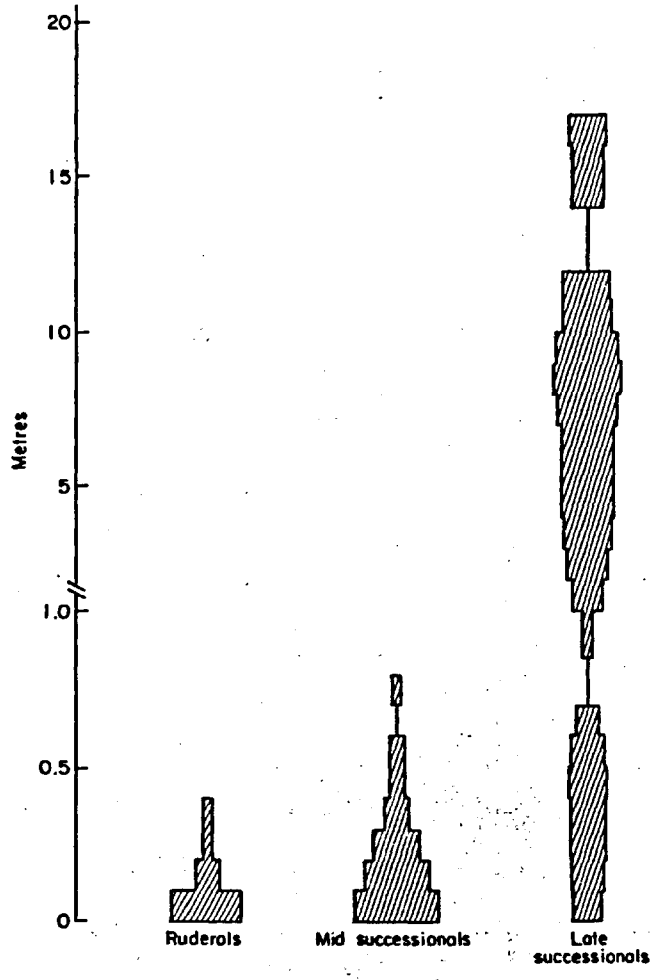


Figure 5. Spatial diversity profiles for the vegetation. (Note: scale change on vertical axis.)

The species accumulation curves for the insects in the Young Field over two seasons are shown in Fig. 7 and should be compared with Fig. 1 for the vegetation. The similarities in shape, including the suggestion of a 'ruderal phase' are striking.

α-diversity

The α-diversities of the year's catches of the Coleoptera and Heteroptera of the three sites do not show any major differences (Table 5), but when the dominance diversity curves for samples are examined (Fig. 8) it is noted that the curves become shallower (equitability increases) throughout the succession. In the Woodland site the total number of individuals is high, mainly due to one abundant species (*Kleidocerys resedae*) giving high d values and hence as species richness is slightly greater, diversity is marginally lower, than in the Old Field (Appendix 3). When the samples from the Young Field for the first few months of the succession are considered they have a low species richness, although the small number of individuals early in the season may give a high diversity index. The

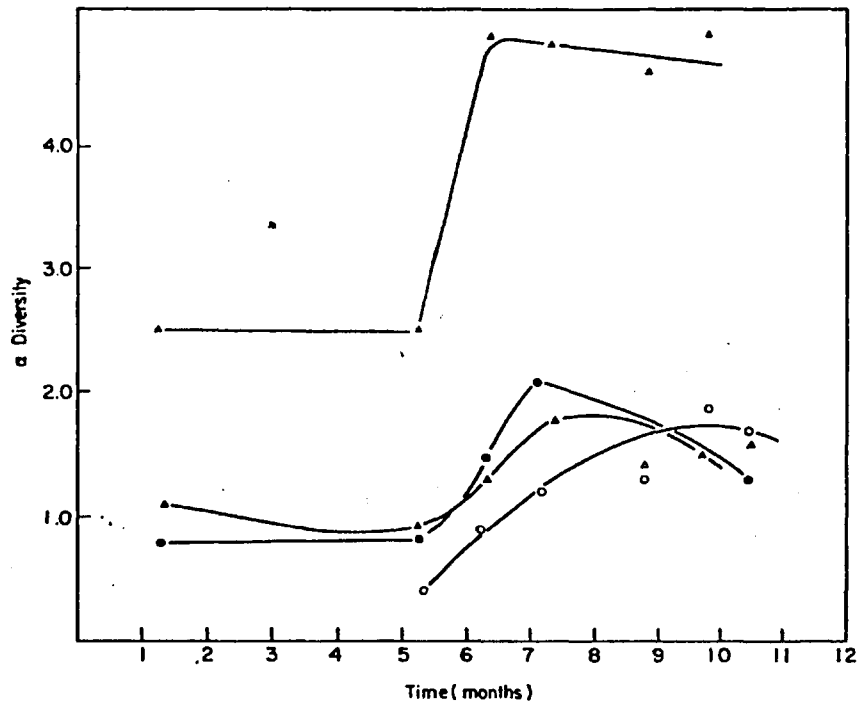


Figure 6. Spatial diversity of vegetation with season. O, Ruderals; ●, Early successionals; △, Mid successionals; ▲, Woodland.

Table 3. Structural diversity of vegetation

Stage/Site	Spatial diversity				Architectural diversity			
	N	S	α	SEα	N	S	α	SEα
Ruderals, Young Field	975	7	1.0	0.42	2205	14	2.0	0.58
Early successionals, Young Field	1204	12	1.9	0.58	4127	14	1.8	0.52
Mid successionals, Old Field	2082	11	1.5	0.49	2969	15	2.1	0.57
Late successionals, Woodland	1696	25	4.2	0.91	4272	20	2.7	0.65

Table 4. Indices of Similarity (I_s) between the Heteroptera and Coleoptera recorded in the different sites between May and October in two seasons

Comparison	Index	
	Heteroptera	Coleoptera
Woodland 1977 v Woodland 1978 (same site)	0.72	0.50
Old Field 1977 v Old Field 1978 (same site)	0.65	0.55
Young Field 1977 v New Young Field 1978 (same age, different site)	0.63	0.54
Young Field 1977 v Young Field 1978 (different age, same site)	0.45	0.45
Young Field 1978 v Old Field 1978 (different age and site)	0.40	0.34
Young Field 1977 v Old Field 1977 (different age and site)	0.18	0.23
New Young Field 1978 v Old Field 1978	0.26	0.21

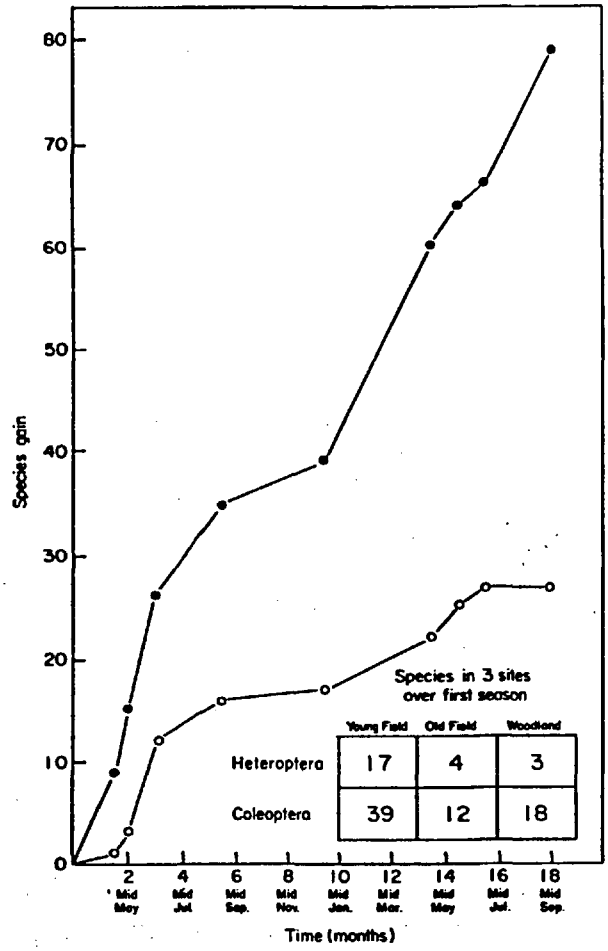


Figure 7. Insect species gain in Young Field over two years. O, Heteroptera; ●, Coleoptera.

Table 5. Total annual diversity (1977) of insects in three sites of different successional age

Site	Heteroptera				Coleoptera			
	N	S	α	SEα	N	S	α	SEα
Young Field	137	16	4.7	1.39	188	40	15.6	3.07
Old Field	118	19	6.4	1.78	378	46	13.8	2.41
Woodland	789	28	5.7	1.20	285	45	15.0	2.71

overall increase in species richness with successional age is shown in Table 6. Thus the α-diversity of the insects studied rises with successional age of the habitat throughout the first 16 months and then remains fairly constant (with seasonal variations), falling only slightly in the Woodland.

Comparison of plant and insect diversities

The above descriptions suggest that whereas plant and insect (Heteroptera and Coleoptera) taxonomic diversities rise together with successional age up to about

Table 6. Species richness of insects in relation to successional age

Site	Stage	1977		1978	
		Heteroptera	Coleoptera	Heteroptera	Coleoptera
Young Field	Ruderal	11	26	12	38
	Early successional			22	61
Old Field	Mid successional	19	46	18	42
Woodland	Late successional	30	50	29	59

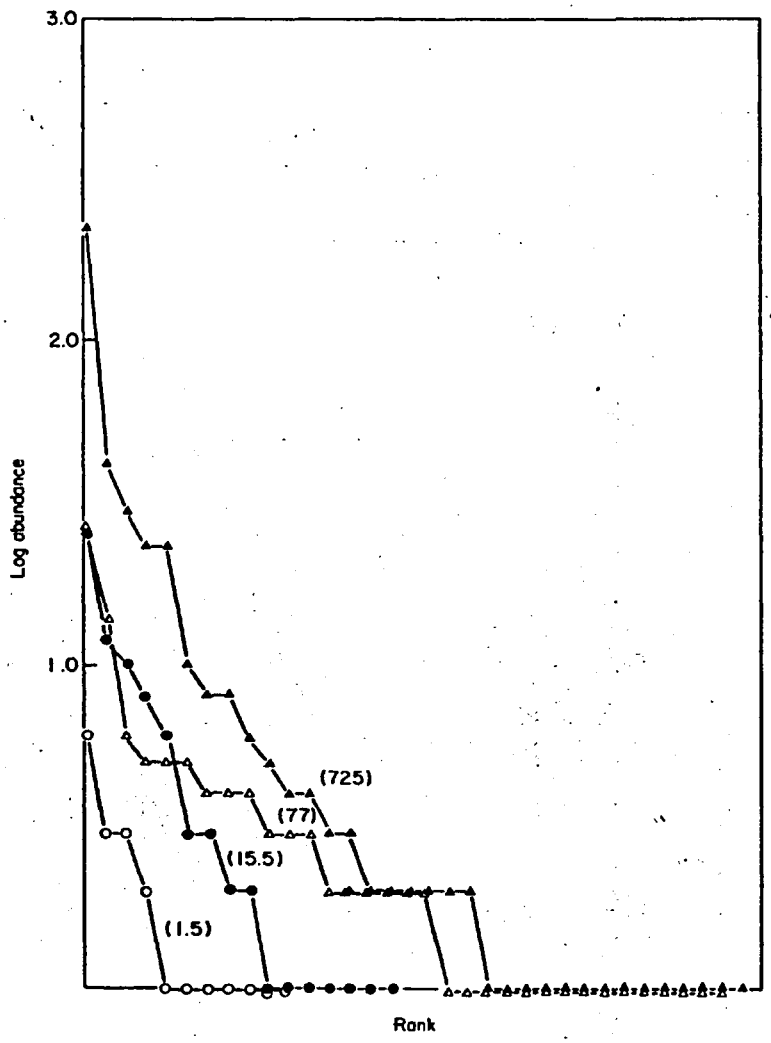


Figure 8. Dominance diversity curves for insects from sites of different successional age (age in months in parenthesis). O, Young Field (age 1.5 months); ●, Young Field (age 15.5 months); Δ, Old Field (age 77 months); ▲, Woodland (age 725 months).

16 months, the diversity of the insects does not fall to the same extent as that of the vegetation in later successional stages. This conclusion is supported by a comparison of the species accumulation curves for the two groups, most easily made by plotting accumulated insect (Heteroptera and Coleoptera) species against accumulated green plant species (Fig. 9). In the Young Field the relationship is virtually linear, the sloped around 45° showing that the rate of accumulation of insect and plant species (excluding fungi) are comparable (correlation coefficient $r=0.99$); there is no asymptote on either axis and this is a reflection of the actual turn-over in species (shown in Fig. 1) by the plants. In the Old Field and Woodland sites the plant species has reached a asymptote, successional change is slower in sites of these ages and so there is very little species turnover. The relatively greater richness of the species of Heteroptera and Coleoptera in these sites is shown by the continued accumulation of species, the differences are particularly striking in regard to the Woodland site.

This relationship is also shown if the mean number of insect species is compared with the mean number of plant species for each site (Fig. 10A). That is, plant and insect taxonomic diversity are not associated in the Woodland site in the way that they are in Young and Old Fields. The diversity of the larger fungi (Appendix 2) appears to show a similar trend to that of these insect groups.

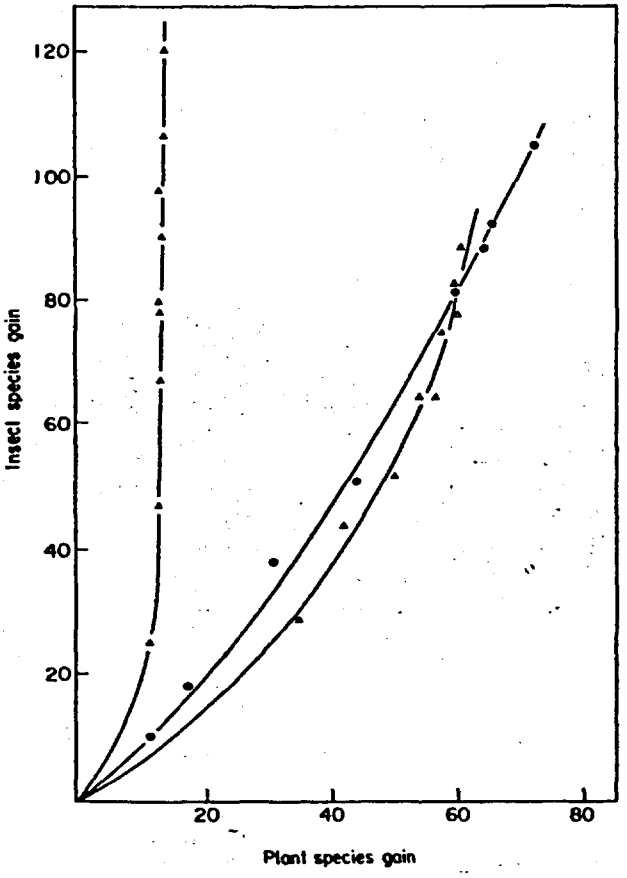


Figure 9. Relationship between insect and plant species accumulation in the three sites over two years. ●, Young Field; △, Old Field; ▲, Woodland.

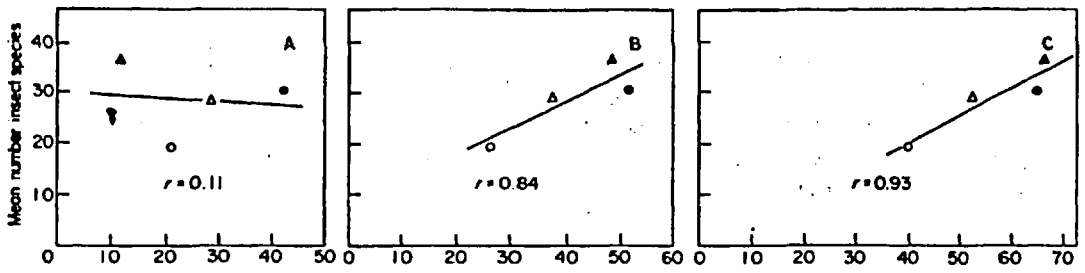


Figure 10. Relationship between number of insect species and A, mean number of plant species; B, with the addition of spatial complexity; C, with the addition of spatial and architectural complexity. O, Ruderals; ●, Early successionals; △, Mid successionals; ▲, Woodland.

If plant structural complexity provides the additional component to explain the high diversity of insects in the later successional stages, then the addition of this to the number of plant species should show a closer correlation for all sites. Spatial complexity was included by incorporating the number of height categories recorded for each sampling occasion to the plant species mean (Fig. 10B). Additionally the other component of structural diversity, architectural diversity, was incorporated in a similar way to give a composite mean for the number of plant species and structures (Fig. 10C). This gave a stronger correlation with the mean number of insect species for each site ($r=0.98$ cf. $r=0.11$).

The details of this relationship may be seen against successional age in Fig. 11.

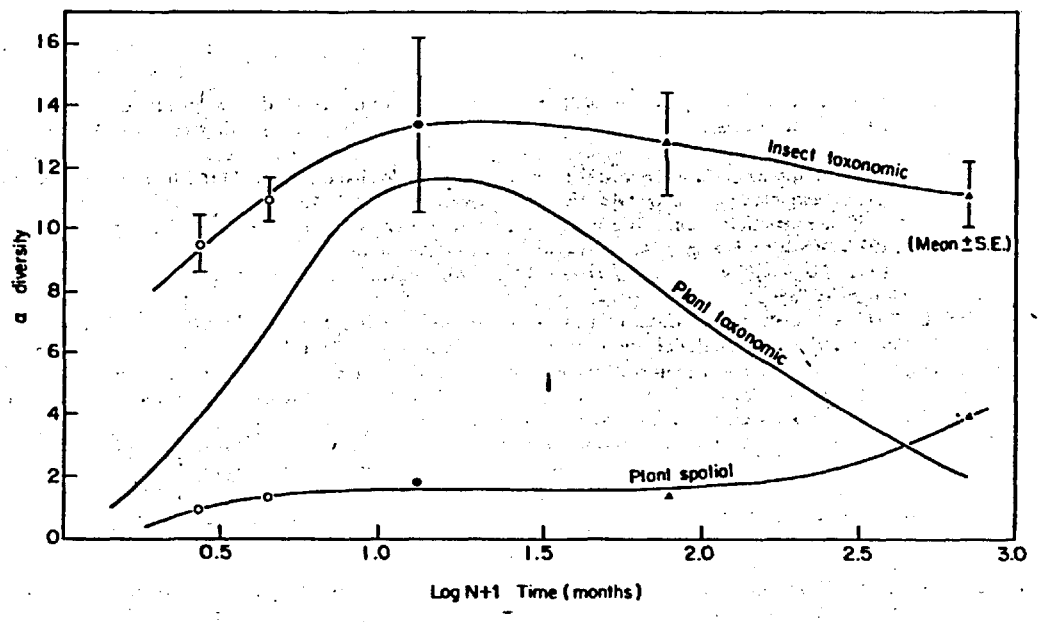


Figure 11. The comparative diversities of plants and insects (Heteroptera and Coleoptera) in relation to log successional age of the habitat. O, Ruderals; ●, Early successionals; △, Mid successionals; ▲, Woodland.

SUMMARY AND CONCLUSION

The taxonomic diversity of the vegetation was seen to rise rapidly in the young sere, but fell after a successional age of about 16 months. The dominance diversity curves are similar to those recorded from Old Fields by Bazzaz (1975), but in the sere he studied, diversity and equitability continued to rise to a greater successional age. Structural complexity, both in terms of spatial and architectural components rose throughout succession.

The taxonomic diversity of the Heteroptera and adult Coleoptera rose proportionally with the taxonomic diversity of the plants in the early seral stages, but in the Woodland stage this fell though not to the same extent as the vegetation. We conclude that Murdoch *et al.* (1972) were correct in associating insect diversity with plant taxonomic diversity in the early seral stages, but in plant communities that are approaching the climax stage their structural attributes become increasingly important, as postulated by Lawton (1978).

ACKNOWLEDGEMENTS

We are most grateful to those colleagues who assisted us with some of the identification of particular groups: Dr P. Hammond (Staphylinidae), Dr C. Johnson (Ptilliidae: *Atomaria, Acrotrichis* spp.), Mr E. E. Green (larger fungi), Mr G. McGavin (Mirid nymphs), Dr J. Bates & Mr J. Kitchenside (Bryophytes), Drs N. Bell & A. Morton (Gramineae); the bulk of the identifications were made by ourselves and one of us (TRES) was largely responsible for Heteroptera and Coleoptera identifications. Several persons kindly assisted us with sampling and sorting our catches, especially Miss E. Mason, Mrs M. Reese and Mr P. Thompson, whilst Dr D. R. Strong critically reviewed the manuscript.

REFERENCES

BAKER, R. R., 1978. *Evolutionary Ecology of Animal Migration:* 1012 pp. London: Hodder & Stoughton.

BAZZAZ, F. A., 1975. Plant species diversity in old field successional ecosystems in southern Illinois. *Ecology, 56:* 485–488.

FEENY, P., 1976. Plant apparency and chemical defense. In J. W. Wallace & M. J. Mansell (Eds), *Biochemical Interaction between Plants and Insects. Recent Advances in Phytochemistry: 10:* 1–40.

FINDLEY, J. S., 1978. Phenetic packing as a measure of faunal diversity. *American Naturalist, 107:* 580–584.

HARPER, J. L., 1977. *Population Biology of Plants:* 892 pp. London: Academic Press.

HORN, H. F., 1971. *The Adaptive Geometry of Trees:* 144 pp. Monographs in Population Biology. New Jersey: Princeton University Press.

JAMES, F. C., 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bulletin, 83:* 215–236.

KARR, J. R., 1968. Habitat and avian density on strip-mined land in east central Illinois. *Condor, 70:* 348–357.

KARR, J. R. & JAMES, F. C., 1974. Eco-morphological configurations and convergent evolution in species and communities. In M. L. Cody & J. M. Diamond (Eds), *Ecology and Evolution of Communities:* 258–288. Cambridge, Massachusetts & London: Harvard University Press.

LAWTON, J. H., 1978. Host-plant influences on insect diversity: the effects of time and space. In L. A. Mound & N. Waloff (Eds), *Diversity of Insect Faunas. Symposium of the Royal Entomological Society of London, 9:* 105–125.

MACARTHUR, R. H., 1960. On the relative abundance of species. *American Naturalist, 94:* 25–36.

MACARTHUR, R. H. & MACARTHUR, J. W., 1961. On bird species diversity. *Ecology, 42:* 594–598.

MAY, R. M., 1976. Patterns in multi-species communities. In R. M. May (Ed.), *Theoretical Ecology:* 142–162. Oxford: Blackwells.

MURDOCH, W. W., EVANS, F. C. & PETERSON, C. H., 1972. Diversity and pattern in plants and insects. *Ecology, 53:* 819–829.

PIANKA, E. R., 1970. On r- and K- selection. *American Naturalist, 104:* 592–597.

RECHER, H. F., 1969. Bird species diversity and habitat diversity in Australia and North America. *American Naturalist, 103:* 75–80.

RICKLEFS, R. E., 1978. *Ecology,* 861 pp. London: Nelson.

SOUTHWOOD, T. R. E., 1977a. Habitat, the templet for ecological strategies? *Journal of Animal Ecology, 46:* 337–365.

SOUTHWOOD, T. R. E., 1977b. The stability of the trophic milieu, its influence on the evolution of behaviour and of responsiveness of trophic signals. *Colloques Internationaux du C.N.R.S., No. 265:* 471–493.

SOUTHWOOD, T. R. E., 1978. *Ecological Methods,* 2nd ed.: 524 pp. London: Chapman & Hall.

STRONG, D. R. & LEVIN, D. A., 1979. Species richness of plant parasites and growth form of their hosts. *The American Naturalist, 113* (7).

TANSLEY, A. G., 1939. *The British Islands and Their Vegetation, 1.* Cambridge University Press.

TAYLOR, L. R., KEMPTON, R. A. & WOIWOOD, I. P., 1976. Diversity statistics and the log-series model. *Journal of Animal Ecology, 45:* 255–272.

VAN VALEN, L., 1965. Morphological variation and width of ecological niche. *American Naturalist, 99:* 377–390.

APPENDIX 1

Trellis diagram of Sørensen's Indices of Similarity for taxonomic composition of the vegetation (bryophytes, pteridophytes and flowering plants)

Age months	Month and year	Sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1.5	May 77	1																		
3.0	July 77	2	0.53																	
6.0	Sept 77	3	0.42	0.53																
13.5	May 78	4	0.28	0.46	0.63															
15.5	July 78	5	0.21	0.34	0.43	0.75														
18.5	Sept 78	6	0.14	0.30	0.50	0.56	0.61													
73	May 77	7	0.15	0.18	0.28	0.28	0.35	0.37												
76	July 77	8	0.11	0.04	0.32	0.23	0.36	0.36	0.64											
78	Sept 77	9	0.10	0.04	0.40	0.27	0.32	0.34	0.58	0.75										
85	May 78	10	0.09	0.07	0.20	0.31	0.41	0.44	0.70	0.70	0.70									
88	July 78	11	0.10	0.11	0.27	0.37	0.42	0.52	0.66	0.65	0.69	0.74								
90	Sept 78	12	0.09	0.15	0.26	0.44	0.41	0.41	0.73	0.70	0.77	0.75	0.71							
720	May 77	13	0.09	0.06	0.04	0.04	0.03	0.05	0.09	0.11	0.05	0.05	0.05	0.05						
723	July 77	14	0.11	0.06	0.04	0.04	0.04	0.05	0.10	0.12	0.06	0.05	0.05	0.05	0.84					
725	Sept 77	15	0.10	0.06	0.04	0.04	0.04	0.05	0.09	0.12	0.05	0.05	0.05	0.05	0.90	0.94				
732	May 78	16													0.84	0.88	0.82			
734	July 78	17													0.95	0.89	0.95	0.89		
737	Sept 78	18													0.80	0.94	0.89	0.74	0.84	

Young Field 1977 / 1978

Old Field 1977 / 1978

Woodland 1977 / 1978

<0.10

APPENDIX 2

Basic taxonomic diversity and indices for the vegetation of the three sites

Successional age months	Sampling date	No. sampling point	N	S	α	SEα	d	Sampling date	No.	N	S	α	SEα	d
Seed bank	=Apr.		48	6	1.8	0.88								
1.5	May 1977	450	133	11	2.8	0.99	0.50	Apr./May	450	56	10	3.5	1.37	0.33
2.25	May/Jun.	225	124	13	3.7	1.19	0.44	Jun.	225	224	17	4.3	1.19	0.16
3.25	Jun./Jul.	225	394	27	6.6	1.45	0.28	Jul.	225	451	24	5.5	1.27	0.20
4.5	Jul./Aug.	225	182	23	7.0	1.73	0.40							
5.25	Aug.	225	393	37	10.0	1.92	0.27	Aug./Sep.	225	334	28	7.3	1.59	0.19
6.25	Sep.	225	349	37	10.5	2.02	0.18	Sep./Oct.	225	389	33	8.6	1.74	0.17
9.75	Jan. 1978	225	364	32	8.5	1.73	0.49							
13.75	May	180	376	46	13.8	2.40	0.35							
14.75	Jun.	180	495	45	12.0	2.09	0.32							
15.75	Jul.	180	410	47	13.7	2.36	0.20							
17.25	Aug.	180	491	42	11.0	1.97	0.15							
18.25	Sep.	180	421	31	7.7	1.59	0.23							
73	May 1977	180	380	34	9.0	1.80	0.33							
74	May/Jun.	90	262	28	7.9	1.76	0.28							
75	Jun./Jul.	180	567	34	7.9	1.55	0.31							
76	late Jul.	180	430	25	5.8	1.32	0.38							
77	Aug.	225	662	26	5.4	1.19	0.38							
78	Sep.	225	741	28	5.8	1.22	0.30							
81	Jan. 1978	225	373	31	8.0	1.67	0.43							
85	Apr./May	225	449	32	7.9	1.60	0.33							
86	Jun.	225	582	34	7.9	1.54	0.28							
87	Jul.	225	527	30	6.9	1.43	0.28							
88	Aug./Sep.	225	695	33	7.2	1.42	0.25							
89	Sep./Oct.	225	627	32	7.1	1.42	0.22							
720	May 1977	450	359	11	2.1	0.72	0.51							
721	May/Jun.	450	410	11	2.1	0.70	0.44							
722	Jun./Jul.	225	457	8	1.4	0.54	0.42							
723	Jul./Aug.	225	455	8	1.4	0.54	0.39							
724	Aug.	225	507	8	1.3	0.52	0.35							
726	Sep.	270	468	9	1.6	0.58	0.38							
732	May 1978	225	331	8	1.5	0.58	0.54							
733	Jun.	225	394	10	1.9	0.65	0.46							
734	Jul.	225	465	10	1.8	0.63	0.41							
735	Aug.	225	416	8	1.4	0.55	0.43							
736	Sep.	225	453	9	1.6	0.58	0.41							
Fungal fruiting bodies		No. m²												
7	Oct. 1977	27.0	8.1	2	0.4	0.29	0.88							
79	Oct. 1977	27.0	5.0	2	1.2	1.23	0.80							
720	Oct. 1977	27.0	8.9	8	2.1	0.88	0.47							

APPENDIX 3

Basic taxonomic diversity data and indices for the insects (Heteroptera and Coleoptera) of the three sites

Successional age Months	Sampling date	N	S	α	SEα	d	Sampling date	N	S	α	SEα	d
1.5	May 1977	20	10	8.0	3.84	0.30	May 1978	71	18	7.8	2.34	0.21
2.0	May/Jun.	19	11	10.9	5.40	0.21	May/Jun.	97	26	11.6	2.95	0.37
4.0	Jul.	152	29	10.6	2.44	0.24	Jul.	68	24	13.2	3.68	0.12
6.0	Sep.	124	27	10.6	2.56	0.44	Sep.	236	31	9.5	2.04	0.42
10.0	Jan. 1978	10	8	18.6	15.16	0.20						
13.5	May	127	41	21.0	4.58	0.39						
14.5	Jun.	114	28	11.9	2.85	0.24						
15.5	Jul.	42	14	7.4	2.64	0.26						
18.5	Sep.	213	38	13.5	2.67	0.32						
73	May 1977	90	29	14.8	3.68	0.20						
74	May/Jun.	96	28	13.3	3.29	0.26						
76	Jul.	68	26	15.4	4.19	0.18						
78	Sep.	109	31	14.5	3.38	0.26						
81	Jan. 1978	129	18	5.7	1.61	0.58						
85	May	50	24	18.1	5.54	0.24						
86	Jun.	86	17	6.4	1.91	0.44						
87	Jul.	23	7	5.4	1.71	0.43						
89	Sep.	175	26	8.5	2.01	0.47						
720	May 1977	177	30	10.4	2.31	0.15						
721	May/Jun.	210	32	10.5	2.24	0.09						
722	Jul.	215	46	17.9	3.31	0.22						
724	Sep.	420	36	9.4	1.82	0.54						
728	Jan. 1978	54	9	3.1	1.25	0.70						
732	May	230	33	10.6	2.21	0.24						
733	Jun.	205	27	8.3	1.91	0.49						
734	Jul.	172	35	13.3	2.79	0.23						
736	Sep.	327	35	9.9	1.97	0.68						