STUDIES ON THE POPULATION DYNAMICS, PHOTOPERIODISM, AND FLIGHT BEHAVIOUR OF THE CABBAGE WHITEFLY, ALEYRODES BRASSICAE (WLK.) HOMOPTERA: ALEYRODIDAE

BY

EMMANUEL UCHECHUKU IHEAGWAM, B.Sc (U.N.N.), M.Sc (LOND.), D.I.C.

Thesis submitted for the Ph.D degree,
University of London

Imperial College of Science & Technology
Silwood Park
Ascot
Berks

September 1976

ABSTRACT

The population parameters of the cabbage whitefly, Aleyrodes brassicae (Wlk.), have been estimated under controlled laboratory conditions. The capacity of the populations to increase was assessed in relation to leaf age, variety, and species of Cruciferae.

Leaf age had no effect upon adult survival. Young leaves were more favourable for both total and maximum fecundities. Fecundity and longevity were influenced by the species of host plant, but these differences did not extend to varieties.

Life-tables have been prepared from weekly fecundity and survival rates at three constant temperatures. Temperature and longevity were inversely related. The intrinsic rate of increase was generally higher at higher temperatures because of faster rate of development and early attainment of maximum fecundity.

Rates and temperature thresholds of development of immature stages were determined. High larval density prolonged the mean development time. Both longevity and fecundity decreased with increased adult density. Virgin females reared on Mustard lived longer and laid more eggs than mated females.

Reproductive diapause was shown to be a function of photoperiod. With LD 14:10 and a temperature of 20°C, 100% diapause occurred. Continuous light (LD 24:0) and a temperature of 25°C respectively prevented diapause.

The critical photoperiod at 15°C was LD $15\frac{3}{4}:8\frac{1}{4}$ with 60% diapause. The photoperiodic cues were monitored by the egg stage and instars I, II, and early III. Chilling facilitated diapause termination.

Flight behaviour of winter and summer females was assessed in the laboratory. Both morphs responded differently in their ability to take-off with age. Take-off and flight of summer morphs were enhanced by mature leaves and food deprivation respectively.

The mean durations of first flights were 14.42 minutes (range 0.57 to 133.67) for winter morphs and 0.31 minute (range 0.03 to 1.13) for summer morphs. The mean rates of climb in the first five seconds of the first flights were 12.57 cm/sec. (range 5 to 21) for winter morphs and -8.92 cm/sec. (range -20 to 7) for summer morphs.

TABLE OF CONTENTS

GENERAL INTRODUCTION

The cabbage whitefly, Aleyrodes brassicae (Wlk.), was stated by Walker (1852) to be possibly a variety of the Chelidonium whitefly. Haupt (1935) and Trehan (1940) have both indicated that brassicae is a synonym of proletella. Since recent authors have used brassicae, it will be used in this investigation for the sake of consistency.

The cabbage whitefly, A. brassicae, is a pest of considerable importance in the southern counties, it occurs sporadically in the midlands, but is almost unknown in the north and in Scotland.

In Europe the greenhouse whitefly, Trialeurodes vaporariorum, is the most important pest in the family Aleyrodidae. In tropical and subtropical countries whitefly are important on a number of crops e.g. citrus (Aleurocanthus woglumi, Dialeurodes citri, Aleurothrixus flocossus), sugar cane (Aleurolobus barodensis, Neomaskellia bergii), coconuts and cashew (Aleurodicus cocosi). On cotton, tobacco, cassava, and pepper, Bemisia tabaci is a pest both in its own right (Mound, 1965c) and as a virus vector (Tarr, 1951; Beck and Chant, 1958). The cabbage whitefly, A. brassicae, has not been reported as a virus vector and it failed to transmit a mossaic disease of broccoli (Caldwell and Prentice, 1942).

Adults and larval stages of the cabbage whitefly, A. brassicae, feed on the undersurfaces of leaves by inserting their stylets into the plant's tissues. Butler (1938) alleged that A. brassicae damages its host plant by the removal of starch and sugar. Peairs (1947) also considered the loss of the sap as the cause of the damage. Mathur (1941) attributed the damage to nitrogen starvation but Husain and Trehan (1942) found higher total nitrogen in infested plants.

The honey dew secreted by adults and immature stages of the cabbage whitefly, A. brassicae, does not only impede photosynthesis but also proves an excellent growth medium for such fungi as Cladosporium herbarum and Alternaria sp.

Different types of host association can be found among the Aleyrodidae. Two species are almost certainly monophagus, Siphoninus immaculata on Hedera and Tetralicia ericae on Erica. At the other extreme are A. fragariae, polyphagous on many herbs and shrubs in Europe, and B. tabaci which is found breeding on a very wide range of host plants. Husain and Trehan (1933) list 44 host species in 12 families of dicotyledons from the Punjab; Avidov (1956) lists 49 host species in 17 families, and the host records in the Nigerian Federal Department of Agricultural Research refer to 29 genera in 10 families.

Some whitefly have a host range which is basically limited to plants of known botanical affinity such as Pealius quercus on Corylaceae and Fagaceae. In other species the host range is not associated with botanical relationship e.g. Aleurotrachelus jelinekii on Viburnum tinus and Arbutus unedo. These two plants belong to widely different families but have hard evergreen leaves. A similar relationship exists between the host plants of A. brassicae, but the leaves are soft.

A. brassicae shows seasonal developmental rhythm which synchronizes with regular variations in environment during the course of the year. In summer, new host plants are cultivated and the overwintering ones produce new foliage. The mean daily temperature at this time is generally near the optimum for A. brassicae and consequently breeding is at its height. The number of generations produced per annum is variable depending on the sum of effective temperatures and availability/suitability of food plants. The generations overlap considerably.

In general, the inability of insects to stand low temperatures during growth and morphogenesis has given rise to specific resting stages in their life cycle. El-Khidir (1963) pointed out that the last generation of *A. brassicae* which emerges in autumn, does not engage in breeding activity. Butler (1938) attributed this cessation of breeding to low winter temperature. However, temperature is only one of the various factors of environment that regularly change during the course of the season. Other factors include humidity and the quality/quantity of food source. But the most reliable signal is that provided by the seasonal change in the day-length, the course of which is not subject to chance fluctuation during the year. It may well be that the short-day in autumn rather than the low temperature is the environmental signal that triggers cessation of breeding in *A. brassicae*.

El-Khidir (1963) observed seasonal dimorphism in *A. brassicae* and studied their daily flight rhythm in the field. The summer morphs are sexually mature on emergence and usually fly from the old lower leaves to the fresh top leaves of the plant. Williams (1935) and Butler (1938) observed mass distribution flight of *A. brassicae* in autumn and early winter.

This thesis represents a study of *A. brassicae* with special reference to:

(i) The population growth statistics on various host plants at constant temperatures;

(ii) Longevity and fecundity of mated and virgin females, larval and adult density effects, rates and temperature thresholds of development of the immature stages;

(iii) Photoperiodism as the environmental factor that induces reproductive diapause; and

(iv) Flight behaviour of the seasonal morphs in the laboratory.

The cabbage whitefly, *A. brassicae*, was chosen for study not only because it is a pest of crucifers, but also the great economic importance of its close relatives in tropical, subtropical, and temperate countries. Its availability all the year round, high population growth rate, and ease of rearing make it an excellent insect for laboratory and indeed field studies.

SECTION Ia: STUDIES ON THE POPULATION DYNAMICS OF THE CABBAGE WHITEFLY, *A. BRASSICAE*, ON DIFFERENT HOST PLANTS

A. INTRODUCTION

Insect/plant association has been in existence for millions of years and the association continues evolving (Southwood, 1972). Consequently much work has been done on their biological relationships (e.g. Davidson, 1925; Painter, 1936; Trouvelot *et al*, 1933; Kennedy, 1953).

The more specialised the association of insects with their food source, the greater is the insects' dependence upon the plant. The dependence is usually influenced by the vicissitudes of changing biochemical composition of the insects' diet resulting from the plants' interaction with the environment.

Host acceptance by many phytophagous insect species is known to be strongly influenced by the presence of 'token substances'. The crucifers contain the best known example of 'token substance' - mustard oil which occurs both in a free form as well as in glucosidal combination. Mustard oils may play an important role in the association between *A. brassicae* and the crucifers.

Extensive work has shown that different species and varieties of host plants can have great effects on the longevity, fecundity rate, and population growth of the insects feeding on them. The webworm, *Hyphantra cunea* (Drury), is larger and lays about 10 times as many eggs when the larvae are reared on the best host plants as compared with less favourable plants (Bohm, 1960). Adults of the grasshopper *Melanoplus bivittatus* (Say) tested on 29 different types of plants, produced nearly 8 times as many eggs on some plants as on others (Tauber *et al*, 1945). The egg output may vary with the species of plant, even if these belong to the same genus. Thus the fecundity of the Colorado beetle, *Leptinotarsa decemlineata* (Say), varies from an average of 35 eggs/batch when the food plant is *Solanum* *edinense* to zero when the food plant is *S. commersonii* (Trouvelot and Grison, 1935). Within the same species different varieties of food plant influence egg production, as when the chinch bug, *Blissus leucopterus* (Say), is fed on different varieties of sorghum (Dahms *et al*, 1936). The cabbage whitefly, *A. brassicae*, can live and breed on some varieties of *Brassica oleracea* e.g. spring cabbage and purple sprouting broccoli but not on *B. campestris* (Butler, 1938).

Different parts of the same plant under different conditions and at different seasons vary in their biochemical composition. This variation affects the fecundity and the longevity of the insects feeding on them. Van Emden and Bashford (1971) found that with increasing age, Brussels Sprout plants become less suitable for the cabbage aphid, *Brevicoryne brassicae* (L.), and much less suitable for the green peach aphid, *Myzus persicae* (Sulzer). Kennedy and Booth (1951) observed that the growing and senescing leaves of certain plants were more susceptible to the aphids *M. persicae* and *Aphis fabae* than the mature green leaves. The fecundity of the cabbage aphid, *B. brassicae*, decreased with leaf age whereas that of the green peach aphid, *M. persicae*, increased (Van Emden, 1969b). The oviposition rate of the greenhouse whitefly, *T. vaporariorum*, declines with leaf age (Hussey and Gurney, 1959).

Living species exhibit a great diversity of patterns of such life history features as total fecundity, maximum longevity and statistical schedules of reproduction and death (Cole, 1954). The rate of increase of any species of insect is determined by the intrinsic rate of increase (r_m) and the restrictions imposed on the intrinsic rate by the environment. The intrinsic rate of increase depends on fecundity rate, speed of development, and longevity.

Some authors have used the intrinsic rate of increase to compare the effect of various environmental conditions on different species. Slobodkin (1962) pointed out its use in delimiting the physical conditions under which organisms are able or unable to survive; Lamb (1961) used it to compare the population growth of the cabbage aphid, *B. brassicae*, on different host plants; and Messenger (1964a) as a measure of population growth as well as index of the effectiveness of parasite. DeLoach (1974) compared three aphid species on the basis of their intrinsic rate of increase.

Among the Homoptera, very many publications are available on life tables and intrinsic rates of increase of aphids e.g. the green peach aphid, *M. persicae* (Barlow, 1962); potato aphid, *Macrosiphum euphorbiae* (Thomas) (Barlow, 1962); spotted alfalfa aphid, *Therioaphis trifolii* (Monell) (Messenger, 1964b); the black bean aphid, *A. fabae*, the vetch aphid, *Megoura viciae*, and biotypes of pea aphid, *Acyrthosiphon pisum* (Milne, 1971); the black bean aphid, *A. fabae*, and the pea aphid, *A. pisum* (Frazer, 1972; Siddiqui *et al*, 1973); cereal aphids, *Metopolophium dirhodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.) (Dean, 1974).

Despite the importance of some whitefly notably *B. tabaci* and *T. vaporariorum* as pests, there seems to be no published work on the life tables and population growth statistics of the aleyrodids.

Since one of the primary objectives of investigating the biology of insect pests of economic importance is to determine how rapidly the insect population will grow, the main aims of the work described in this section were to determine the effects of

i. leaf age,

ii. varieties of *Brassica oleracea*;

iii. species of *Brassica*, and

iv. temperature on longevity, fecundity rate, and population growth statistics of the cabbage whitefly, *A. brassicae*. The life table and population statistics of the greenhouse whitefly, *T. vaporariorum*, were also computed for comparison with those of the cabbage whitefly.

B. MATERIALS AND METHODS

1. Plant types

The following experimental plants were selected:

(a) *Brassica oleracea* (var. Earliest)
(b) *B. oleracea* (var. Large Blood Red)
(c) *B. oleracea* (var. June Star)
(d) *B. oleracea* (var. Golden Acre)
(e) *B. oleracea* (var. Purple Sprout)
(f) *B. alba* Mustard
(g) *B. rapa* Turnip

Seeds were obtained from Suttons Seeds Ltd., Reading, Berkshire.

Plants were grown in 10 cm pots. The soil used in all cases was John Innes 1 (J.1). Plants were raised in glasshouses under natural day-length in summer and artificial lighting by fluorescent tubes connected to time switch to ensure 16 hr light in autumn and winter.

Since the total nitrogen of Brussels Sprout plants decrease after a peak at 6-9 weeks (Van Emden and Bashford, 1971), only plants within this age range were used in all experiments.

2. Assessment of leaf age

The arbitrary scale of leaf types described by Kennedy and Booth (1950) for classifying leaves by age was used:

(a) Unfurled leaves but paler than the darkest green leaves were treated as young leaves.

(b) The darkest green and most glossy leaves were treated as mature leaves.

3. Leaf cages

Clip-on leaf cages were made from rings of perspex (2 cm. inner diameter, 2.5 cm. outer diameter, and 1 cm. high). Each cage was provided with a tightly fitting but detachable lid covered with Terylene muslin.

4. Whitefly culture

Laboratory cultures of cabbage whitefly were started with over-wintering females collected from field plots of Brussels Sprout in Silwood Bottom. Cultures were maintained on Brussels Sprout (var. Irish Elegance) enclosed in cages (45 cm. x 45 cm. x 45 cm.) with muslin walls and kept in rooms held at 25°, 20° and 15°C respectively. Lighting was provided by an array of fluorescent tubes and a 16 hr photoperiod was maintained. Cultures were renewed monthly during which old host plants were discarded, cages cleaned, and new cultures set up. Regular availability of newly emerged adults was ensured throughout the duration of the experiment.

5. Host preference

(a) Variety

Eight potted plants of each of the four varieties of cabbage were selected. Each plant was pruned down to two young leaves and inserted through a hole in the cork into a tube (7.5 cm. high and 2.5 cm. diameter) containing tap water. Non-absorbent cotton was used to keep the plants erect. The plants were arranged in a cage (45 cm. x 45 cm. x 45 cm) with muslin walls, in a completely randomized design (Cochran and Cox, 1957) and were approximately at the same height and non-overlapping. About 200 newly emerged female and male whitefly were released into the cage. The source of light was a set of fluorescent tubes above the cage and the temperature was 20°C.

After 48 hrs the experiment was stopped and records of the number of eggs laid on the various plants were taken and subjected to analysis of variance. Differences between the mean number of eggs were compared using Duncan's new multiple range test (Steel and Torrie, 1960).

(b) Species

The method used was similar to that described above for the varieties.

6. Leaf age experiments

To study the effect of leaf age on fecundity, longevity, and statistical schedules of reproduction and death, one newly emerged female and one male were reared throughout their life either on young or on mature leaves. They were confined on the undersurface of the respective leaf types by means of leaf cages which were supported with forked sticks. Cardon dioxide applied from "Sparklets Corkmaster" was used to anaesthetise the insects during handling.

Daily egg counts were made with the aid of the "ZEISS" hand lens. Occasionally females sat over the eggs making it difficult for them to be seen and counted. However, with a gentle blow from the mouth, the females were displaced and eggs rendered visible.

Insects were transferred to new leaves of the same physiological age usually daily at 25°, every other day at 20°, and at 4 day intervals at 15°C. To effect the transfer, insects were induced to withdraw their stylets from the leaf tissues by prodding them gently with the edge of a small tube into which they hopped. This regular transfer of insects ensured accurate counting of eggs and also reduced any undesirable effect of high egg density on oviposition. Any male that was accidentally lost or that died before the female, was replaced. The record was completed with the death of the female.

7. Construction of life tables

Population performance on the leaf and plant types was assessed by constructing life tables at each temperature regime. For experimental convenience, figures for the mean developmental periods and the age - specific fecundity of the adults were determined separately. Mortality of immature stages was negligible except, however, at very high densities.

Life tables were constructed using the method outlined by Andrewartha and Birch (1954).

The developmental cycle and adult life were divided into weekly intervals. Egg laying and death were assumed to occur at the mid-point in each week (Howe, 1953b). For example, the duration of development at 20°C was 3 weeks and oviposition by adults commenced in their first week of life. These eggs were assumed laid at 3.5 weeks.

In the life tables,

x is the age of whitefly,

lx is the proportion of whitefly still alive at age x,

m_x is the total eggs laid per female in the age interval x, divided by 2, because the sex ratio of the cabbage whitefly is 1:1.

lxm_x is the expected female offspring of an average female at age x.

$\sum lxm_x$ is the expected lifetime production of female offspring for a newborn female. This quantity is called the net reproductive rate (Ro).

$\sum m_x$ is the expected reproduction of a female that lived through all of the age groups in the table. This quantity is the gross reproductive rate (G.R.R.).

8. Calculation of intrinsic rate of natural increase (r_m)

Using the values of lx and m_x, the intrinsic rate of increase can be calculated by iterative substitution of values of r_m in the equation of Birch (1948):

$$\sum e^{-r_m x}\, lx\, m_x = 1$$

In practice both sides of the equation are usually multiplied by e^k. Thus,

$$e^7 \sum e^{-r_m x}\, lx\, m_x = e^7$$

$$\sum e^{7-r_m x}\, lx\, m_x = 1096.6$$

The values of r_c calculated from the formula

$$r_c = \frac{\log e\ Ro}{Tc}$$

were taken as possible values of r_m and then two provisional values arbitrarily selected on either side of them, differing in the second decimal place.

The values

$r_m x$

$7 - r_m x$

$e^{7-r_m x}$

$e^{7-r_m x}\, lx\, m_x$ were calculated using the Hewlett-Packard HP 45 calculator.

The values of $\sum e^{7-r_m x}\, lx\, m_x$ departed from 1097 by an extent depending on how close the trial r_m is to the true value. The true r_m was found graphically by plotting the two provisional r_m's against their sums

(Birch, 1948; Watson, 1964; Southwood, 1968). The values of r_m derived by interpolation were taken to the third decimal place and this was considered appropriate for detecting slight differences between leaf and plant types.

9. Generation Time (T)

The mean duration of a generation is the mean time from birth of parents to birth of offspring. It is calculated from the equation:

$$T = \frac{\log_e R_o}{r_m}$$

10. Finite nett rate of natural increase (λ)

This is the number of multiplications per female per week. It is defined by the equation:

$$\lambda = e^{r_m}$$

11. Population growth curves (theoretical approach)

λ increases in a geometric manner, hence the population growth resulting from it is said to show a geometric population growth.

Curves for various values of λ for different leaf and plant types under different temperature regimes were drawn to illustrate how small differences in the values of λ could cause enormous differences in the numbers that would be reached after several weeks.

C. RESULTS

1. Preference for varieties of cabbage

A summary of the results is shown in Table 1(a) and the analysis of variance in Table 1(b). Table 1(c) is the comparison of mean number of eggs by Duncan's new multiple range test.

The highest mean number of eggs was laid on Large Blood Red (101.67) and the lowest on Golden Acre (37.5).

The variance ratio~~s~~ (F) for effects of variety was not significant. The differences between the means were also not significant.

2. Longevity and fecundity on young and mature leaves of cabbage varieties at 25°, 20°, and 15°C

(a) Longevity and age-specific survival rates (lx)

Longevity of *A. brassicae* females on young and mature leaves of the varieties is presented as mean longevity (Table 2 and Fig. 1(b)) and as age-specific survival rates (Tables 10-21 and Figs. 2-6). The average time for the populations to reach 50% mortality (LT_{50}) is shown in Table 3.

The mean longevity results increased with decreasing temperature. Analysis of variance showed that the effect of leaf age on longevity was significant at all three constant temperatures ($p < .01$ at 25°, $p = .05$ at 20°, $p < .01$ at 15°C) (see Tables 4a, b; 5a, b; and 6a, b).

The variance ratio (F) for effect of variety was significant ($p = .01$) only at 25°C.

Comparison of mean longevities by Duncan's new multiple range test showed that at 25°C the value on Large Blood Red was significantly different ($p = .05$) from the values on June Star and Earliest both of which

Table 1(a): Number of eggs laid by *A. brassicae* on four varieties of cabbage in a varietal preference experiment

	Varieties			
	Earliest	Large Blood Red	June Star	Golden Acre
Replicates	No. of eggs			
1	86	58	59	10
2	102	30	20	29
3	86	18	144	24
4	92	426	37	15
5	78	22	74	79
6	75	56	33	68
Total	519	610	367	225
$\bar{x}$	86.5	101.67	61.17	37.5

Table 1(b): Analysis of variance for Table 1(a)

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Varieties	3	14385.8	4795.27	0.67 (N.S.)
Residual	20	142415.2	7120.76	
Total	23	156801		

N.S. denotes not significant

Table 1(c): Comparison of varietal means by Duncan's new multiple range test

Value of p	2	3	4	5
Significant Studentized Range (SSR)	2.95	3.10	3.18	3.25
Least Significant Range (LSR)	101.63	106.80	109.55	111.96

Ranked means

Golden Acre	June Star	Earliest	Large Blood Red
37.50	61.17	86.50	101.67

Any two values underscored by the same line are not significantly different. Any two values not underscored by the same line are significantly different (p = .05).

do not differ but differ significantly ($p = .05$) from the value on Golden Acre (Table 4(c)).

At 20°C, the values on Earliest, Large Blood Red, and June Star were not significantly different but were significantly higher ($p = .05$) than the value on Golden Acre (Table 5(c)).

At 15°C, the mean longevities on Earliest and Large Blood Red were not significantly different. They differed significantly ($p = .05$) from values on June Star and Golden Acre (Table 6(c)).

The time taken for the populations to reach 50% mortality increased with decreasing temperature with the exception of a few odd cases (June Star and Golden Acre at 20°C).

Survival at all temperatures was longer on young leaves than on mature leaves except on Earliest at 25°C and on June Star at 20°C where it was equal.

At 25°C, there was no difference between the survival rates on all young leaves (3 weeks) except on Golden Acre (2 weeks).

On mature leaves it was longest on Earliest (3 weeks), followed by Large Blood Red and June Star (2 weeks respectively) and shortest on Golden Acre (1 week).

Survival on young leaves of Earliest and Large Blood Red at 20°C was longer (4 weeks respectively) than at 25°C, but shorter on young leaves of June Star (2 weeks), and equal on Golden Acre.

Mature leaves of Earliest and Large Blood Red had the same survival time (3 weeks respectively) June Star (2 weeks), and Golden Acre (1 week).

At 15°C, survival times on young leaves were 12 weeks on all varieties except June Star (11 weeks).

On mature leaves it was longest on Large Blood Red and Golden Acre (11 weeks respectively) and shortest on Earliest and June Star (8 weeks respectively).

The times taken to reach 50% mortality on the leaf types of all varieties at different temperatures were subjected to analysis of variance. The variance ratios (F) for leaf age and for variety effects were not significant and the differences between the mean times were not significant by Duncan's new multiple range test.

At all temperatures the survivorship curves (lx) on young leaves were higher than those on mature leaves with occasional overlapping of the two. The shapes of the lx curves at 25° and 20°C were similar and correspond to Slobodkin's type IV (Slobodkin, 1962) in which mortality acted early in the life of the adults. At 15°C, the lx curves were of type I, with mortality acting on the old individuals.

(b) <u>Fecundity and age-specific fecundity rate</u> (m_x)

Fecundity was consistently higher on young than on mature leaves of all varieties at the three constant temperatures. On both leaf types, fecundity increased with decreasing temperature. The results at different temperatures are compared in Table 2.

At 25°C, the mean numbers of eggs laid on young leaves of Earliest and Large Blood Red were highest (63.1 and 62.6 respectively) and least on Golden Acre (24.9).

On mature leaves, Earliest had the greatest mean number of eggs (34.5) while Golden Acre had the lowest (19.5) (Table 7(a)).

Figure 1(a). Mean fecundity of A. brassicae reared on young and mature leaves of four varieties of cabbage at 25°, 20°, and 15°C.

(b). Mean longevity of A. brassicae females reared on young and mature leaves of four varieties of cabbage at 25°, 20°, and 15°C.

Vertical lines indicate standard deviation.

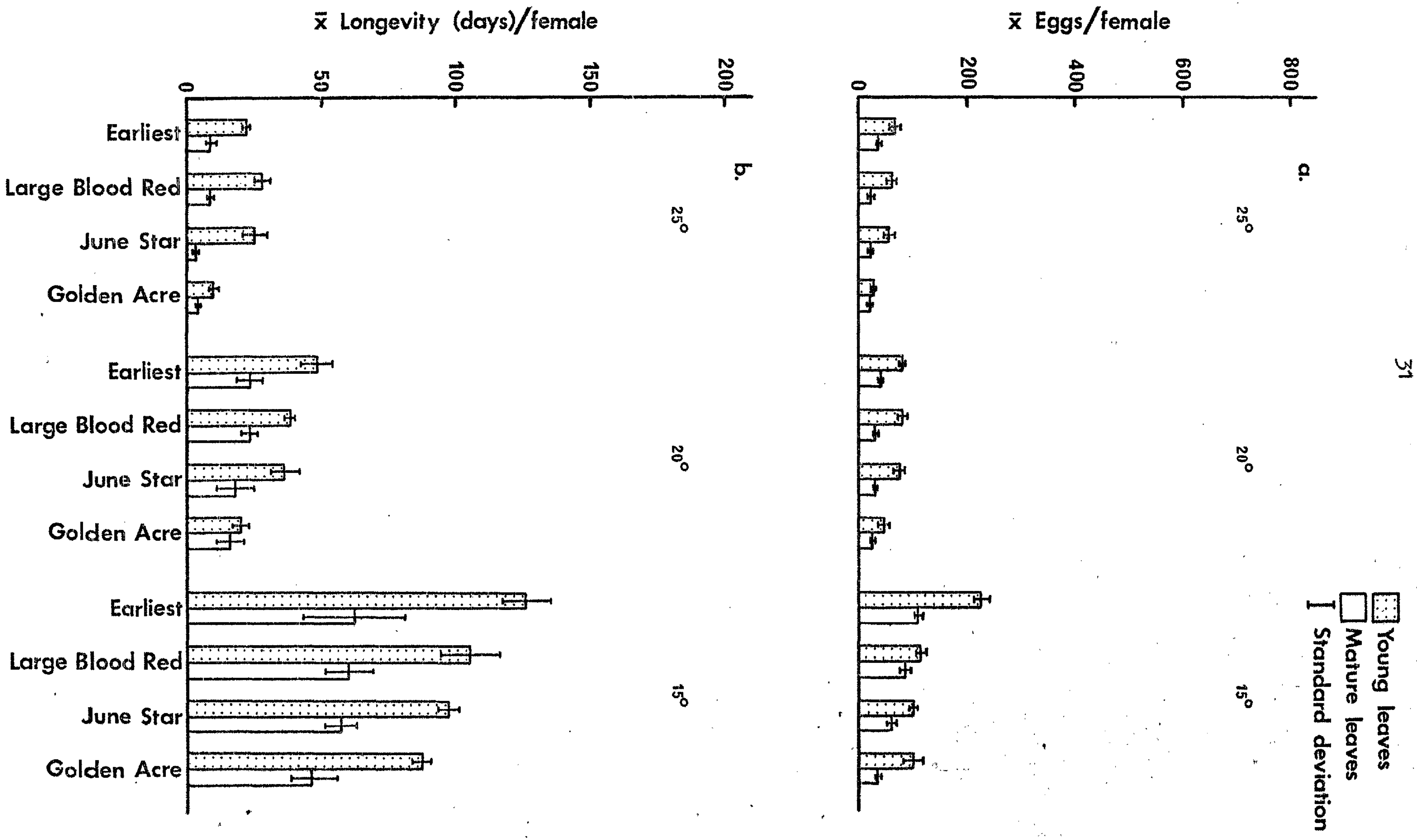

x̄ Eggs/female
0
200
400
600
800
a.
x̄ Longevity (days)/female
0
50
100
150
200
b.
25°
20°
15°
Earliest
Large Blood Red
June Star
Golden Acre
Earliest
Large Blood Red
June Star
Golden Acre
Earliest
Large Blood Red
June Star
Golden Acre
Young leaves
Mature leaves
Standard deviation

Table 2: Mean fecundity and longevity of *A. brassicae* females reared on young and mature leaves of four varieties of cabbage at 25°, 20° and 15°C.

Host plant (variety)		25°C		20°C		15°C	
		Leaf types					
		Young	Mature	Young	Mature	Young	Mature
Earliest	No. of females	11	10	10	11	16	11
	$\bar{x}$ no. of eggs/♀	63.1±6.04	34.5±5.36	80.6± 5.26	42.2±7.79	224.3±13.92	108.9± 8.01
	$\bar{x}$ longevity (days)/♀	21.9±1.17	15.8±1.84	48.0± 5.58	28.3±5.25	126 ± 9.65	82.4±19.23
Large Blood Red	No. of females	10	8	12	10	7	7
	$\bar{x}$ no. of eggs/♀	62.6±9.42	21.8±3.56	78.8±10.29	31.9±3.7	115.5± 8.09	83.9± 8.68
	$\bar{x}$ longevity (days)/♀	27.8±2.88	19.2±1.42	37.8± 2.69	22.0±7.74	105.8±10.99	80.4± 9.50
June Star	No. of females	10	9	10	15	11	8
	$\bar{x}$ no. of eggs/♀	55.3±9.49	19.8±2.36	77.0± 7.60	28.5±3.50	101.2± 7.54	58.1± 8.29
	$\bar{x}$ longevity (days)/♀	25.7±4.92	13.3±0.40	36.5± 5.17	20.7±7.03	97.7± 4.50	57.0± 6.22
Golden Acre	No. of females	10	10	10	10	8	10
	$\bar{x}$ no. of eggs/♀	24.9±4.5	19.5±2.61	44.7± 7.9	23.9±4.23	98.0±18.52	37.7± 4.06
	$\bar{x}$ longevity (days)/♀	10.2±1.69	6.6±0.68	19.6± 3.42	16.8±4.68	87.9± 4.94	55.6± 8.36

Table 3: Duration (weeks) for populations of adult *A. brassicae* females to reach 50% mortality level on both young and mature leaves of four varieties of cabbage at three constant temperatures.

Varieties	25°C		20°C		15°C	
	Young	Mature	Young	Mature	Young	Mature
Earliest	3	3	4	3	12	8
Large Blood Red	3	2	4	3	12	11
June Star	3	2	2	2	11	8
Golden Acre	2	1	2	1	12	11

Table 4(a): Longevity of *A. brassicae* females on young and mature leaves of four varieties of cabbage at 25°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	21.9	15.8	37.7	18.85
Large Blood Red	27.8	19.2	47.0	23.50
June Star	25.7	13.3	39.0	19.50
Golden Acre	10.2	6.6	16.8	8.40
Age totals	85.6	54.9	140.5	70.25

Table 4(b): Analysis of variance for Table 4(a).

Source of Variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	117.81	117.81	61.04*
Variety	3	249.24	83.08	43.05*
Residual	3	5.80	1.93	
Total	7	372.85		

* denotes significance at 1% level

Table 4(c): Comparison of varietal means by Duncan's new multiple range test

Value of p	2	3	4	5
Significant Studentized Range (SSR)	4.5	4.5	4.5	4.5
Least Significant Range (LSR)	3.13	3.13	3.13	3.13

Ranked means

Golden Acre	June Star	Earliest	Large Blood Red
8.40	19.50	18.85	23.50

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 5(a): Longevity of *A. brassicae* females on young and mature leaves of four varieties of cabbage at 20°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	48.0	28.3	76.3	38.15
Large Blood Red	37.8	22.0	59.8	29.90
June Star	36.5	20.7	57.2	28.60
Golden Acre	19.6	16.8	36.4	18.20
Age totals	141.90	87.80	229.70	114.85

Table 5(b): Analysis of variance for Table 5(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	365.85	365.85	13.43*
Variety	3	402.01	134.00	4.92 (N.S.)
Residual	3	81.75	27.25	
Total	7	849.61		

* denotes significant at 5% level

N.S. denotes not significant

Table 5(c): Comparison of varietal means by Duncan's new multiple range test

Value of p	2	3	4	5
Significant Studentized Range (SSR)	4.5	4.5	4.5	4.5
Least Significant Range (LSR)	11.75	11.75	11.75	11.75

Ranked means

Golden Acre	June Star	Large Blood Red	Earliest
18.2	28.6	29.9	38.15

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 6(a): Longevity of *A. brassicae* females on young and mature leaves of four varieties of cabbage at 15°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	126.0	82.4	208.4	104.20
Large Blood Red	105.8	80.4	186.2	93.10
June Star	97.7	57.0	154.7	77.35
Golden Acre	87.9	55.6	143.5	71.75
Age totals	417.4	274.8	692.8	346.40

Table 6(b): Analysis of variance for Table 6(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	2437.97	2437.97	39.54*
Variety	3	1316.20	438.73	7.12 (N.S.)
Residual	3	184.97	61.66	
Total	7	3939.14		

* denotes significance at 1% level

N.S. denotes not significant

Table 6(c): Comparison of varietal means by Duncan's new multiple range test

Value of p	2	3	4	5
Significant Studentized Range (SSR)	4.5	4.5	4.5	4.5
Least Significant Range (LSR)	12.5	12.5	12.5	12.5

Ranked means

Golden Acre	June Star	Large Blood Red	Earliest
71.75	77.35	93.10	104.20

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

The variance ratio (F) for leaf age effect was significant ($p = .05$) but that for varietal effect was not significant (Table 7(b)). The differences between the varietal means were not significant by Duncan's new multiple range test.

Results at 20°C followed the trend observed at 25°C (Tables 8a, b).

At 15°C, the variance ratio (F) for leaf age effect was significant ($p = .05$) and the mean fecundity on Earliest was significantly different from those on Large Blood Red, June Star and Golden Acre by Duncan's new multiple range test ($p = .05$) (Tables 9a, b, c).

The age-specific fecundity rates (m_x) (Tables 10-21) are illustrated in Figs. 2-6. Fecundity rate on all varieties at all three constant temperatures reached a peak early in the reproductive periods of the populations, followed by a decline.

Peaks were reached within 2-3 weeks of the onset of oviposition on both young and mature leaves at 25° (Fig. 2) and 20°C (Figs. 3 and 4). But at 15°C, (Figs. 5 and 6) the peaks of m_x on the varieties generally were erratic, occurring in the 3rd week on Earliest, 5th week on Large Blood Red and 9th week on June Star and Golden Acre respectively.

The age-specific fecundity curves were higher on young leaves than on mature leaves in almost all cases. Early in the reproductive periods, m_x curves for both leaf types rose sharply, being quite close to each other at 25°C, but separating gradually with decreased temperature. After peaks had been attained, m_x curves for young and mature leaves separated considerably at 25° and 20°C but closed up again towards the termination of oviposition. However, in some cases e.g. Earliest and

Large Blood Red at 25°C, the curves kept wide apart to the end of oviposition.

A feature common to all the longevity and age-specific curves was the rather abrupt termination of m_x curves. This was because of no obvious post oviposition period as most of the females died with the oviposition of their last batch of eggs.

3. Population growth statistics on young and mature leaves of cabbage varieties at 25°, 20°, and 15°C.

(a) Gross reproductive rate (G.R.R.)

The age-specific fecundity rates (m_x) on young and mature leaves of all four varieties at 25°, 20°, and 15°C are indicated in m_x columns of the life tables (Tables 10-21). The sum of these values which represent the gross reproductive rates are presented in Table 22.

On both young and mature leaves of all varieties, the gross reproductive rates increased with decreasing temperature, the highest values occurring at 15°C.

At all temperatures the gross reproductive rates on young leaves of Earliest were highest (58.2 at 25°C and 111.5 at 15°C) and lowest on young leaves of Golden Acre (44.9 at 25°C and 75.9 at 15°C).

The gross reproductive rate on mature leaves of Earliest was higher than the rates on other varieties except at 25°C where Large Blood Red was highest (36.6 and 52 respectively). Golden Acre had the lowest values (27.8 at 25°C and 33.3 at 15°C).

(b) Net reproductive rate (Ro)

The net reproductive rate (Ro) increased as temperature decreased.

Table 7(a): Fecundity of *A. brassicae* reared on young and mature leaves of four varieties of cabbage at 25°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	63.09	34.50	97.59	48.80
Large Blood Red	62.60	21.75	84.35	42.18
June Star	55.30	19.78	75.08	37.54
Golden Acre	24.90	19.50	44.40	22.20
Age totals	205.89	95.53	301.42	150.71

Table 7(b): Analysis of variance for Table 7(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	1522.42	1522.42	12.48*
Variety	3	766.79	255.60	2.09 (N.S.)
Residual	3	366.06	122.02	
Total	7	2655.27		

* denotes significance at 5% level

N.S. denotes not significant

Table 8(a): Fecundity of *A. brassicae* reared on young and mature leaves of four varieties of cabbage at 20°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	80.60	42.18	112.78	56.39
Large Blood Red	78.83	31.90	110.73	55.37
June Star	77.00	28.47	105.47	52.74
Golden Acre	44.70	23.90	68.60	34.30
Age totals	281.13	126.45	397.58	198.80

Table 8(b): Analysis of variance for Table 8(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	3997.19	3997.19	28.95*
Variety	3	646.00	215.33	1.56 (N.S.)
Residual	3	414.20	138.07	
Total	7	5057.40		

* denotes significance at 5% level

N.S. denotes not significant

Table 9(a): Fecundity of *A. brassicae* reared on young and mature leaves of four varieties of cabbage at 15°C.

Varieties	AGE OF LEAF		Varietal totals	Varietal means
	Young	Mature		
Earliest	224.31	108.91	333.22	166.61
Large Blood Red	115.50	83.88	199.38	99.69
June Star	101.18	58.13	159.31	79.66
Golden Acre	98.00	37.70	135.70	67.85
Age totals	538.99	288.62	827.61	413.81

Table 9(b): Analysis of variance for Table 9(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	7835.65	7835.65	11.37*
Variety	3	11673.77	3891.26	5.65 (N.S.)
Residual	3	2067.54	689.18	
Total	7	21576.96		

* denotes significance at 5% level

N.S. denotes not significant

Table 9(c): Comparison of varietal means by Duncan's new multiple range test

Value of p	2	3	4	5
Significant Studentized Range (SSR)	4.5	4.5	4.5	4.5
Least Significant Range (LSR)	59.07	59.07	59.07	59.07

Ranked means

Golden Acre	June Star	Large Blood Red	Earliest
67.85	79.66	99.69	166.61

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Maximum values were obtained at 15°C (Table 22).

Leaf age affected Ro with higher values on young than on mature leaves (Table 22 and Fig. 7).

Though highest Ro values occurred on Earliest at all temperatures, the differences between the varieties at 25° and 20°C were not particularly striking. At 15°, however, the differences became more apparent with 90.9 on Earliest, 60.9 on Large Blood Red, 48.2 and 47.2 on June Star and Golden Acre respectively.

Similarly, on mature leaves the Ro values were quite close with Earliest and Large Blood Red approximately equal at 15°C (48.9 and 52.3 respectively) and June Star and Golden Acre also approximately equal (21.5 and 25.1 respectively).

(c) Intrinsic rate of natural increase (r_m)

Values of the intrinsic rate of natural increase (r_m) on young and mature leaves of all four cabbage varieties at 25°, 20°, and 15°C are presented in Table 22.

r_m values decreased with decreasing temperature, highest at 25°C and lowest at 15°C.

Leaf age affected the values of r_m. Higher values were consistently recorded on young than on mature leaves at all three constant temperatures.

Among the varieties, highest r_m values were obtained on young leaves of Earliest (1.040 at 25°, .775 at 20°, and .429 at 15°C). The lowest values occurred on Golden Acre at 25°C and 20°C (.903 and .807 respectively). But at 15°C, the r_m on Golden Acre was higher than that on

June Star (.330 and .299 respectively). This was due to a shorter mean generation time (T) on Golden Acre (Table 22).

On mature leaves, Earliest had highest r_m values at all temperatures except at 25°C where Large Blood Red was higher (.921 and .963 respectively). r_m on Golden Acre which was lowest in all cases was, however, higher than r_m on June Star at 15°C for the same explanation given above.

(d) Mean generation time (T)

The mean generation time (T) on varietal young and mature leaves at 25°, 20°, and 15°C are shown in Table 22.

T increased with decreasing temperature, shortest at 25°C and longest at 15°C (Fig. 7).

Leaf age had no outstanding effects on T.

T (in weeks) on young leaves ranged from 3.17 (min.) on Golden Acre - 3.45 (max.) on June Star at 25°C, 4.22 (min.) on Golden Acre - 4.77 (max.) on Large Blood Red at 20°C, and 10.27 (min.) on Earliest - 12.96 (max.) on June Star at 15°C.

On mature leaves the ranges were 2.81 (min.) on Golden Acre - 3.42 (max.) on Earliest at 25°C, 4.46 (min.) on June Star - 4.70 (max.) on Golden Acre at 20°C, and 10.40 (min.) on Earliest - 12.62 (max.) on June Star at 15°C.

(e) Finite rate of increase (λ)

The different values of λ for leaf age and varietal effects at the three constant temperatures are presented in Table 22 and Fig. 7. Since these values were derived from r_m ($\lambda = e^{r_m}$), they followed the trend already described for r_m.

(f) Population growth curves

Values of λ on all varietal young leaves at 25°, 20°, and 15°C ranged from 1.35 (min.) to 2.83 (max.), and on mature leaves from 1.28 (min.) to 2.62 (max.) (Table 23).

Though the differences seem quite small, the sizes of populations resulting from them at any given time differ considerably (Fig. 8). For example, on young leaves of Earliest at 25°C ($\lambda = 2.83$), the size of the population reached in 4 weeks by one female (64 insects) would take about $5\frac{1}{2}$ weeks at 20°C ($\lambda = 2.51$) and about 10 weeks at 15°C ($\lambda = 1.55$).

4. Preference for host plant species

The number of eggs laid on each host plant is shown in Table 23(a). These were subjected to analysis of variance (Table 23(b)) and the means compared by Duncan's new multiple range test (Table 23(c)).

The highest mean (94.88) was recorded on Mustard, followed by Purple Sprout (29.5), and the least (20.25) on Turnip.

The variance ratio (F) for effect of different species was significant ($p = .05$).

The mean number of eggs on Mustard was significantly higher ($p = .05$) than those on Purple Sprout and Turnip. The difference between the mean values on Purple Sprout and Turnip was not significant. Thus, Mustard was the most preferred of the three species.

5. Longevity and fecundity on young and mature leaves of different host plant species at 25°, 20°, and 15°C

(a) Mean longevity and age-specific survival rates (lx)

Tables 24, 25(a), 26(a), 27(a) and Fig. 9(b) show mean longevity

Table 10(a): Life table data for A. brassicae females reared on young leaves of Earliest at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					1.05				1.00			
x	lx	mx	lxmx	xlxmx	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.95	9.32	8.85	22.13	2.63	4.37	79.04	699.54	2.50	4.50	90.20	796.65
3.5	.75	13.47	10.10	35.35	3.68	3.32	27.66	279.37	3.50	3.50	33.12	334.47
4.5	.50	11.33	5.67	25.52	4.73	2.27	9.68	54.88	4.50	2.50	12.18	69.07
5.5	.40	10.83	4.33	23.82	5.78	1.22	3.39	14.67	5.50	1.50	4.48	19.41
6.7	.30	8.25	2.48	16.62	6.83	0.17	1.19	2.94	6.50	0.50	1.65	4.09
7.5	.10	5.00	0.50	3.75	7.88	-0.88	0.41	0.21	7.50	-0.50	0.61	0.30
					Total			1051.61	Total			1223.99

Ro = 31.93

r_m = 1.04

T = 3.33

λ = 2.83

Table 10(b): Life table data for *A. brassicae* females reared on mature leaves of Earliest at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.93				0.92			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
2.5	.81	6.53	5.29	13.23	2.33	4.67	106.70	564.43	2.30	4.70	109.95	581.62
3.5	.75	12.30	9.23	32.31	3.26	3.74	42.10	388.56	3.22	3.78	43.82	404.42
4.5	.60	9.25	5.55	24.98	4.19	2.81	16.61	92.19	4.14	2.86	17.46	96.91
5.5	.45	5.00	2.25	12.38	5.12	1.88	6.55	14.75	5.06	1.94	6.96	15.66
6.5	.30	3.50	1.05	6.83	6.05	0.95	2.59	2.71	5.98	1.02	2.77	2.91
					Total			1062.64	Total			1101.52

$R_o = 23.37$

$r_m = 0.921$

$T = 3.42$

$\lambda = 2.51$

Table 11(a): Life table data for A. brassicae females reared on young leaves of Large Blood Red at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					1.05				1.00			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
2.5	.97	9.65	9.36	23.40	2.63	4.37	79.04	739.85	2.50	4.50	90.02	842.56
3.5	.73	11.15	8.14	28.49	3.68	3.32	27.66	225.16	3.50	3.50	33.12	269.56
4.5	.42	13.20	5.54	24.93	4.73	2.27	9.68	53.62	4.50	2.50	12.18	67.49
5.5	.24	9.00	2.16	11.88	5.78	1.22	3.39	7.32	5.50	1.50	4.48	9.68
6.5	.14	7.65	1.07	6.96	6.83	0.17	1.19	1.27	6.50	0.50	1.65	1.76
7.5	.14	3.50	0.47	3.53	7.88	-0.88	0.41	0.20	7.50	-0.50	0.61	0.30
	Ro	=	26.76		Total			1027.42	Total			1191.35
	r_m	=	1.03									
	T	=	3.19									
	λ	=	2.80									

Table 11(b): Life table data for A. brassicae females reared on mature leaves of Large Blood Red at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.97				0.96			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
2.5	.75	11.00	8.25	20.63	2.43	4.57	96.54	796.49	2.40	4.60	99.48	820.75
3.5	.64	9.15	5.86	20.51	3.40	3.60	36.60	214.47	3.36	3.64	38.09	223.22
4.5	.30	10.00	3.00	13.50	4.37	2.63	13.87	41.62	4.32	2.68	14.59	43.76
5.5	.27	9.60	2.59	14.25	5.34	1.66	5.26	13.62	5.28	1.72	5.58	14.46
6.5	.20	8.50	1.70	11.05	6.31	0.69	1.99	3.39	6.24	0.76	2.14	3.64
7.5	.20	3.75	0.75	5.63	7.28	-0.28	0.76	0.57	7.20	-0.20	0.82	0.61
					Total			1070.16	Total			1106.44

Ro = 22.15

r_m = 0.963

T = 3.22

λ = 2.62

Figure 2: Longevity and age-specific fecundity of *A. brassicae* reared on young and mature leaves of (a) Earliest, (b) Large Blood Red, (c) June Star, (d) Golden Acre at 25°C.

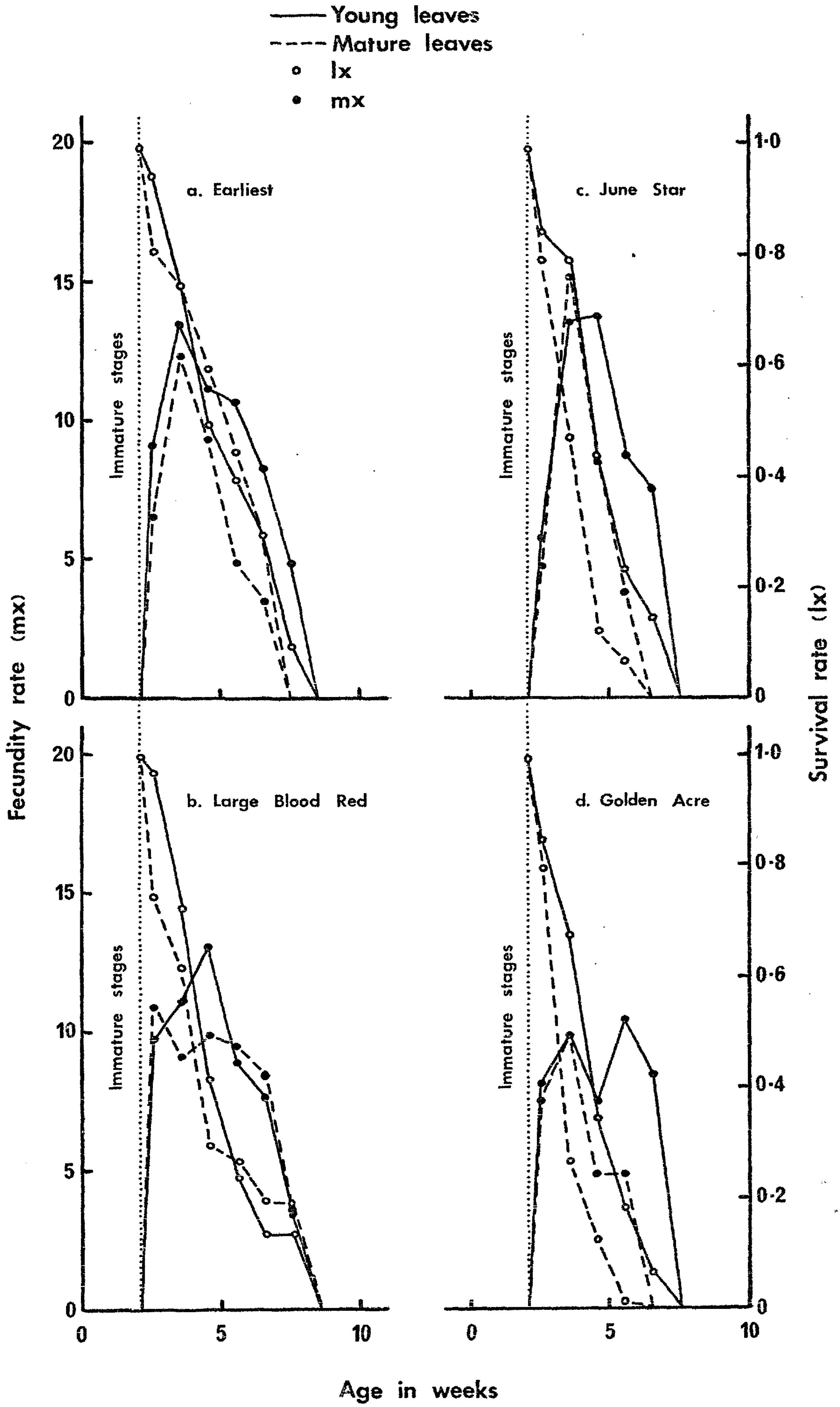

Young leaves
Mature leaves
lx
mx
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
Immature stages
a. Earliest
b. Large Blood Red
c. June Star
d. Golden Acre
0
5
10
15
20
0·2
0·4
0·6
0·8
1·0

Table 12(a): Life table data for A. brassicae females reared on young leaves of June Star at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.94				0.93			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.85	6.13	5.21	13.03	2.35	4.65	104.58	544.89	2.33	4.67	106.70	555.90
3.5	.75	13.76	10.32	36.12	3.29	3.71	40.85	421.61	3.26	3.74	42.10	434.45
4.5	.45	14.08	6.34	28.53	4.23	2.77	15.96	101.18	4.19	2.81	16.61	105.31
5.5	.24	9.00	2.16	11.88	5.17	1.83	6.23	13.47	5.12	1.88	6.55	14.16
6.5	.15	7.75	1.16	7.54	6.11	0.89	2.44	2.82	6.05	0.95	2.59	3.00
	Ro = 25.19				Total			1083.97	Total			1112.82
	r_m = 0.936											
	T = 3.45											
	λ = 2.55											

Table 12(b): Life table data for A. brassicae females reared on mature leaves of June Star at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.81				0.80			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.80	5.05	4.04	10.10	2.03	4.97	144.03	581.87	2.00	5.00	148.41	599.59
3.5	.48	15.50	7.44	26.04	2.84	4.16	64.07	476.69	2.80	4.20	66.69	496.15
4.5	.13	4.75	0.62	2.79	3.65	3.35	28.50	17.67	3.60	3.40	29.96	18.58
5.5	.07	4.00	0.28	1.54	4.46	2.54	12.68	3.55	4.40	2.60	13.46	3.77
					Total			1079.78	Total			1118.09

$Ro = 12.38$

$r_m = 0.806$

$T = 3.12$

$\lambda = 2.24$

Table 13(a): Life table data for *A. brassicae* females reared on young leaves of Golden Acre at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.94				0.93			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
2.5	.85	8.29	7.05	17.63	2.35	4.65	104.58	737.32	2.33	4.67	106.70	752.22
3.5	.68	10.13	6.89	24.12	3.29	3.71	40.85	281.48	3.22	3.78	43.82	301.89
4.5	.35	7.50	2.63	11.84	4.23	2.77	15.96	41.97	4.19	2.81	16.61	43.68
5.5	.19	10.50	2.00	11.00	5.17	1.83	6.23	12.47	5.12	1.88	6.55	3.93
6.5	.07	8.50	0.60	3.90	6.11	0.89	2.44	1.46	6.05	0.95	2.59	1.55
					Total			1074.70	Total			1103.27

$R_o = 19.17$

$r_m = 0.932$

$T = 3.17$

$\lambda = 2.54$

Table 13(b): Life table data for *A. brassicae* females reared on mature leaves of Golden Acre at 25°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.81				0.80			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
2.5	.80	7.74	6.19	15.48	2.03	4.97	144.03	891.53	2.00	5.00	148.41	918.68
3.5	.27	10.08	2.72	9.52	2.84	4.16	64.07	174.27	2.80	4.20	66.69	181.39
4.5	.13	5.00	0.65	2.93	3.65	3.35	28.50	18.53	3.60	3.40	29.96	19.48
5.5	.02	5.00	0.10	0.55	4.46	2.54	12.68	1.27	4.40	2.60	13.46	1.35
					Total			1085.60	Total			1120.90

$R_o = 9.66$

$r_m = 0.807$

$T = 2.81$

$\lambda = 2.24$

Table 14(a): Life table data for *A. brassicae* females reared on young leaves of Earliest at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.78				0.77			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	1	8.18	8.18	28.63	2.73	4.27	71.52	585.05	2.70	4.30	73.70	602.86
4.5	.78	13.19	10.29	46.31	3.51	3.49	32.79	337.37	3.47	3.53	34.12	351.14
5.5	.58	12.42	7.20	39.60	4.29	2.71	15.03	108.21	4.24	2.76	15.80	113.76
6.5	.50	8.84	4.42	28.73	5.07	1.93	6.89	30.45	5.01	1.99	7.32	32.33
7.5	.35	8.49	2.97	22.28	5.85	1.15	3.16	9.38	5.78	1.22	3.39	10.06
8.5	.29	6.63	1.92	16.32	6.63	0.37	1.45	2.78	6.55	0.45	1.57	3.01
9.5	.24	5.88	1.41	13.40	7.41	-0.41	0.66	0.94	7.32	-0.32	0.73	1.02
10.5	.18	4.59	0.83	8.72	8.19	-1.19	0.30	0.25	8.09	-1.09	0.34	0.28
11.5	.10	5.75	0.58	6.67	8.97	-1.97	0.14	0.08	8.86	-1.86	0.16	0.09
	Ro = 37.8				Total			1074.50	Total			1114.55
	r_m = 0.775											
	T = 4.69											
	λ = 2.17											

Table 14(b): Life table data for A. brassicae females reared on mature leaves of Earliest at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.69				0.68			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.97	5.43	5.27	18.45	2.42	4.58	97.51	513.90	2.38	4.62	101.49	534.87
4.5	.73	11.47	8.37	37.67	3.11	3.89	48.91	409.38	3.06	3.94	51.42	430.37
5.5	.43	9.83	4.23	23.27	3.80	3.20	24.53	103.77	3.74	3.26	26.05	110.19
6.5	.25	7.25	1.81	11.77	4.55	2.45	11.59	20.97	4.42	2.58	13.20	23.89
7.5	.23	5.25	1.21	9.08	5.18	1.82	6.17	7.47	5.10	1.90	6.69	8.09
8.5	.23	7.50	1.73	14.71	5.87	1.13	3.10	5.36	5.78	1.22	3.39	5.86
9.5	.23	6.34	1.46	13.87	6.56	0.44	1.55	2.27	6.46	0.54	1.72	2.51
10.5	.07	5.12	0.36	3.78	7.25	-0.25	0.78	0.28	7.14	-0.14	0.87	0.31
	Ro = 24.44				Total			1063.40	Total			1116.09

$Ro = 24.44$

$r_m = 0.684$

$T = 4.67$

$\lambda = 1.98$

Table 15(a): Life table data for *A. brassicae* females reared on young leaves of Large Blood Red at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.75				0.74			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
3.5	.96	6.58	6.32	22.12	2.63	4.37	79.04	499.56	2.59	4.41	82.27	519.94
4.5	.69	14.60	10.07	45.32	3.38	3.62	37.34	375.99	3.33	3.67	39.25	395.27
5.5	.54	12.09	6.53	35.92	4.13	2.87	17.64	115.17	4.07	2.93	18.73	122.29
6.5	.53	10.23	5.42	35.23	4.88	2.12	8.33	45.15	4.81	2.19	8.94	48.43
7.5	.37	6.71	2.48	18.60	5.63	1.37	3.94	9.76	5.55	1.45	4.26	10.57
8.5	.30	5.00	1.50	12.75	6.38	0.62	1.86	2.79	6.29	0.71	2.03	3.05
9.5	.30	3.63	1.09	10.36	7.13	-0.13	0.88	0.96	7.03	-0.03	0.97	1.06
10.5	.25	3.17	0.79	8.30	7.88	-0.88	0.41	0.33	7.77	-0.77	0.46	0.37
					Total			1049.71	Total			1100.98

$R_o = 34.20$

$r_m = 0.741$

$T = 4.77$

$\lambda = 2.10$

Table 15(b): Life table data for *A. brassicae* females reared on mature leaves of Large Blood Red at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.64				0.63			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.85	4.62	3.93	13.76	2.24	4.76	116.75	458.81	2.21	4.79	120.30	472.78
4.5	.78	10.00	7.80	35.10	2.88	4.12	61.56	480.16	2.84	4.16	64.07	499.76
5.5	.48	6.00	2.88	15.84	3.52	3.48	32.46	93.48	3.47	3.53	34.12	98.28
6.5	.48	3.00	1.44	9.36	4.16	2.84	17.12	24.65	4.10	2.90	18.17	26.17
7.5	.35	4.00	1.40	10.50	4.80	2.20	9.03	12.64	4.73	2.27	9.68	13.55
8.5	.30	4.00	1.20	10.20	5.44	1.56	4.76	5.71	5.36	1.64	5.16	6.19
					Total			1075.45	Total			1116.73

Ro = 18.65

r_m = 0.635

T = 4.61

λ = 1.89

Figure 3: Longevity and age-specific fecundity of _A. brassicae_ reared on young and mature leaves of (a) Earliest, (b) Large Blood Red at 20°C.

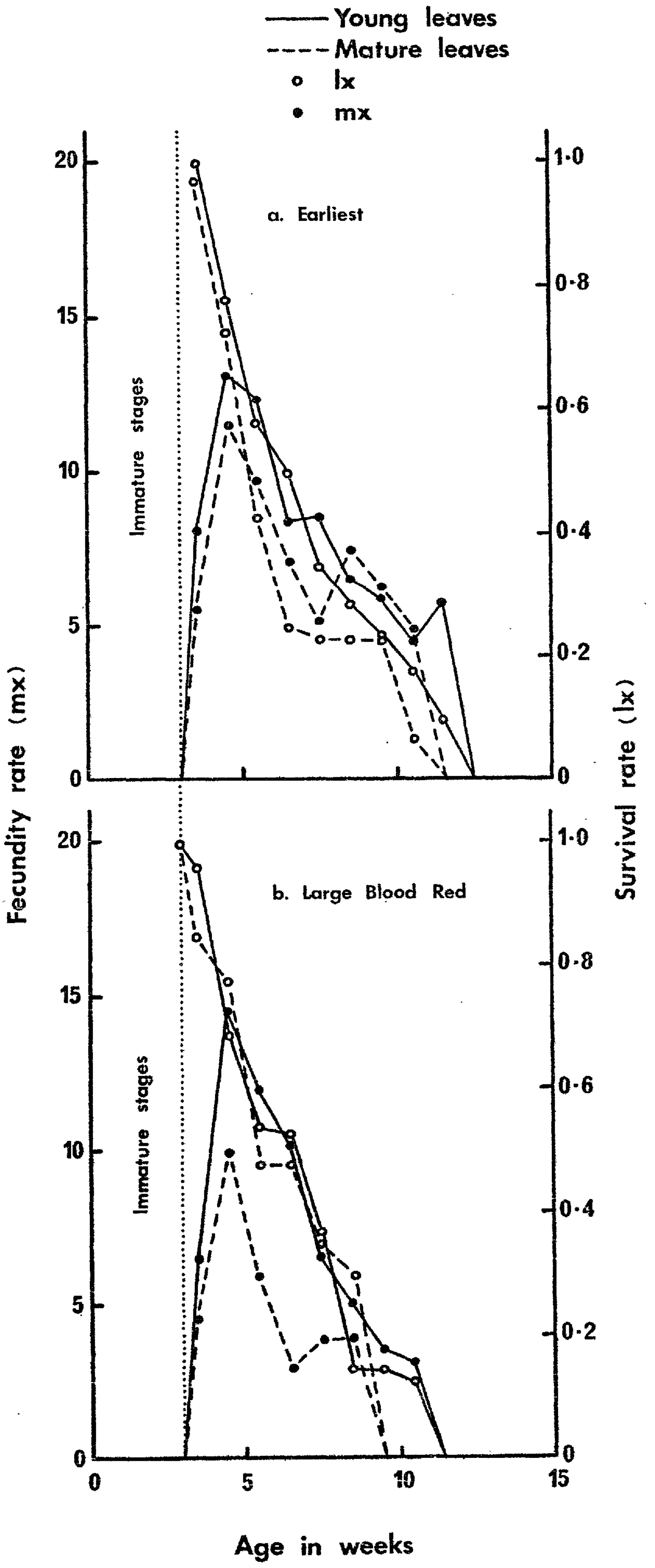

Young leaves
Mature leaves
lx
mx
a. Earliest
b. Large Blood Red
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
0
0·2
0·4
0·6
0·8
1·0
0
5
10
15

Table 16(a): Life table data for A. brassicae females reared on young leaves of June Star at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.72				0.71			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.85	7.68	6.53	22.86	2.52	4.48	88.23	576.17	2.49	4.51	90.92	593.72
4.5	.48	16.86	8.09	36.41	3.24	3.76	42.95	347.45	3.20	3.80	44.70	361.63
5.5	.39	13.06	5.09	28.00	3.96	3.04	20.91	106.41	3.91	3.09	21.98	111.86
6.5	.31	8.17	2.53	16.45	4.68	2.32	10.18	25.74	4.62	2.38	10.80	27.34
7.5	.18	11.02	1.98	14.85	5.40	1.60	4.95	9.81	5.33	1.67	5.31	10.52
8.5	.13	5.25	0.68	5.78	6.12	0.88	2.41	1.64	6.04	0.96	2.61	1.78
9.5	.13	2.50	0.33	3.14	6.84	0.16	1.17	0.39	6.75	0.25	1.28	0.42
10.5	.05	0	0	0	-	-	-	-	-	-	-	-
					Total			1067.61	Total			1107.27

Ro = 25.23

r_m = 0.713

T = 4.53

λ = 2.04

Table 16(b): Life table data for A. brassicae females reared on mature leaves of June Star at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.61				0.60			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.80	5.14	4.11	14.39	2.14	4.86	129.02	530.29	2.10	4.90	134.29	551.93
4.5	.50	10.60	5.30	23.85	2.75	4.25	70.11	371.56	2.70	4.30	73.70	390.61
5.5	.41	8.00	3.28	18.04	3.36	3.64	38.09	124.94	3.30	3.70	40.45	132.67
6.5	.21	6.00	1.26	8.19	3.97	3.03	20.70	26.08	3.90	3.10	22.20	27.97
7.5	.14	3.50	0.49	3.68	4.58	2.42	11.25	5.51	4.50	2.50	12.18	5.97
8.5	.10	2.50	0.25	2.13	5.19	1.81	6.11	1.53	5.10	1.90	6.69	1.67
9.5	.03	2.00	0.06	0.57	5.80	1.20	3.32	0.20	5.70	1.30	3.67	0.22
	Ro	=	14.75		Total			1060.11	Total			1111.04
	r_m	=	0.603									
	T	=	4.46									
	λ	=	1.83									

Figure 4: Longevity and age-specific fecundity of A. *brassicae* reared on young and mature leaves of (a) June Star, (b) Golden Acre at 20°C.

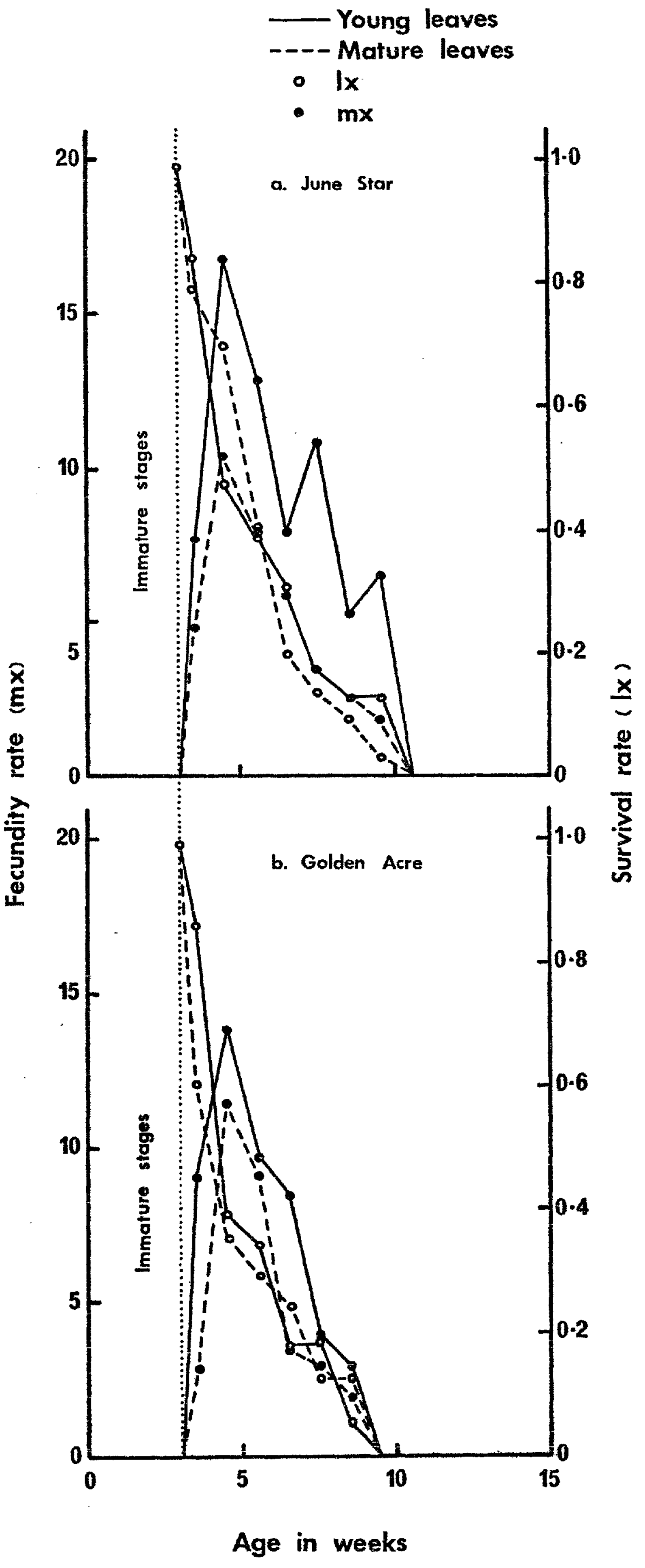

——— Young leaves
- - - - Mature leaves
o lx
• mx
a. June Star
b. Golden Acre
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
0
0·2
0·4
0·6
0·8
1·0
0
5
10
15

Table 17(a): Life table data for A. brassicae females reared on young leaves of Golden Acre at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.71				0.70			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.87	9.16	7.97	27.90	2.49	4.51	90.92	724.65	2.45	4.55	94.63	754.22
4.5	.40	14.01	5.60	25.20	3.20	3.80	44.70	250.33	3.15	3.85	46.99	263.16
5.5	.35	9.83	3.44	18.92	3.91	3.09	21.98	75.60	3.85	3.15	23.34	80.28
6.5	.19	8.50	1.62	10.53	4.62	2.38	10.80	17.50	4.55	2.45	11.59	18.77
7.5	.19	4.00	0.76	5.70	5.33	1.67	5.31	4.04	5.25	1.75	5.75	4.37
8.5	.06	3.00	0.18	1.53	6.04	0.96	2.61	0.47	5.95	1.05	2.86	0.51
					Total			1072.59	Total			1121.31

Ro = 19.57

r_m = 0.705

T = 4.22

λ = 2.02

Table 17(b): Life table data for A. brassicae females reared on mature leaves of Golden Acre at 20°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.49							
x	lx	mx	lxmx	xlxmx	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxmx$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxmx$
3.5	.61	3.04	1.85	6.48	1.72	5.28	196.37	363.28				
4.5	.36	11.50	4.14	18.63	2.21	4.79	120.30	498.05				
5.5	.30	8.21	2.46	13.53	2.70	4.30	73.70	181.30				
6.5	.25	3.50	0.88	5.72	3.19	3.81	45.15	39.73				
7.5	.13	3.00	0.39	2.93	3.68	3.32	27.66	10.79				
8.5	.13	2.00	0.26	2.21	4.17	2.83	16.95	4.41				
					Total			1097.56				

Ro = 9.98

r_m = 0.490

T = 4.70

λ = 1.63

Table 18(a): Life table data for A. brassicae females reared on young leaves of Earliest at 15°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.43				0.42			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	6.19	6.19	46.43	3.23	3.77	43.38	268.52	3.15	3.85	46.99	290.89
8.5	1	10.67	10.67	90.70	3.66	3.34	28.22	301.11	3.57	3.43	30.88	329.45
9.5	1	11.53	11.53	109.54	4.09	2.91	18.36	211.65	3.99	3.01	20.29	233.91
10.5	.96	11.40	10.94	114.91	4.52	2.48	11.94	130.64	4.41	2.59	13.33	145.83
11.5	.94	9.97	9.37	107.78	4.95	2.05	7.77	72.79	4.83	2.17	8.76	82.07
12.5	.94	8.81	8.28	103.52	5.38	1.62	5.05	41.84	5.25	1.75	5.75	47.65
13.5	.94	9.05	8.51	114.84	5.81	1.19	3.29	27.97	5.67	1.33	3.78	32.18
14.5	.85	6.58	5.59	81.10	6.24	0.76	2.14	11.95	6.09	0.91	2.48	13.89
15.5	.76	6.41	4.87	75.51	6.67	0.33	1.39	6.77	6.51	0.49	1.63	7.95
16.5	.68	5.41	3.68	60.70	7.10	-0.10	0.90	3.33	6.93	0.07	1.07	3.95
17.5	.58	5.54	3.21	56.23	7.53	-0.53	0.59	1.89	7.35	-0.35	0.70	2.26
18.5	.50	3.92	1.96	36.26	7.96	-0.96	0.38	0.75	7.77	-0.77	0.46	0.91
19.5	.50	4.54	2.27	44.27	8.39	-1.39	0.25	0.57	8.19	-0.19	0.30	0.69
20.5	.46	3.81	1.75	35.93	8.82	-1.82	0.16	0.28	8.61	-1.61	0.20	0.35
21.5	.38	1.98	0.75	16.18	9.25	-2.25	0.11	0.08	9.03	-2.03	0.13	0.10

Table 18(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.43				0.42			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
22.5	.31	2.11	0.65	14.72	9.68	-2.68	0.07	0.04	9.45	-2.45	0.09	0.06
23.5	.25	1.16	0.29	6.82	10.11	-3.11	0.04	0.01	9.87	-2.87	0.06	0.02
24.5	.23	0.98	0.23	5.52	10.54	-3.54	0.03	0.01	10.29	-3.29	0.04	0.01
25.5	.16	0.80	0.13	3.26	10.97	-3.97	0.02	0	10.71	-3.71	0.02	0
26.5	.07	0.60	0.04	1.11	-	-	-	-	-	-	-	-
					Total			1080.20	Total			1192.17

R_o = 90.91

r_m = 0.429

T = 10.27

λ = 1.55

Table 18(b): Table data for A. brassicae females reared on mature leaves of Earliest at 15°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.38				0.37			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	4.30	4.30	32.25	2.85	4.15	63.43	272.77	2.78	4.22	68.03	292.54
8.5	1	6.30	6.30	53.55	3.23	3.77	43.38	273.29	3.15	3.85	46.99	296.06
9.5	.92	6.27	5.77	54.82	3.61	3.39	29.61	171.17	3.52	3.48	32.46	187.29
10.5	.92	6.91	6.36	66.78	3.99	3.01	20.29	129.03	3.89	3.11	22.42	142.60
11.5	.92	6.46	5.94	68.31	4.37	2.63	13.87	82.41	4.26	2.74	15.49	91.99
12.5	.92	6.68	6.15	76.88	4.75	2.25	9.49	58.35	4.63	2.37	10.70	65.79
13.5	.82	4.22	3.46	46.71	5.13	1.87	6.49	22.45	5.00	2.00	7.39	25.57
14.5	.55	4.75	2.61	37.85	5.51	1.49	4.44	11.58	5.37	1.63	5.10	13.32
15.5	.37	6.76	2.50	38.75	5.89	1.11	3.03	7.59	5.74	1.26	3.53	8.81
16.5	.33	4.39	1.45	23.93	6.27	0.73	2.08	3.01	6.11	0.89	2.44	3.53
17.5	.23	5.05	1.16	20.30	6.65	0.35	1.42	1.65	6.48	0.52	1.68	1.95
18.5	.17	7.00	1.19	22.02	7.03	-0.03	0.97	1.15	6.85	0.15	1.16	1.38
19.5	.12	4.75	0.57	11.12	7.41	-0.41	0.66	0.38	7.22	-0.22	0.80	0.46
20.5	.07	7.50	0.53	10.87	7.79	-0.79	0.45	0.24	7.59	-0.59	0.55	0.29
21.5	.07	2.50	0.18	3.76	8.17	-1.17	0.31	0.06	7.96	-0.96	0.38	0.07

Table 18(b): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.38				0.37			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
22.5	.07	2.50	0.18	4.05	8.55	-1.55	0.21	0.04	8.33	-1.33	0.26	0.05
23.5	.07	2.00	0.14	3.29	8.93	-1.93	0.15	0.02	8.70	-1.70	0.18	0.03
24.5	.07	2.00	0.4	3.43	9.31	-2.31	0.10	0.01	9.07	-2.07	0.13	0.02
	R_o = 48.92 r_m = 0.374 T = 10.40 λ = 1.45				Total			1035.20	Total			1131.75

Figure 5: Longevity and age-specific fecundity of A. brassicae reared on young and mature leaves of (a) Earliest, (b) Large Blood Red at 15°C.

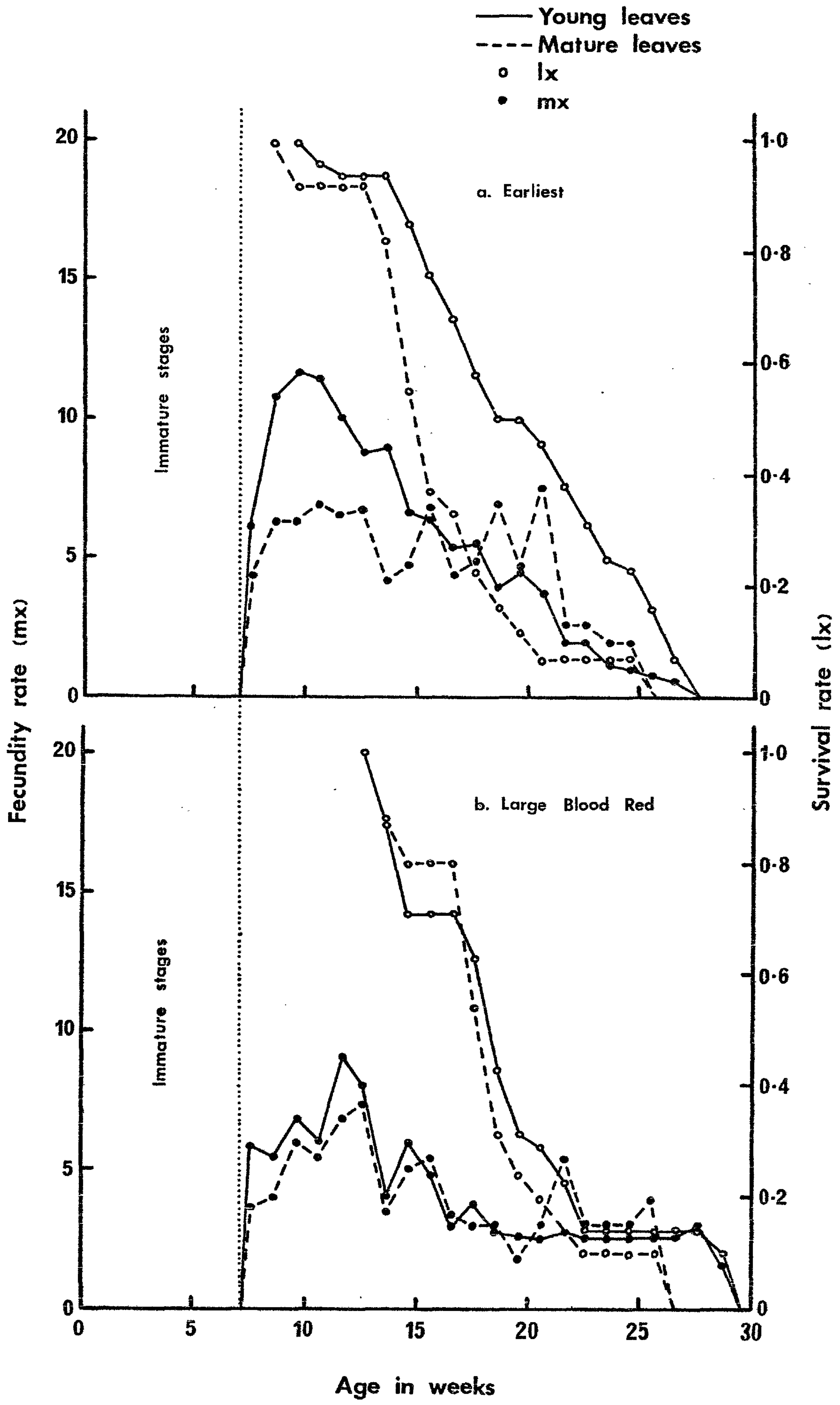

Young leaves
Mature leaves
lx
mx
a. Earliest
b. Large Blood Red
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
25
30
0
5
10
15
20
0
0·2
0·4
0·6
0·8
1·0

Table 19(a): Life table data for A. brassicae females reared on young leaves of Large Blood Red at 15°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.39				0.38			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
7.5	1	5.72	5.72	42.90	2.93	4.07	58.56	334.95	2.85	4.15	63.43	362.84
8.5	1	5.36	5.36	45.56	3.32	3.68	39.65	212.50	3.23	3.77	43.38	232.52
9.5	1	6.71	6.71	63.75	3.71	3.29	26.84	180.12	3.61	3.39	29.67	199.06
10.5	1	5.92	5.92	62.16	4.10	2.90	18.17	107.59	3.99	3.01	20.29	120.10
11.5	1	8.99	8.99	103.39	4.49	2.51	12.30	110.62	4.37	2.63	13.87	124.73
12.5	1	7.87	7.87	98.38	4.88	2.12	8.33	65.57	4.75	2.25	9.49	74.67
13.5	.88	4.07	3.58	48.33	5.27	1.73	5.64	20.19	5.13	1.87	6.49	23.23
14.5	.71	6.00	4.26	61.77	5.66	1.34	3.82	16.27	5.51	1.49	4.44	18.90
15.5	.71	4.70	3.34	51.77	6.05	0.95	2.59	8.65	5.89	1.11	3.03	10.13
16.5	.71	3.00	2.13	35.15	6.44	0.56	1.75	3.73	6.27	0.73	2.08	4.42
17.5	.63	3.68	2.32	40.60	6.83	0.17	1.19	2.75	6.65	0.35	1.42	3.29
18.5	.43	2.79	1.20	22.20	7.22	-0.22	0.80	0.96	7.03	-0.03	0.97	1.16
19.5	.30	2.55	0.77	15.02	7.61	-0.61	0.54	0.42	7.41	-0.41	0.66	0.52
20.5	.29	2.50	0.73	14.97	8.00	-1.00	0.37	0.27	7.79	-0.79	0.45	0.33
21.5	.23	2.75	0.63	13.55	8.39	-1.39	0.25	0.16	8.17	-1.17	0.31	0.20

Table 19(a): Continued

Pivotal age (weeks) x	lx	m_x	l_xm_x	xl_xm_x	Provisional r_m's							
					0.39				0.38			
					r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
22.5	.14	2.50	0.35	7.88	8.78	-1.78	0.17	0.06	8.55	-1.55	0.21	0.07
23.5	.14	2.50	0.35	8.23	9.17	-2.17	0.11	0.04	8.93	-1.93	0.15	0.05
24.5	.14	3.00	0.42	10.29	9.56	-2.56	0.08	0.03	9.31	-2.31	0.10	0.04
25.5	.14	2.50	0.35	8.93	9.95	-2.95	0.05	0.02	9.69	-2.69	0.07	0.02
26.5	.14	2.50	0.35	9.28	10.34	-3.34	0.04	0.01	10.07	-3.07	0.05	0.02
27.5	.14	3.00	0.42	11.55	10.73	-3.73	0.02	0.01	10.45	-3.45	0.03	0.01
28.5	.10	1.50	0.15	4.28	11.12	-4.12	0.02	0	10.83	-3.83	0.02	0
	R_o = 61.92 r_m = 0.387 T = 10.66 λ = 1.47				Total			1064.92	Total			1176.30

Table 19(b): Life table for A. brassicae females reared on mature leaves of Large Blood Red at 15°C and table showing calculations for r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.37				0.36			
x	lx	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
7.5	1	3.60	3.60	27.00	2.78	4.22	68.03	244.92	2.70	4.30	73.70	265.32
8.5	1	3.95	3.95	35.58	3.15	3.85	46.99	185.62	3.06	3.94	51.42	203.10
9.5	1	5.95	5.95	56.53	3.52	3.48	32.46	193.14	3.42	3.58	35.87	213.45
10.5	1	5.40	5.40	56.70	3.89	3.11	22.42	121.07	3.78	3.22	25.03	135.15
11.5	1	6.70	6.70	77.05	4.26	2.74	15.49	103.76	4.14	2.86	17.46	116.99
12.5	1	7.20	7.20	90.00	4.63	2.37	10.70	77.02	4.50	2.50	12.18	87.71
13.5	.87	3.25	2.83	38.21	5.00	2.00	7.39	20.91	4.86	2.14	8.50	24.05
14.5	.80	5.00	4.00	58.00	5.37	1.63	5.10	20.42	5.22	1.78	5.93	23.72
15.5	.80	5.38	4.30	66.65	5.74	1.26	3.53	15.16	5.58	1.42	4.14	17.79
16.5	.80	3.32	2.66	43.89	6.11	0.89	2.44	6.48	5.94	1.06	2.89	7.68
17.5	.54	3.05	1.65	28.88	6.48	0.52	1.68	2.78	6.30	0.70	2.01	3.32
18.5	.31	3.09	0.96	17.76	6.85	0.15	1.16	1.12	6.66	0.34	1.40	1.35
19.5	.24	1.84	0.44	8.58	7.22	-0.22	0.80	0.35	7.02	-0.02	0.98	0.43
20.5	.20	3.00	0.60	12.30	7.59	-0.59	0.55	0.33	7.38	-0.38	0.68	0.41
21.5	.14	5.50	0.77	16.56	7.96	-0.96	0.38	0.29	7.74	-0.74	0.48	0.37

Table 19(b): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.37				0.36			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
22.5	.10	3.00	0.30	6.75	8.33	-1.33	0.26	0.08	8.10	-1.10	0.33	0.10
23.5	.10	3.00	0.30	7.05	8.70	-1.70	0.18	0.05	8.46	-1.46	0.23	0.07
24.5	.10	2.50	0.25	6.13	9.07	-2.07	0.13	0.03	8.82	-1.82	0.16	0.04
25.5	.10	4.00	0.40	10.20	9.44	-2.44	0.09	0.03	9.18	-2.18	0.11	0.05
					Total			993.56	Total			1101.10

$R_o = 52.26$

$r_m = 0.360$

$T = 10.98$

$\lambda = 1.43$

Table 20(a): Life table data for *A. brassicae* females reared on young leaves of June Star at 15°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.29			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	1.28	1.28	9.60	2.25	4.75	115.58	147.95	2.18	4.82	123.97	158.68
8.5	1	2.23	2.23	18.95	2.55	4.45	85.63	190.95	2.47	4.53	92.76	206.85
9.5	1	1.64	1.64	15.58	2.85	4.15	63.43	104.03	2.76	4.24	69.41	113.83
10.5	1	2.08	2.08	21.84	3.15	3.85	46.99	97.75	3.05	3.95	51.94	108.03
11.5	1	3.68	3.68	42.32	3.45	3.55	34.81	128.11	3.34	3.66	38.86	173.32
12.5	1	4.46	4.46	55.75	3.75	3.25	25.79	115.02	3.63	3.37	29.08	129.69
13.5	.99	5.88	5.82	78.57	4.05	2.95	19.11	111.20	3.92	3.08	21.56	125.48
14.5	.77	5.71	4.40	63.80	4.35	2.65	14.15	62.28	4.21	2.79	16.28	71.64
15.5	.73	7.76	5.66	87.73	4.65	2.35	10.49	59.35	4.50	2.50	12.18	68.95
16.5	.68	6.39	4.35	71.78	4.95	2.05	7.77	33.79	4.79	2.21	9.12	39.67
17.5	.48	5.45	2.62	45.85	5.25	1.75	5.75	15.08	5.08	1.92	6.82	17.87
18.5	.36	4.64	1.67	30.90	5.55	1.45	4.26	7.12	5.37	1.63	5.10	8.52
19.5	.36	3.90	1.40	27.30	5.85	1.15	3.16	4.42	5.66	1.34	3.82	5.35
20.5	.36	5.26	1.89	38.75	6.15	0.85	2.34	4.42	5.95	1.05	2.86	5.40
21.5	.33	5.15	1.70	36.55	6.45	0.55	1.73	2.95	6.24	0.76	2.14	3.64

Table 20(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.29			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
22.5	.27	4.50	1.22	27.45	6.75	0.25	1.28	1.57	6.53	0.47	1.60	1.95
23.5	.27	4.66	1.26	29.61	7.05	-0.05	0.95	1.20	6.82	0.18	1.20	1.51
24.5	.24	3.49	0.84	20.58	7.35	-0.35	0.70	0.59	7.11	-0.11	0.90	0.75
	Ro	=	48.20		Total			1087.78	Total			1241.13
	r_m	=	0.299									
	T	=	12.96									
	λ	=	1.35									

Table 20(b): Life table data for *A. brassicae* females reared on mature leaves of June Star at 15°C and table showing calculations of r_m with two provisional r_m's

Pivotal age (weeks)					Provisional r_m's							
					0.25				0.24			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	0.66	0.66	4.95	1.88	5.12	167.34	110.44	1.80	5.20	181.27	119.64
8.5	1	1.67	1.67	14.20	2.13	4.87	130.32	217.64	2.04	4.96	142.59	238.13
9.5	1	1.66	1.66	15.77	2.38	4.62	101.49	168.48	2.28	4.72	112.17	186.20
10.5	1	1.59	1.59	16.70	2.63	4.37	79.04	125.68	2.52	4.48	88.23	140.29
11.5	.93	1.66	1.54	17.75	2.88	4.12	61.56	94.80	2.76	4.24	69.41	106.89
12.5	.83	1.30	1.08	13.49	3.13	3.87	47.94	51.78	3.00	4.00	54.60	58.97
13.5	.75	1.39	1.04	12.57	3.38	3.62	37.34	38.83	3.24	3.76	42.95	44.67
14.5	.57	5.18	2.95	42.81	3.63	3.37	29.08	85.78	3.48	3.52	33.78	99.66
15.5	.45	5.25	2.36	26.85	3.88	3.12	22.65	53.45	3.72	3.28	26.58	62.72
16.5	.45	3.25	1.46	17.70	4.13	2.87	17.64	25.75	3.96	3.04	20.91	30.52
17.5	.45	2.75	1.24	15.88	4.38	2.62	13.74	17.03	4.20	2.80	16.44	20.39
18.5	.33	1.25	0.41	5.09	4.63	2.37	10.70	4.39	4.44	2.56	12.94	5.30
19.5	.22	2.50	0.55	10.73	4.88	2.12	8.33	4.58	4.68	2.32	10.18	5.60
20.5	.22	4.50	0.99	20.30	5.13	1.87	6.49	6.42	4.92	2.08	8.00	7.92
21.5	.22	4.50	0.99	21.29	5.38	1.62	5.05	5.00	5.16	1.84	6.30	6.23

Table 20(b): Continued.

Pivotal age (weeks)					Provisional r_m's							
					0.25				0.24			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
22.5	.17	3.50	0.60	13.39	5.63	1.37	3.94	2.36	5.40	1.60	4.95	2.97
23.5	.17	3.00	0.51	11.99	5.88	1.12	3.06	1.56	5.64	1.36	3.90	1.99
24.5	.12	1.50	0.18	4.41	6.13	0.87	2.39	0.43	5.88	1.12	3.06	0.55
R_o = 21.48					Total			1014.40	Total			1138.64
r_m = 0.243												
T = 12.62												
λ = 1.28												

Figure 6: Longevity and age-specific fecundity of _A. brassicae_ reared on young and mature leaves of (a) June Star, (b) Golden Acre at 15°C.

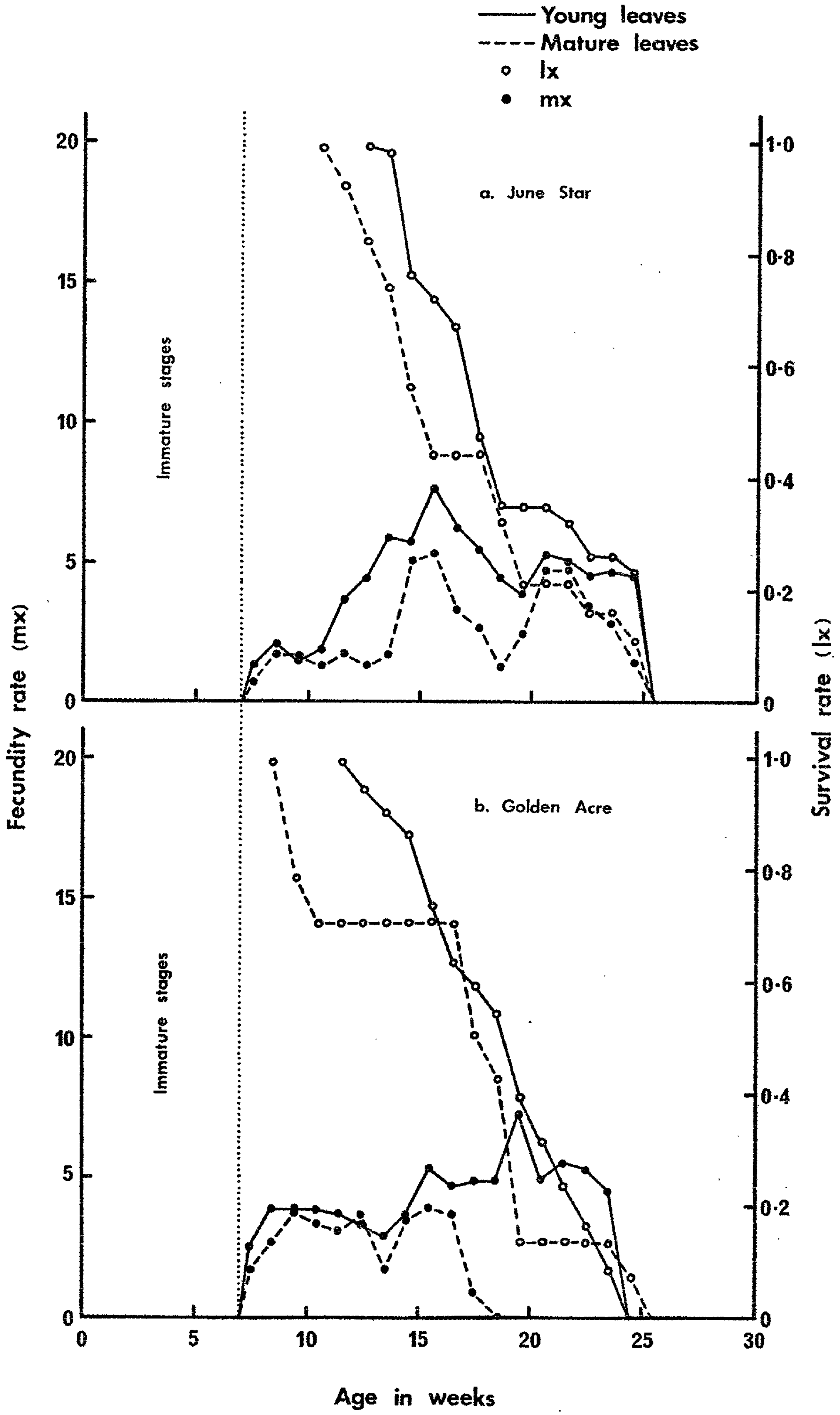

Young leaves
Mature leaves
lx
mx
a. June Star
b. Golden Acre
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
25
30
0·2
0·4
0·6
0·8
1·0

Table 21(a): Life table data for *A. brassicae* females reared on young leaves of Golden Acre at 15°C and table showing calculation of r_m.

Pivotal age (weeks)					Provisional r_m							
					0.33							
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
7.5	1	2.50	2.50	18.75	2.48	4.52	91.84	229.59				
8.5	1	4.05	4.05	34.43	2.81	4.19	66.02	267.39				
9.5	1	3.90	3.90	37.05	3.14	3.86	47.47	185.11				
10.5	1	3.96	3.96	41.58	3.47	3.53	34.12	135.13				
11.5	1	3.77	3.77	43.36	3.80	3.20	24.53	92.49				
12.5	.95	3.29	3.13	39.13	4.13	2.87	17.64	55.20				
13.5	.91	3.10	2.82	38.07	4.46	2.54	12.68	35.76				
14.5	.87	3.80	3.31	48.00	4.79	2.21	9.12	30.17				
15.5	.74	5.26	3.89	60.30	5.12	1.88	6.55	25.49				
16.5	.64	4.65	2.98	49.17	5.45	1.55	4.71	14.04				
17.5	.60	4.85	2.91	50.93	5.78	1.22	3.39	9.86				
18.5	.55	5.00	2.75	50.88	6.11	0.89	2.44	6.70				
19.5	.40	7.48	2.99	58.31	6.44	0.56	1.75	5.23				
20.5	.32	5.02	1.61	33.01	6.77	0.23	1.26	2.03				
21.5	.24	5.50	1.32	28.38	7.10	-0.10	0.90	1.19				

Table 21(a): Continued.

Pivotal age (weeks)					Provisional r_m							
					0.33							
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
22.5	.17	5.25	0.89	20.03	7.43	-0.43	0.65	0.58				
23.5	.09	4.50	0.41	9.64	7.76	-0.76	0.47	0.19				
					Total			1096.15				

Ro = 47.19

r_m = 0.330

T = 11.68

λ = 1.39

Table 21(b): Life table data for A. brassicae females reared on mature leaves of Golden Acre at 15°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.28			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
7.5	1	1.80	1.80	11.25	2.25	4.75	115.58	208.05	2.10	4.90	134.29	241.72
8.5	1	2.93	2.93	24.91	2.55	4.45	85.63	250.89	2.38	4.62	101.49	297.38
9.5	.79	3.92	3.10	29.45	2.85	4.15	63.43	196.65	2.66	4.34	76.71	237.79
10.5	.71	3.30	2.34	24.60	3.15	3.85	46.99	109.96	2.94	4.06	57.97	135.66
11.5	.71	3.20	2.27	26.13	3.45	3.55	34.81	79.03	3.22	3.78	43.82	99.46
12.5	.71	3.80	2.70	33.73	3.75	3.25	25.79	69.63	3.50	3.50	33.12	89.41
13.5	.71	1.80	1.28	17.25	4.05	2.95	19.11	24.46	3.78	3.22	25.03	32.04
14.5	.71	3.60	2.56	37.06	4.35	2.65	14.15	36.23	4.06	2.94	18.92	48.42
15.5	.71	4.00	2.84	44.02	4.65	2.35	10.49	29.78	4.34	2.66	14.30	40.60
16.5	.71	3.80	2.70	44.52	4.95	2.05	7.77	20.97	4.62	2.38	10.80	29.17
17.5	.51	1.00	0.51	8.93	5.25	1.75	5.75	2.93	4.90	2.10	8.17	4.16
18.5	.43	0.17	0.07	1.35	5.55	1.45	4.26	0.30	5.18	1.82	6.17	0.43
19.5	.14	0	0	0	-	-	-	-	-	-	-	-
20.5	.14	0	0	0	-	-	-	-	-	-	-	-
21.5	.14	0	0	0	-	-	-	-	-	-	-	-

Table 21(b): Continued.

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.28			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
22.5	.14	0	0	0	-	-	-	-	-	-	-	-
23.5	.14	0	0	0	-	-	-	-	-	-	-	-
24.5	.08	0	0	0	-	-	-	-	-	-	-	-
	Ro = 25.10				Total			1028.88	Total			1256.24
	r_m = 0.287											
	T = 11.23											
	λ = 1.33											

Table 22: Population growth statistics of A. brassicae on young and mature leaves of four varieties of cabbage at 25°, 20°, and 15°C.

Population statistics	Host plants (variety)	25°C		20°C		15°C	
		Leaf types					
		Young	Mature	Young	Mature	Young	Mature
G.R.R. (♀/♀)	Earliest	58.20	36.58	73.97	58.19	111.46	90.34
	Large Blood Red	54.12	52.00	62.01	31.62	90.11	78.73
	June Star	50.72	29.30	64.54	37.74	80.95	47.11
	Golden Acre	44.92	27.80	48.50	31.25	75.88	33.32
Ro (♀/♀)	Earliest	31.93	23.37	37.80	24.44	90.91	48.92
	Large Blood Red	26.76	22.15	34.20	18.65	61.92	52.26
	June Star	25.19	12.38	25.23	14.75	48.20	21.48
	Golden Acre	19.17	9.66	19.57	9.98	47.19	25.10
r_m (♀/♀/week)	Earliest	1.040	0.921	0.775	0.684	0.429	0.374
	Large Blood Red	1.030	0.963	0.741	0.635	0.387	0.360
	June Star	0.936	0.806	0.713	0.603	0.299	0.243
	Golden Acre	0.932	0.807	0.705	0.490	0.330	0.287
T (weeks)	Earliest	3.33	3.42	4.69	4.67	10.27	10.40
	Large Blood Red	3.19	3.22	4.77	4.61	10.66	10.98
	June Star	3.45	3.12	4.53	4.46	12.96	12.62
	Golden Acre	3.17	2.81	4.22	4.70	11.68	11.23
λ (♀/♀/week)	Earliest	2.83	2.51	2.17	1.98	1.55	1.45
	Large Blood Red	2.80	2.62	2.10	1.89	1.47	1.43
	June Star	2.55	2.24	2.04	1.83	1.35	1.28
	Golden Acre	2.54	2.24	2.02	1.63	1.39	1.33

Figure 7: Relationship between the finite rate of increase (λ), net reproduction rate (Ro), generation time (T), and temperature.

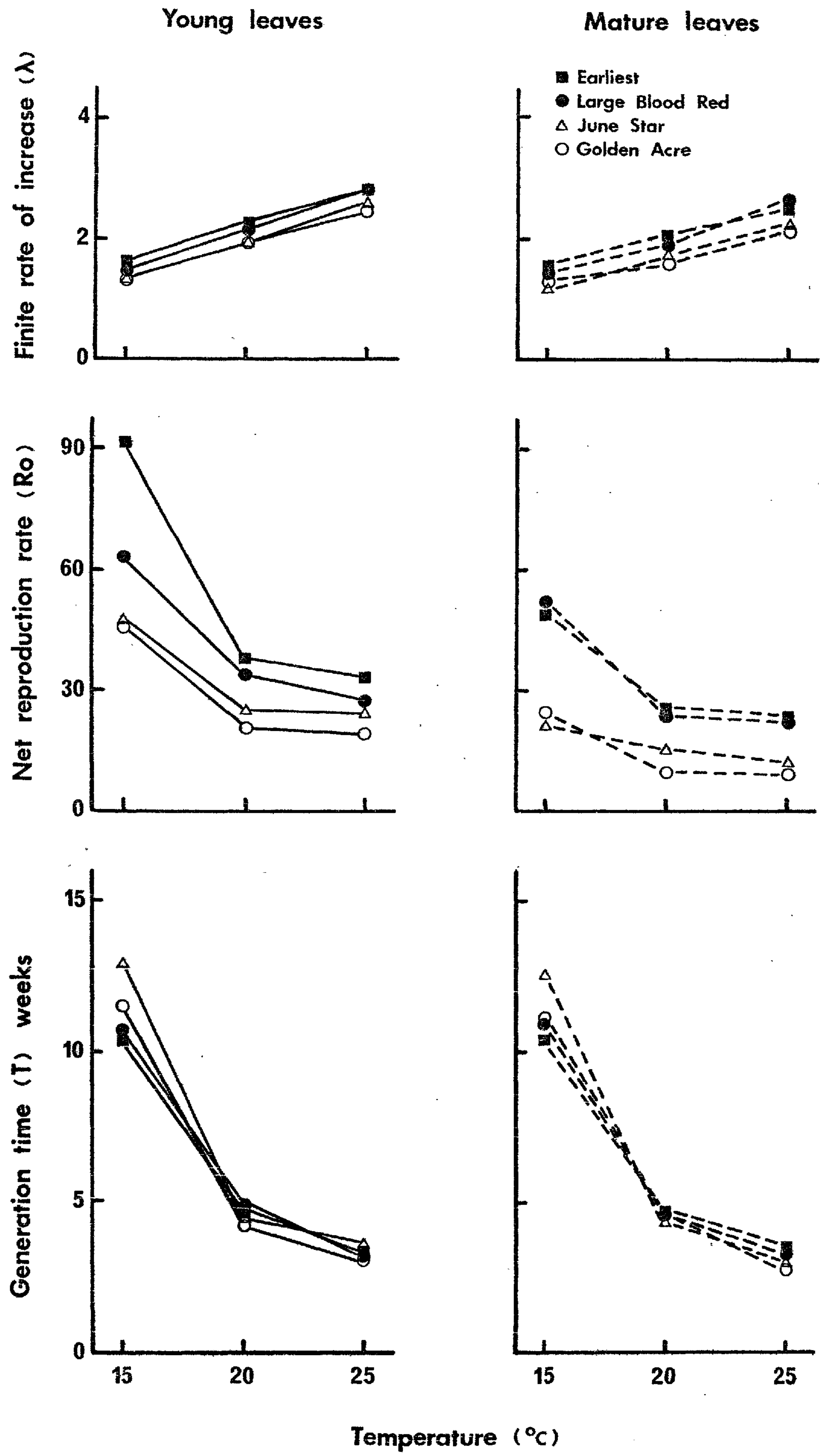
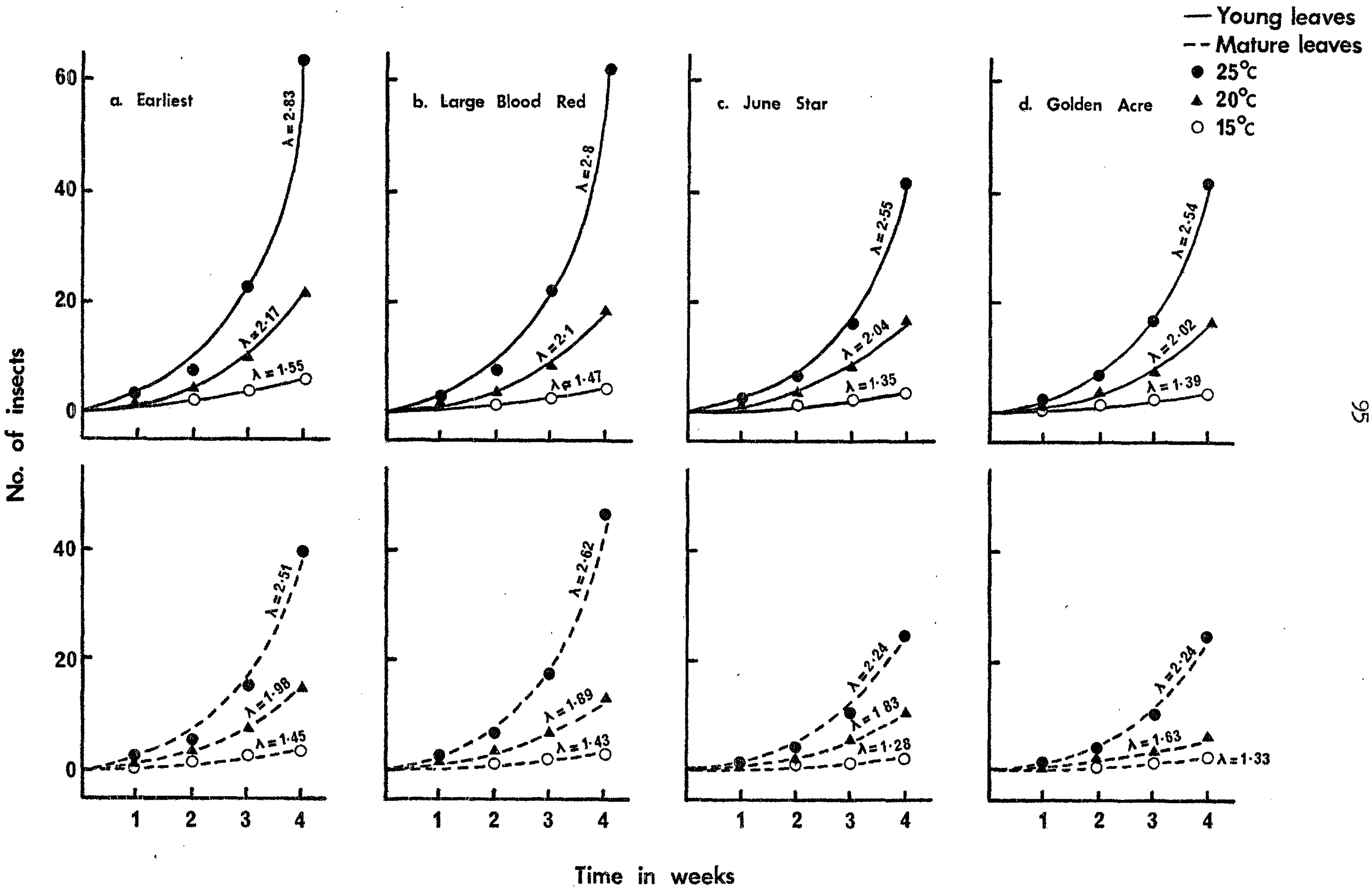

Young leaves
Mature leaves
Earliest
Large Blood Red
June Star
Golden Acre
Finite rate of increase (λ)
0
2
4
Net reproduction rate (Ro)
0
30
60
90
Generation time (T) weeks
0
5
10
15
15
20
25
15
20
25
Temperature (°c)

Figure 8: Curves for various values of λ/♀/week, showing population growth of *A. brassicae* on young (———), and mature (-----) leaves of (a) Earliest, (b) Large Blood Red, (c) June Star, (d) Golden Acre at 25°, 20°, and 15°C.



— Young leaves
-- Mature leaves
● 25°C
▲ 20°C
○ 15°C
a. Earliest
b. Large Blood Red
c. June Star
d. Golden Acre
λ = 2·83
λ = 2·17
λ = 1·55
λ = 2·8
λ = 2·1
λ = 1·47
λ = 2·55
λ = 2·04
λ = 1·35
λ = 2·54
λ = 2·02
λ = 1·39
λ = 2·51
λ = 1·98
λ = 1·45
λ = 2·62
λ = 1·89
λ = 1·43
λ = 2·24
λ = 1·83
λ = 1·28
λ = 2·24
λ = 1·63
λ = 1·33
No. of insects
60
40
20
0
40
20
0
1
2
3
4
Time in weeks

Table 23(a): Number of eggs laid by *A. brassicae* on three Brassica species in a species preference experiment.

Replicates	Species		
	Mustard	Purple Sprout	Turnip
	No. of eggs		
1	30	9	16
2	63	29	8
3	39	67	25
4	72	20	37
5	52	61	50
6	267	3	18
7	191	26	1
8	45	21	7
Total	759	236	162
$\bar{x}$	94.88	29.5	20.25

Table 23(b): Analysis of variance for Table 23(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Species	2	26475.63	13237.81	4.82*
Residual	21	57666.37	2746.02	
Total	23	84142		

* denotes significance at 5%

Table 23(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	2.93	3.08	3.17
Least Significant Range (LSR)	54.29	57.06	58.73

Ranked means

Turnip	Purple Sprout	Mustard
20.25	29.5	94.88

Any two values not underscored by the same line are significantly different ($p = .05$). Any two values underscored by the same line are not significantly different.

of adult A. brassicae females on young and mature leaves of three species of Cruciferae at three constant temperatures. Age-specific survival rates (lx) are presented in Tables 34-42 and illustrated graphically in Figs. 10-15. Tables 28(a), 29(a) and 30(a) show the average time for the populations to reach 50% mortality (LT_{50}).

Longevity increased with decreasing temperature on both leaf types of all species.

Analysis of variance showed that the effect of leaf age on longevity was not significant (Tables 28(b), 29(b) and 30(b)).

The effect of host plant species was not significant except at 20°C ($p = .05$) (Table 29(b)).

Mean longevity on different species was tested for differences using Duncan's new multiple range test. All means were not significantly different at 25°C. But at 20°C, longevity on Mustard was significantly different ($p = .05$) (Table 26(c)). Mean longevities on Mustard and Purple Sprout were not significantly different but each was significantly different from Turnip at 15°C ($p = .05$) (Table 27(c)).

Time for populations to reach 50% mortality, like the mean longevity, increased with decreasing temperature.

Results of analysis of variance showed that the variance ratio (F) for leaf age effect was not significant at any of the constant temperatures (Tables 28(b), 29(b) and 30(b)). The variance ratio (F) for species effect was not significant at 15° but was significant at 20° ($p < .01$) and at 25°C ($p < .05$) (Tables 28(b) and 29(b)).

Duncan's new multiple range test was used to test the differences between species means. Survival on each species was significantly different ($p = .05$) at 25° and 20°C respectively. But at 15°C, Mustard and Purple Sprout were not significantly different though each was significantly different from Turnip ($p = .05$) (Tables 28(c), 29(c), and 30(c)).

The lx curves for Mustard at 25° (Fig. 10) and 20°C (Fig. 12) represented an abbreviated form of Slobodkin's type I (Slobodkin, 1962), with mortality acting on the middle aged individuals. But for Purple Sprout and Turnip, (Figs. 11 and 13), the curves were typical of type IV, mortality acting on young individuals. At 15°C, the curves for all species were of type I where mortality was delayed till old age (Figs. 14 and 15).

lx curves for mature leaves of Purple Sprout and Turnip were generally under those for young leaves whereas the curves for mature leaves of Mustard were either superior to those for young leaves or were very close to them.

(b) Fecundity and age-specific fecundity rate (m_x)

At all constant temperatures, more eggs were laid on young leaves than on mature leaves. The highest fecundity was recorded on Mustard and the least on Turnip (Fig. 9(a)).

Fecundity increased with decreasing temperature except in the case of Mustard where maximum fecundity occurred at 20°C (Table 24 and Fig. 9(a)).

The variance ratio (F) was significant ($p = .05$) for leaf age effect and for species effect ($p < .01$) at 25° (Tables 31(a) and (b)) and 20° (Tables 32(a) and (b)) respectively. At 15°C, the variance ratio (F) was also significant ($p = .05$) for leaf age and species effects respectively (Tables 33(a) and (b)).

Figure 9(a). Mean fecundity of A. brassicae reared on young and mature leaves of three species of Brassica at 25°, 20°, and 15°C.

(b). Mean longevity of A. brassicae females reared on young and mature leaves of three species of Brassica at 25°, 20°, and 15°C.

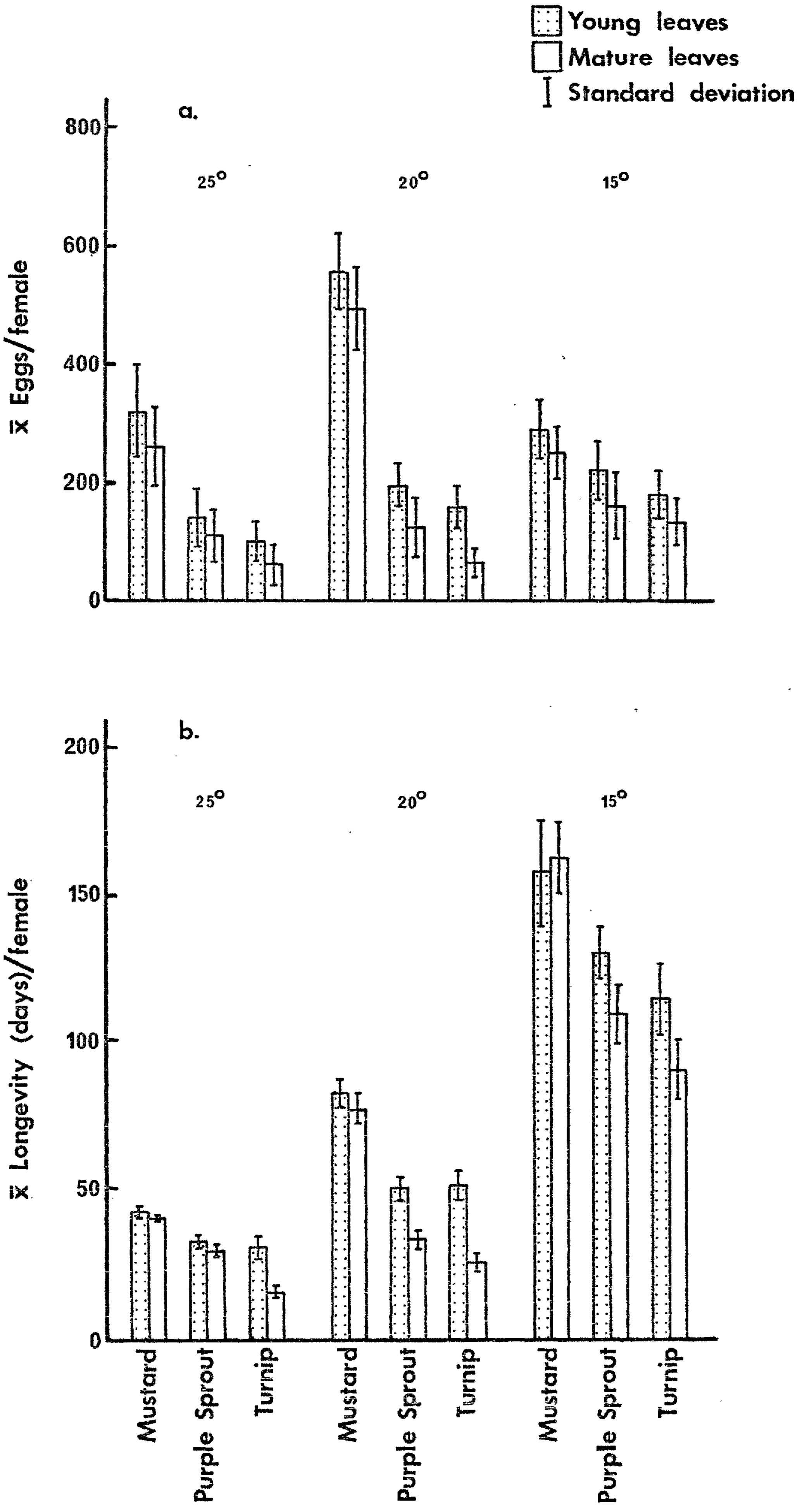

Young leaves
Mature leaves
Standard deviation
a.
x̄ Eggs/female
800
600
400
200
0
25°
20°
15°
b.
x̄ Longevity (days)/female
200
150
100
50
0
25°
20°
15°
Mustard
Purple Sprout
Turnip
Mustard
Purple Sprout
Turnip
Mustard
Purple Sprout
Turnip

Table 24: Mean fecundity and longevity of A. brassicae females reared on young and mature leaves of three species of Cruciferae at 25°, 20°, and 15°C.

Host plants (Species)		25°C		20°C		15°C	
		Leaf types					
		Young	Mature	Young	Mature	Young	Mature
Mustard	No. of females	19	19	18	17	6	8
	$\bar{x}$ no. of eggs/♀	318.9±15.9	259.2±12.9	553 ±12.9	493.2±14.59	279 ±10.48	250.3± 9.39
	$\bar{x}$ longevity (days)/♀	42.6± 1.88	41.4± 1.36	83.2± 5.07	77.9± 5.2	157.9±18.4	163.3±12.08
Purple Sprout	No. of females	14	13	17	12	6	7
	$\bar{x}$ no. of eggs/♀	140 ±10.12	107.4± 9.12	193.9± 6.99	126.2±10.67	220 ±10.66	157.1±11.17
	$\bar{x}$ longevity (days)/♀	33.1± 1.57	30.3± 1.78	51.4± 3.58	33.8± 3.02	131.2± 8.54	110.2± 9.5
Turnip	No. of females	10	9	12	9	9	5
	$\bar{x}$ no. of eggs/♀	98.6± 7.35	61.1± 6.95	160.4± 7.6	64.7± 4.77	180.2± 8.23	134.8± 8.26
	$\bar{x}$ longevity (days)/♀	31.2± 3.72	15.8± 1.84	51.5± 5.06	25.5± 2.8	114.6±11.81	90.5±10.09

Table 25(a): Mean longevity of *A. brassicae* females on young and mature leaves of three species of Cruciferae at 25°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	42.6	41.4	84.0	42.0
Purple Sprout	33.1	30.3	63.4	31.7
Turnip	31.2	15.8	47.0	23.5
Age totals	106.9	87.5	194.4	97.2

Table 25(b): Analysis of variance for Table 25(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	62.73	62.73	2.07 (N.S.)
Species	2	343.72	171.86	5.68 (N.S.)
Residual	2	60.49	30.25	
Total	5	466.94		

N.S. denotes not significant

Table 26(a): Mean longevity of *A. brassicae* females on young and mature leaves of three species of Cruciferae at 20°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	83.2	77.9	161.1	80.6
Purple Sprout	51.4	33.8	85.2	42.6
Turnip	51.5	25.5	77.0	38.5
Age totals	186.1	137.2	323.3	161.65

Table 26(b): Analysis of variance for Table 26(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	398.53	398.53	7.35 (N.S.)
Species	2	2150.15	1075.08	19.82*
Residual	2	108.47	54.24	
Total	5	2657.07		

* denotes significance at 5% level

N.S. denotes not significant

Table 26(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	25.9	25.9	25.9

Ranked means

Turnip	Purple Sprout	Mustard
38.5	42.6	80.6

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 27(a): Mean longevity of *A. brassicae* females on young and mature leaves of three species of Cruciferae at 15°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	157.9	163.3	321.2	160.6
Purple Sprout	131.2	110.2	241.4	120.7
Turnip	114.6	90.5	205.1	102.6
Age totals	403.7	364.0	767.7	383.9

Table 27(b): Analysis of variance for Table 27(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	262.67	262.67	1.76 (N.S.)
Species	2	3491.28	1745.64	11.68 (N.S.)
Residual	2	299.02	149.51	
Total	5	4052.97		

N.S. denotes not significant

Table 27(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	42.99	42.99	42.99

Ranked means

Turnip	Purple Sprout	Mustard
102.6	120.7	160.6

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 28(a): Time for populations of adult *A. brassicae* females to reach 50% mortality levels on both young and mature leaves of three species of Cruciferae at 25°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	6	6	12	6.0
Purple Sprout	5	4	9	4.5
Turnip	3	2	5	2.5
Age totals	14	12	26	13.0

Table 28(b): Analysis of variance for Table 28(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	0.66	0.66	3.88 (N.S.)
Species	2	12.33	6.17	36.29*
Residual	2	0.34	0.17	
Total	5	13.33		

* denotes significance at less than 5% level

N.S. denotes not significant

Table 28(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	1.45	1.45	1.45

Ranked means

Turnip	Purple Sprout	Mustard
2.5	4.5	6.0

Any two values not underscored by the same line are significantly different (p = .05).

Table 29(a): Time for populations of adult A. brassicae females to reach 50% mortality levels on both young and mature leaves of three species of Cruciferae at 20°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	12	11	23	11.5
Purple Sprout	6	5	11	5.5
Turnip	5	3	8	4.0
Age totals	23	19	42	21.0

Table 29(b): Analysis of variance for Table 29(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	2.66	2.66	15.65 (N.S.)
Species	2	63.00	31.50	185.29*
Residual	2	0.34	0.17	
Total	5	66.00		

* denotes significance at less than .1%

N.S. denotes not significant

Table 29(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	1.44	1.44	1.44

Ranked means

Turnip	Purple Sprout	Mustard
4.0	5.5	11.5

Any two values not underscored by the same line are significantly different (p = .05).

Table 30(a): Time for populations of adult *A. brassicae* females to reach 50% mortality levels on both young and mature leaves of three species of Cruciferae at 15°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	21	23	44	22.0
Purple Sprout	17	15	32	16.0
Turnip	20	19	39	19.5
Age totals	58	57	115	57.5

Table 30(b): Analysis of variance for Table 30(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	0.16	0.16	0.07 (N.S.)
Species	2	36.33	18.17	8.04 (N.S.)
Residual	2	4.51	2.26	
Total	5	41.00		

N.S. denotes not significant

Table 30(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	5.29	5.29	5.29

Ranked means

Purple Sprout	Turnip	Mustard
16	19.5	22

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Duncan's new multiple range test showed that the species means were significantly different ($p = .05$) at all temperatures (Tables 31(c), 32(c), and 33(c)).

Age-specific fecundity rates (m_x) are shown in m_x columns of the life tables (Tables 34-42) and illustrated graphically in Figs. 10-15.

Maximum m_x was generally reached in the second week of the reproductive period. m_x values were highest on Mustard: 36.93 (young) and 37.21 (mature) and lowest on Turnip: 16.41 (young) and 13.71 (mature), at 25°C. One prominent m_x peak occurred at this temperature for each species leaf type.

At 20°C, two or more peaks were observed but only such peaks that occurred before 50% mortality of the population, were considered important. This was necessary because of the ability of some last remnants in a population to lay high numbers of eggs before they died, thus distorting the true picture.

On Mustard, three m_x peaks occurred in the 2nd week (29.93), 6th week (30.24), and 10th week (24.39) of the reproductive periods. A similar trend was followed on mature leaves. Only one of the several m_x peaks on Purple Sprout and Turnip occurred before a 50% mortality was reached.

At 15°C, m_x values rose gradually and tended to remain either fairly constant or fluctuated with very low amplitudes.

On Mustard at 15°C, the middle portion of the graph for mature leaves was significantly higher than that for young leaves. The explanation for this could be seen from the lx curve, for while survival on young leaves had decreased considerably, that on mature leaves was still unity.

Table 31(a): Fecundity of A. brassicae reared on young and mature leaves of three species of Cruciferae at 25°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	318.94	259.00	577.94	288.97
Purple Sprout	140.00	107.38	247.38	123.69
Turnip	98.60	61.11	159.71	79.86
Age totals	557.54	427.49	985.03	492.52

Table 31(b): Analysis of variance for Table 31(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	2818.83	2818.83	26.55*
Species	2	48645.37	24322.68	229.07**
Residual	2	212.36	106.18	
Total	5	51676.56		

* denotes significance at 5% level

** denotes significance at less than 1% level

Table 31(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	36.24	36.24	36.24

Ranked means

Turnip	Purple Sprout	Mustard
79.86	123.69	288.97

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 32(a): Fecundity of *A. brassicae* reared on young and mature leaves of three species of Cruciferae at 20°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	553.00	493.18	1046.18	523.09
Purple Sprout	193.85	126.17	320.02	160.01
Turnip	160.35	64.67	225.02	112.51
Age totals	907.20	684.02	1591.22	795.61

Table 32(b): Analysis of variance for Table 32(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	8301.552	8301.552	46.73*
Species	2	201772.85	100886.425	567.92**
Residual	2	355.284	177.642	
Total	5			

* denotes significance at 5% level

** denotes significance at less than 1% level

Table 32(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	46.89	46.89	46.89

Ranked means

Turnip	Purple Sprout	Mustard
112.51	160.01	523.09

Any two values not underscored by the same line are significantly different (p = .05). Any two values underscored by the same line are not significantly different.

Table 33(a): Fecundity of *A. brassicae* reared on young and mature leaves of three species of Cruciferae at 15°C.

Species	AGE OF LEAF		Species totals	Species means
	Young	Mature		
Mustard	279.00	250.30	529.30	264.65
Purple Sprout	220.00	157.14	377.14	188.57
Turnip	180.22	134.80	315.02	157.51
Age totals	679.22	542.24	1221.46	610.73

Table 33(b): Analysis of variance for Table 33(a).

Source of variation SV	Degree of freedom DF	Sum of squares SS	Mean squares MS	Variance ratio F
Leaf age	1	3127.25	3127.25	21.44*
Species	2	12154.58	6077.29	41.66*
Residual	2	291.77	145.89	
Total	5	15573.6		

* denotes significance at 5% level

Table 33(c): Comparison of species means by Duncan's new multiple range test

Value of p	2	3	4
Significant Studentized Range (SSR)	6.09	6.09	6.09
Least Significant Range (LSR)	42.47	42.47	42.47

Ranked means

Turnip	Purple Sprout	Mustard
157.51	188.57	264.65

Any two values not underscored by the same line are significantly different (p = .05).

6. Population growth statistics on young and mature leaves of different host species at 25°, 20°, and 15°C

(a) Gross reproductive rate (G.R.R.)

In the case of Purple Sprout and Turnip, the gross reproductive rates increased with decreasing temperature, the highest values being obtained at 15°C. For Mustard, the G.R.R. was highest at 20° and lowest at 25°C (Table 43).

The variance ratio (F) for leaf age effect was significant at 25° ($p < .05$) and at 20°C ($p < .05$). F for species effect was significant at 25° ($p < .01$) and at 20°C ($p < .01$). F was not significant for both leaf age and species effects at 15°C.

At all temperatures except 15°C, the mean G.R.R. for Mustard was significantly different by Duncan's new multiple range test ($p = .05$).

(b) Net reproductive rate (Ro)

The trend in the values of Ro with respect to temperature was similar to that of G.R.R. (Table 43 and Fig. 16).

Analysis of variance showed that at 25° and 20°C, F was not significant for leaf age effect. But species effects were significant at 25° ($p < .01$) and at 20°C ($p < .01$). At 15°C, the F values for leaf age and species effects were not significant.

Duncan's new multiple range test showed that the mean Ro for Mustard was significantly different at 25° ($p = .05$) and at 20°C ($p = .05$). At 15°C, the means were not significantly different.

(c) Intrinsic rate of natural increase (r_m)

Values of r_m are shown in Table 43.

r_m values on young leaves were consistently higher than those on mature leaves though the differences are not particularly striking.

r_m decreased with decreasing temperature. At each temperature regime and for each leaf age, the highest values were obtained on Mustard while the lowests were on Turnip.

The trend in the results of analysis of variance is similar to that outlined below for λ since λ was derived from r_m.

(d) Mean generation time (T)

The mean generation times on young and mature leaves of the three species at 25°, 20°, and 15°C are compared in Table 43 and Fig. 16.

T increased with decreasing temperature.

From the results of analysis of variance, the values of T were neither influenced by leaf age nor by species type.

(e) Finite rate of increase (λ)

The various values of λ are shown in Table 43. λ was highest at 25°C and lowest at 15°C (Fig. 16).

The variance ratio for leaf age effect was not significant at any of the constant temperatures. F for species effect was also not significant except at 25°C ($p < .01$).

(f) Population growth curves

Curves for various values of λ/♀/week showing population growth on young and mature leaves of the different species are illustrated in Fig. 17.

The curves for population growth on young and mature leaves of each species were similar. This is not surprising since their variance ratios were not significantly different (see λ above).

The variance ratio for species effect was significant at 25°C. At this temperature, the theoretical size of the population reached after 4 weeks by one female on young leaves of Mustard (329) would be approximately twice that on Purple Sprout (112) and approximately 5 times that on Turnip (61).

The time taken to reach a given population size increased with decreasing temperature. For example, the size of the population by one female on young leaves of Mustard at 25°C after 4 weeks (329) would take about 7½ weeks at 20°C and about 15 weeks at 15°C.

Table 34(a): Life table data for A. brassicae females reared on young leaves of Mustard at 25°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.45				1.44			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
2.5	1	26.30	26.30	65.75	3.63	3.37	29.08	764.77	3.60	3.40	29.96	788.06
3.5	.99	36.93	36.56	127.96	5.08	1.92	6.82	249.37	5.04	1.96	7.10	259.55
4.5	.95	34.39	32.67	147.02	6.53	0.47	1.60	52.27	6.48	0.52	1.68	54.95
5.5	.80	31.42	25.14	138.27	7.98	-0.98	0.38	9.44	7.92	-0.92	0.40	10.02
6.5	.67	26.33	17.64	114.66	9.43	-2.43	0.09	1.55	9.36	-2.36	0.09	1.67
7.5	.42	15.36	6.45	48.38	10.88	-3.88	0.02	0.13	10.80	-3.80	0.02	0.14
8.5	.19	10.84	2.06	17.51	12.33	-5.33	0	0	12.24	-5.24	0.01	0.01
9.5	.11	6.25	0.69	6.56	-	-	-	-	-	-	-	-
10.5	.04	1.00	0.04	0.42	-	-	-	-	-	-	-	-
	Ro	=	147.55		Total			1077.5	Total			1113.4
	r_m	=	1.445									
	T	=	3.45									
	λ	=	4.24									

Table 34(b): Life table data for A. brassicae females reared on mature leaves of Mustard at 25°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.50				1.40			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
2.5	1	25.17	25.17	62.93	3.75	3.25	25.79	649.14	3.50	3.50	33.12	833.52
3.5	1	37.21	37.21	130.24	5.25	1.75	5.75	214.13	4.90	2.10	8.17	303.86
4.5	1	28.03	28.03	126.14	6.75	0.25	1.28	35.99	6.30	0.70	2.01	56.45
5.5	.98	26.14	25.62	140.91	8.25	-1.25	0.29	7.34	7.70	-0.70	0.50	12.81
6.5	.82	20.97	17.20	111.80	9.75	-2.75	0.06	1.10	9.10	-2.10	0.12	2.06
7.5	.54	13.12	7.08	53.10	11.25	-4.25	0.01	0.10	10.50	-3.50	0.03	0.21
8.5	.15	5.43	0.81	6.89	12.75	-5.75	0	0	11.90	-4.90	0.01	0.01
9.5	.07	1.50	0.11	1.05	14.25	-7.25	0	0	13.30	-6.30	0	0
					Total			907.8	Total			1208.92

$R_o = 141.23$

$r_m = 1.436$

$T = 3.45$

$\lambda = 4.20$

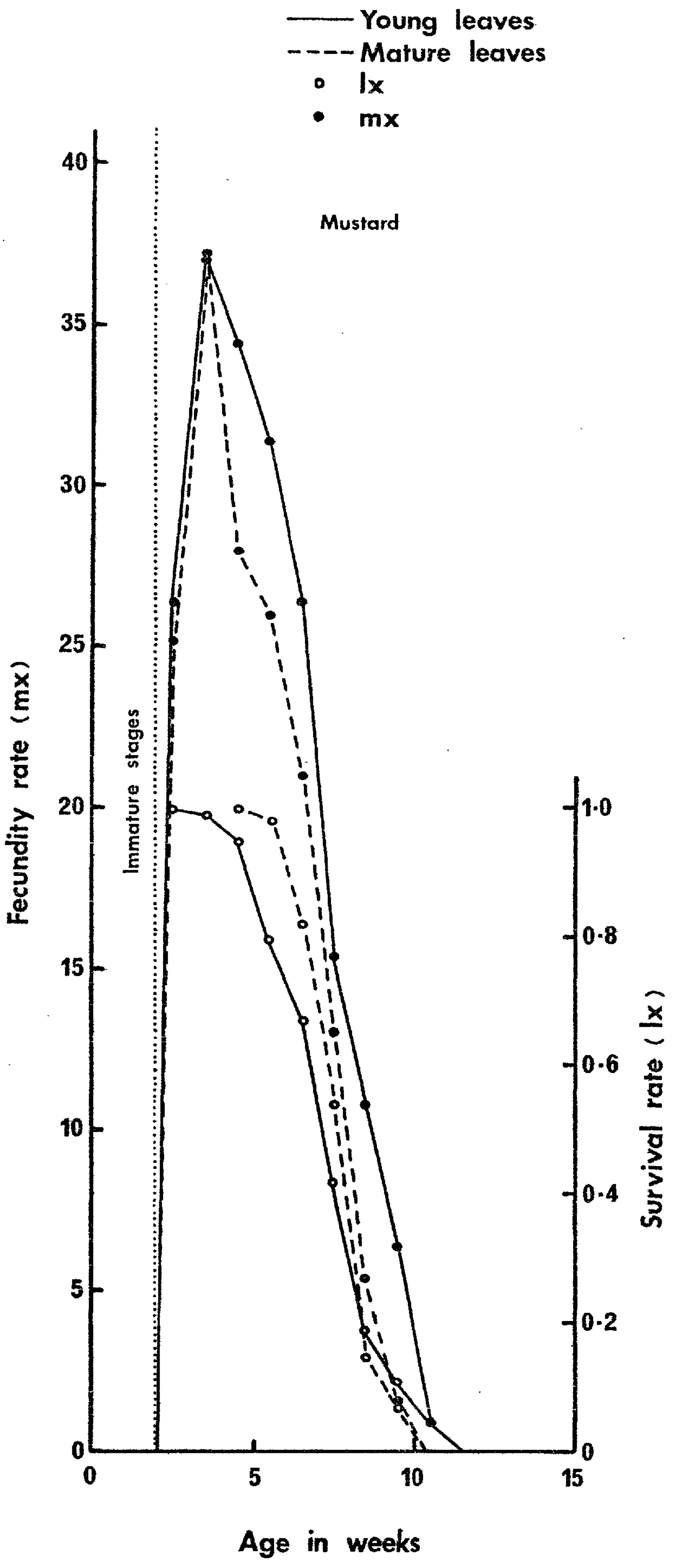

Young leaves
Mature leaves
lx
mx
Mustard
Immature stages
Fecundity rate (mx)
40
35
30
25
20
15
10
5
0
Survival rate (lx)
1·0
0·8
0·6
0·4
0·2
0
0
5
10
15
Age in weeks

Table 35(a): Life table data for A. brassicae females reared on young leaves of Purple Sprout at 25°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.21				1.20			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
2.5	.98	13.04	12.78	31.95	3.03	3.97	52.98	677.14	3.0	4.0	54.60	697.76
3.5	.92	21.22	19.52	68.32	4.24	2.76	15.80	308.41	4.2	2.8	16.44	321.00
4.5	.80	17.26	13.81	62.15	5.45	1.55	4.71	65.07	5.4	1.6	4.95	68.40
5.5	.73	11.30	8.25	45.38	6.66	0.34	1.40	11.59	6.6	0.4	1.49	12.31
6.5	.44	10.56	4.65	30.23	7.87	-0.87	0.42	1.95	7.8	-0.8	0.45	2.09
7.5	.16	11.00	1.76	13.20	9.08	-2.08	0.12	0.22	9	-2.0	0.14	0.24
8.5	.02	0	0	0	-	-	-	-	-	-	-	-
	Ro	=	60.77		Total			1064.38	Total			1101.80
	r_m	=	1.201									
	T	=	3.42									
	λ	=	3.32									

Table 35(b): Life table data for A. brassicae females reared on mature leaves of Purple Sprout at 25°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.19				1.18			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.99	13.97	13.83	34.58	2.98	4.02	55.70	770.35	2.95	4.05	57.40	793.81
3.5	.80	18.38	14.70	51.45	4.17	2.83	16.95	249.10	4.13	2.87	17.64	259.26
4.5	.63	12.81	8.07	36.32	5.36	1.64	5.16	41.60	5.31	1.69	5.42	43.74
5.5	.45	11.67	5.25	28.88	6.55	0.45	1.57	8.23	6.49	0.51	1.67	8.74
6.5	.27	9.59	2.59	16.84	7.74	-0.74	0.63	1.62	7.67	-0.67	0.51	1.33
7.5	.06	3.25	0.20	1.50	8.93	-1.93	0.15	0.03	8.85	-1.85	0.16	0.03
	Ro	=	44.64		Total			1070.93	Total			1106.91
	r_m	=	1.188									
	T	=	3.20									
	λ	=	3.28									

Figure 11: Longevity and age-specific fecundity of *A. brassicae* reared on young and mature leaves of (a) Purple Sprout, (b) Turnip at 25°C.

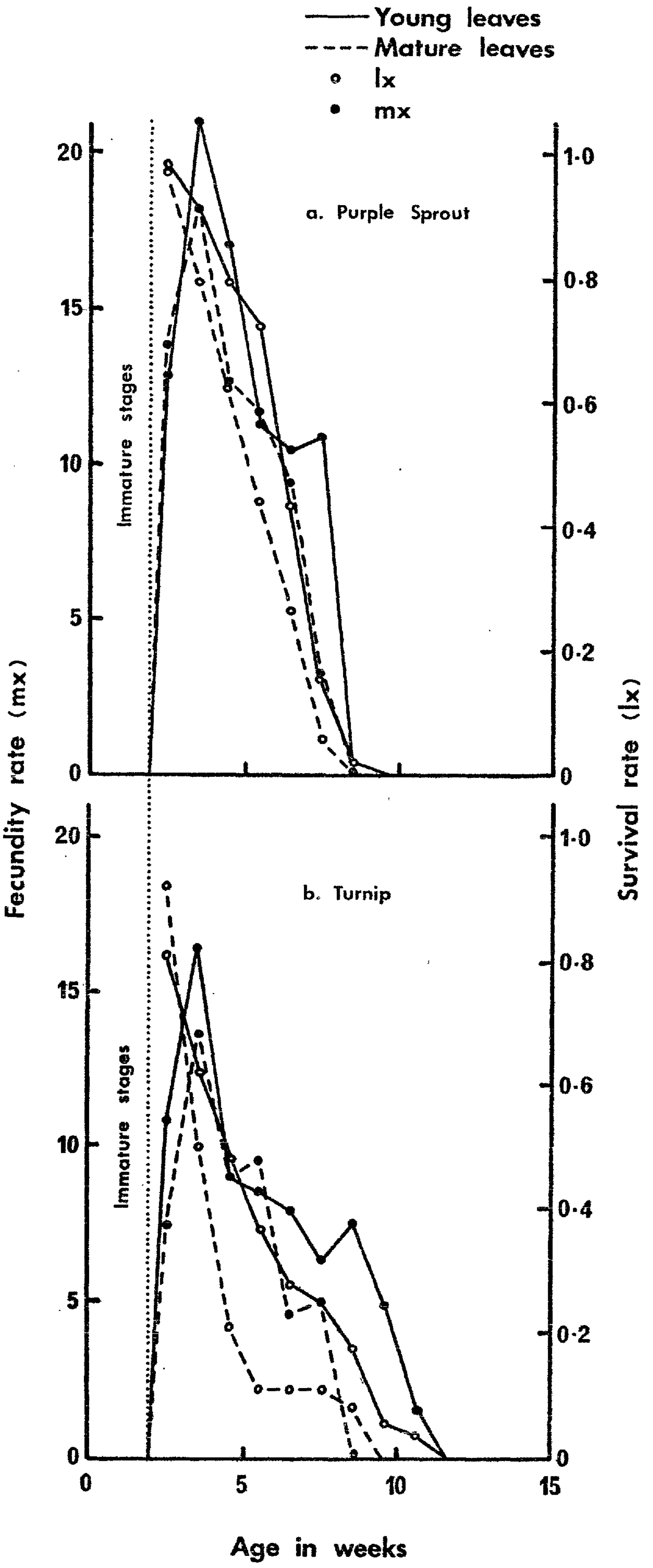

Young leaves
Mature leaves
lx
mx
a. Purple Sprout
b. Turnip
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
0
0·2
0·4
0·6
0·8
1·0

Table 36(a): Life table data for A. brassicae females reared on young leaves of Turnip at 25°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.03				1.02			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
2.5	.81	10.87	8.80	22.00	2.58	4.42	83.10	731.25	2.55	4.45	85.63	753.52
3.5	.62	16.41	10.17	35.60	3.61	3.39	29.67	301.70	3.57	3.43	30.88	314.02
4.5	.48	9.07	4.35	19.58	4.64	2.36	10.59	46.07	4.59	2.41	11.13	48.43
5.5	.37	8.72	3.23	17.77	5.67	1.33	3.78	12.21	5.61	1.39	4.01	12.97
6.5	.28	7.88	2.21	14.37	6.70	0.30	1.35	2.98	6.63	0.37	1.45	3.20
7.5	.25	6.39	1.60	12.00	7.73	-0.73	0.48	0.77	7.65	-0.65	0.52	0.84
8.5	.18	7.64	1.38	11.73	8.76	-1.76	0.17	0.24	8.67	-1.67	0.19	0.26
9.5	.06	5.00	0.30	2.85	9.79	-2.79	0.06	0.02	9.69	-2.69	0.07	0.02
10.5	.04	1.50	0.06	0.63	10.82	-3.82	0.02	0	10.71	-3.71	0.02	0
					Total			1095.24	Total			1133.26

R_o = 32.1

r_m = 1.030

T = 3.37

λ = 2.80

Table 36(b): Life table data for A. brassicae females reared on mature leaves of Turnip at 25°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.93				0.92			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.92	7.58	6.97	24.41	2.60	4.40	81.45	567.71	2.30	4.70	109.95	766.33
3.5	.50	13.71	6.86	30.85	3.26	3.74	42.10	288.79	3.22	3.78	43.82	300.58
4.5	.21	8.85	1.86	10.22	4.19	2.81	16.61	30.89	4.14	2.86	17.46	32.48
5.5	.11	9.50	1.05	6.79	5.12	1.88	6.55	6.88	5.06	1.94	6.96	7.31
6.5	.11	4.50	0.50	3.71	6.05	0.95	2.59	1.29	5.98	1.02	2.77	1.39
7.5	.11	5.00	0.55	4.68	6.98	0.02	1.02	0.56	6.90	0.10	1.11	0.61
8.5	.08	0	0	0	-	-	-	-	-	-	-	-
					Total			896.12	Total			1108.70

Ro = 17.79

r_m = 0.92

T = 3.13

λ = 2.51

Table 37(a): Life table for A. brassicae females reared on young leaves of Mustard at 20°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.01				1.00			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	1	17.14	17.14	59.99	3.54	3.46	31.82	545.34	3.5	3.5	33.12	567.60
4.5	1	29.93	29.93	134.69	4.55	2.45	11.59	346.81	4.5	2.5	12.18	364.62
5.5	1	29.01	29.01	159.56	5.56	1.44	4.22	122.44	5.5	1.5	4.48	130.01
6.5	.94	24.51	23.04	149.76	6.57	0.43	1.54	35.42	6.5	0.5	1.65	37.99
7.5	.85	26.29	22.35	167.63	7.58	-0.58	0.56	12.51	7.5	-0.5	0.61	13.56
8.5	.85	30.24	25.71	218.84	8.59	-1.59	0.20	5.24	8.5	-1.5	0.22	5.74
9.5	.82	24.61	20.18	191.71	9.60	-2.60	0.07	1.50	9.5	-2.5	0.08	1.66
10.5	.77	20.99	16.16	169.68	10.61	-3.61	0.03	0.44	10.5	-3.5	0.03	0.49
11.5	.66	20.07	13.25	152.38	11.62	-4.62	0.01	0.13	11.5	-4.5	0.01	0.15
12.5	.64	24.39	15.61	195.13	12.63	-5.63	0	0	12.5	-5.5	0	0
13.5	.58	21.88	12.69	171.32	-	-	-	-	-	-	-	-
14.5	.49	19.63	9.62	139.49	-	-	-	-	-	-	-	-
15.5	.39	19.88	7.75	120.13	-	-	-	-	-	-	-	-
16.5	.31	13.49	4.18	68.97	-	-	-	-	-	-	-	-
17.5	.20	11.50	2.30	40.25	-	-	-	-	-	-	-	-

Table 37(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					1.01				1.00			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
18.5	.11	8.67	0.95	17.58	-	-	-	-	-	-	-	-
19.5	.01	0	0	0	-	-	-	-	-	-	-	-
	Ro = 249.87 r_m = 1.005 T = 5.47 λ = 2.75				Total			1069.86	Total			1121.82

Figure 12: Longevity and age-specific fecundity of A. brassicae reared on young and mature leaves of Mustard at 20°C.

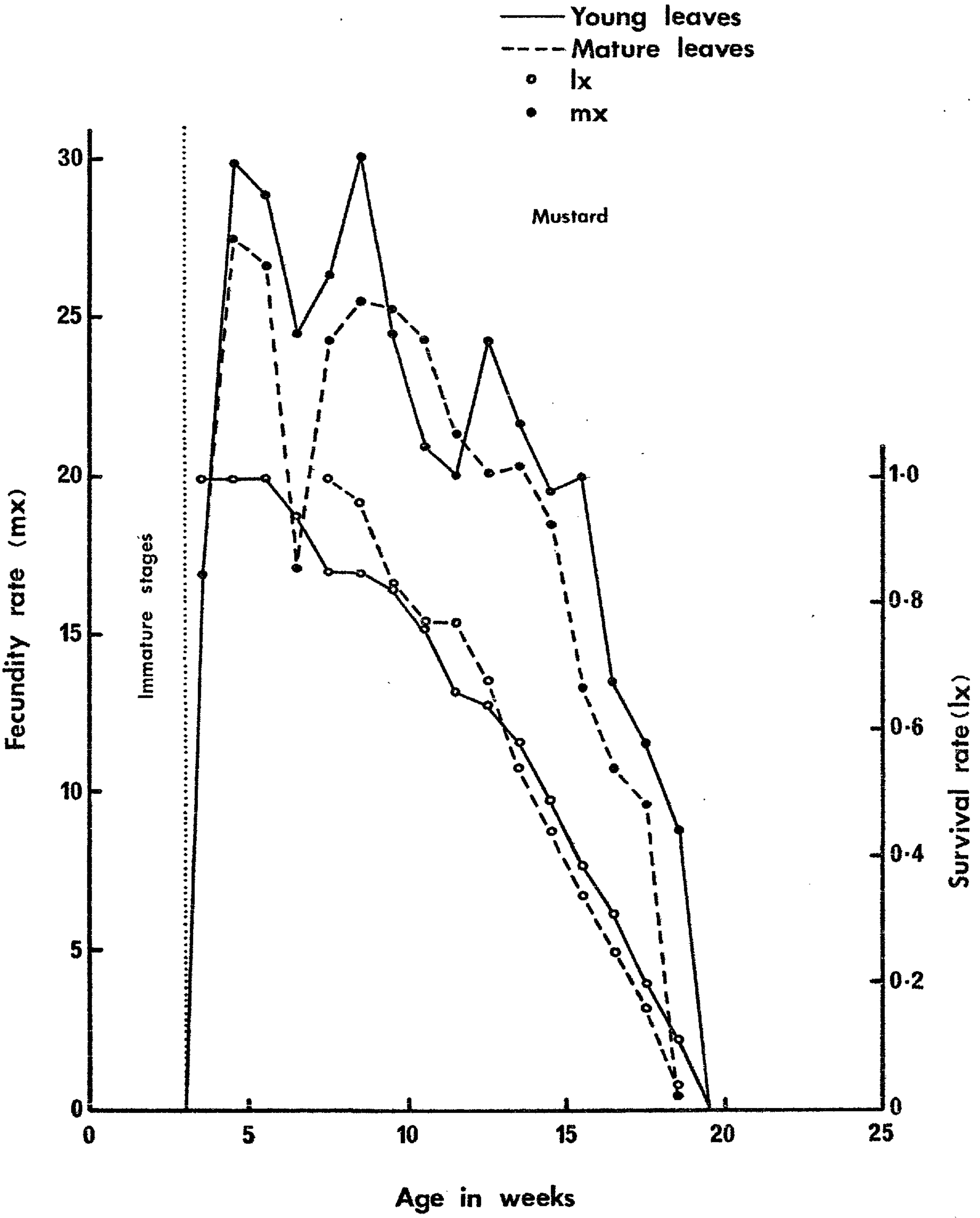

Young leaves
Mature leaves
lx
mx
Mustard
Immature stages
Fecundity rate (mx)
0
5
10
15
20
25
30
Survival rate (lx)
0
0·2
0·4
0·6
0·8
1·0
Age in weeks
0
5
10
15
20
25

Table 37(b): Life table data for A. brassicae females reared on mature leaves of Mustard at 20°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					1.00				0.99			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
3.5	1	17.02	17.02	59.57	3.5	3.5	33.12	563.62	3.47	3.53	34.12	580.79
4.5	1	27.47	27.47	123.62	4.5	2.5	12.18	334.65	4.46	2.54	12.68	348.31
5.5	1	26.71	26.71	146.91	5.5	1.5	4.48	119.71	5.45	1.55	4.71	125.84
6.5	1	17.32	17.32	112.58	6.5	0.5	1.65	28.56	6.44	0.56	1.75	30.32
7.5	1	24.31	24.31	182.33	7.5	-0.5	0.61	14.74	7.43	-0.43	0.65	15.81
8.5	.96	25.60	24.58	208.93	8.5	-1.5	0.22	5.48	8.42	-1.42	0.24	5.94
9.5	.83	25.39	21.07	200.17	9.5	-2.5	0.08	1.73	9.41	-2.41	0.09	1.89
10.5	.78	24.32	18.97	199.19	10.5	-3.5	0.03	0.57	10.40	-3.40	0.03	0.63
11.5	.78	21.33	16.64	191.36	11.5	-4.5	0.01	0.17	11.39	-4.39	0.01	0.21
12.5	.68	20.19	13.73	171.63	12.5	-5.5	0	0	12.38	-5.38	0	0
13.5	.54	20.32	10.97	148.10	-	-	-	-	-	-	-	-
14.5	.44	18.45	8.12	117.74	-	-	-	-	-	-	-	-
15.5	.34	13.43	4.57	70.84	-	-	-	-	-	-	-	-
16.5	.25	10.73	2.68	44.22	-	-	-	-	-	-	-	-
17.5	.16	9.63	1.54	26.95	-	-	-	-	-	-	-	-

Table 37(b): Continued

Pivotal age (weeks)					Provisional r_m's							
					1.00				0.99			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
18.5	.04	0.25	0.01	0.19	-	-	-	-	-	-	-	-
	Ro = 235.71 r_m = 0.9923 T = 5.50 λ = 2.70				Total			1069.23	Total			1109.74

Table 38(a): Life table data for A. brassicae females reared on young leaves of Purple Sprout at 20°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.87				0.86			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
3.5	.98	9.41	9.22	32.27	3.05	3.95	51.94	478.84	3.01	3.99	54.05	498.39
4.5	.94	17.53	16.48	74.16	3.92	3.08	21.76	358.58	3.87	3.13	22.87	376.96
5.5	.87	19.24	16.74	92.07	4.79	2.21	9.12	152.60	4.73	2.27	9.68	162.03
6.5	.80	14.08	11.26	73.19	5.66	1.34	3.82	43.00	5.59	1.41	4.10	46.12
7.5	.71	13.43	9.54	71.55	6.53	0.47	1.60	15.26	6.45	0.55	1.73	16.54
8.5	.58	13.31	7.72	65.62	7.40	-0.40	0.67	5.17	7.31	-0.31	0.73	5.66
9.5	.43	11.83	5.09	48.36	8.27	-1.27	0.28	1.43	8.17	-1.17	0.31	1.58
10.5	.38	13.63	5.18	54.39	9.14	-2.14	0.12	0.61	9.03	-2.03	0.13	0.68
11.5	.20	9.51	1.90	21.85	10.01	-3.01	0.05	0.09	9.89	-2.89	0.06	0.29
12.5	.11	11.00	1.21	15.13	10.88	-3.88	0.02	0.02	10.75	-3.75	0.02	0.03
13.5	.11	6.75	0.74	9.99	11.75	-4.75	0.01	0.01	11.61	-4.61	0.01	0.01
14.5	.04	5.00	0.20	2.90	-	-	-	-	-	-	-	-

Table 38(a): Continued

Ro = 85.28	Total	1055.61	Total	1108.29
r_m = 0.861				
T = 5.16				
λ = 2.37				

Table 38(b): Life table data for A. brassicae females reared on mature leaves of Purple Sprout at 20°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks) x	lx	mx	lxm_x	$xlxm_x$	Provisional r_m's							
					0.75				0.74			
					r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
3.5	.95	6.8	6.46	22.61	2.63	4.37	79.04	510.62	2.59	4.41	82.27	531.46
4.5	.85	9.99	8.49	38.21	3.38	3.62	37.34	317.00	3.33	3.67	39.25	333.25
5.5	.75	9.92	7.44	40.92	4.13	2.87	17.64	131.22	4.07	2.93	18.73	139.33
6.5	.65	11.56	7.51	48.84	4.88	2.12	8.33	62.57	4.81	2.19	8.94	67.10
7.5	.50	13.25	6.63	49.69	5.63	1.37	3.94	26.09	5.55	1.45	4.26	28.26
8.5	.45	6.75	3.04	25.82	6.38	0.62	1.86	5.65	6.29	0.71	2.03	6.18
9.5	.39	8.50	3.32	31.49	7.13	-0.13	0.88	2.92	7.03	-0.03	0.97	3.22
10.5	.25	7.50	1.88	19.69	7.88	-0.88	0.41	0.78	7.77	-0.77	0.46	0.87
11.5	.14	5.00	0.70	8.05	8.63	-1.63	0.20	0.14	8.51	-1.51	0.22	0.15
	Ro = 45.47				Total			1056.99	Total			1109.82
	r_m = 0.7425											
	T = 5.14											
	λ = 2.10											

Figure 13: Longevity and age-specific fecundity of A. brassicae reared on young and mature leaves of (a) Purple Sprout, (b) Turnip at 20°C.

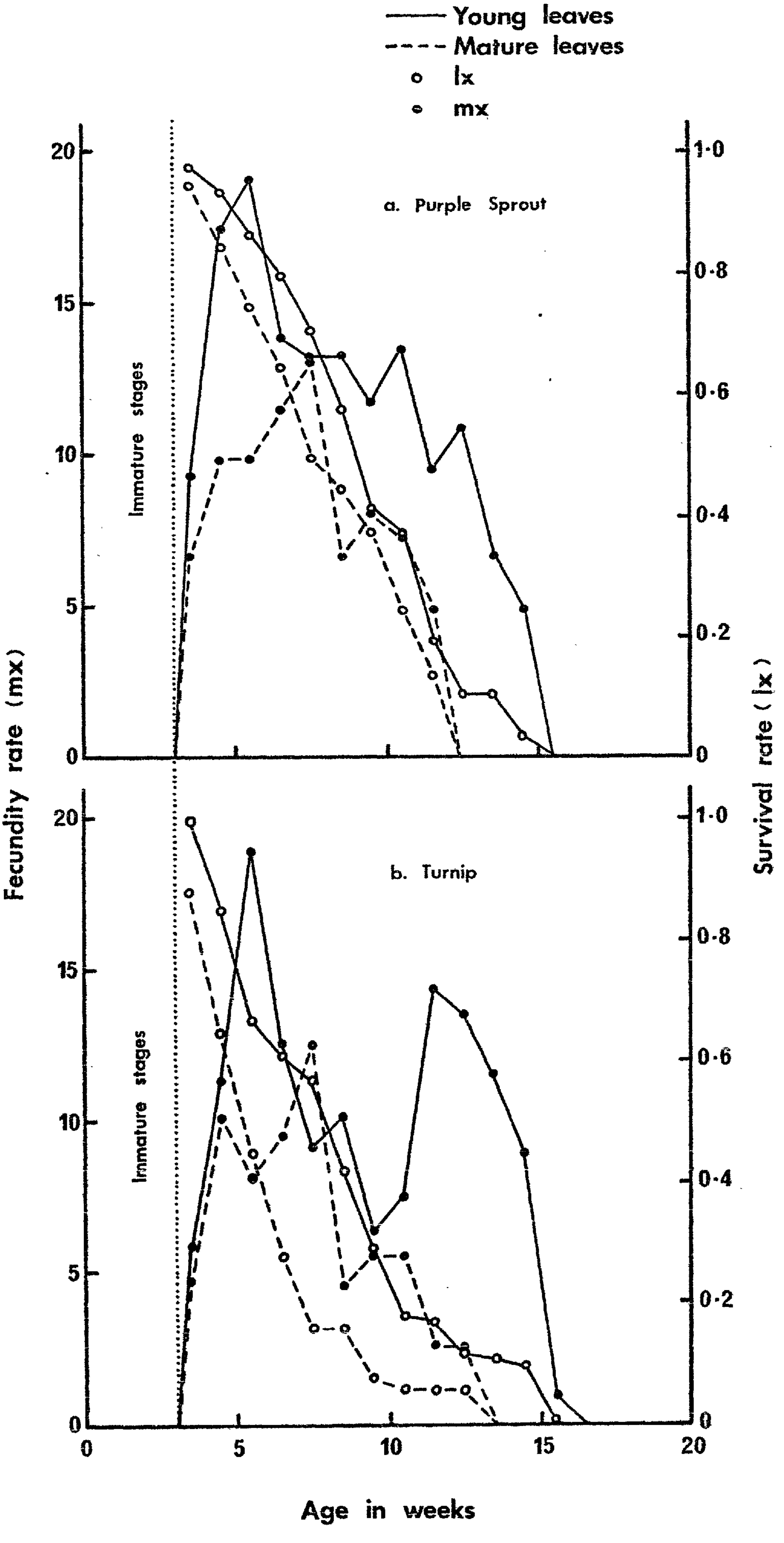

Young leaves
Mature leaves
lx
mx
a. Purple Sprout
b. Turnip
Immature stages
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
0
0·2
0·4
0·6
0·8
1·0

Table 39(a): Life table data for A. brassicae females reared on young leaves of Turnip at 20°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks) x	l_x	m_x	l_xm_x	xl_xm_x	Provisional r_m's							
					0.77				0.76			
					r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
3.5	1	5.99	5.99	20.97	2.70	4.30	73.70	441.46	2.66	4.34	76.71	459.48
4.5	.85	11.38	9.67	43.52	3.47	3.53	34.12	329.98	3.42	3.58	35.87	346.90
5.5	.67	18.90	12.66	69.63	4.24	2.76	15.80	200.03	4.18	2.82	16.78	212.39
6.5	.61	12.59	7.68	49.92	5.01	1.99	7.32	56.18	4.94	2.06	7.85	60.26
7.5	.57	9.16	5.22	39.15	5.78	1.22	3.39	17.68	5.70	1.30	3.67	19.15
8.5	.42	10.23	4.30	36.55	6.55	0.45	1.57	6.74	6.46	0.54	1.72	7.38
9.5	.29	6.45	1.87	17.77	7.32	-0.32	0.73	1.36	7.22	-0.22	0.80	1.50
10.5	.18	7.55	1.36	14.28	8.09	-1.09	0.34	0.46	7.98	-0.98	0.38	0.51
11.5	.17	14.49	2.46	28.29	8.86	-1.86	0.16	0.38	8.74	-1.74	0.18	0.43
12.5	.12	13.50	1.62	20.25	9.63	-2.63	0.07	0.12	9.50	-2.50	0.08	0.13
13.5	.11	11.50	1.27	17.15	10.40	-3.40	0.03	0.04	10.26	-3.26	0.04	0.05
14.5	.10	9.00	0.90	13.05	11.17	-4.17	0.02	0.01	11.02	-4.02	0.02	0.02
15.5	.01	1.00	0.01	0.16	11.94	-4.84	0.01	0	11.78	-4.78	0.01	0

Table 39(a): Continued

Ro = 55.01	Total	1054.44	Total	1108.20
r_m = 0.762				
T = 5.26				
λ = 2.14				

Table 39(b): Life table data for A. brassicae females reared on mature leaves of Turnip at 20°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.65				0.64			
x	l_x	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
3.5	.88	4.86	4.28	14.98	2.28	4.72	112.17	480.08	2.24	4.76	116.75	499.67
4.5	.65	10.27	6.68	30.06	2.93	4.07	58.56	391.16	2.88	4.12	61.56	411.22
5.5	.45	8.25	3.71	20.41	3.58	3.42	30.57	113.41	3.52	3.48	32.46	120.43
6.5	.28	9.50	2.66	17.29	4.23	2.77	15.96	42.45	4.16	2.84	17.12	45.53
7.5	.16	12.50	2.00	15.00	4.88	2.12	8.33	16.66	4.80	2.20	9.03	18.05
8.5	.16	4.50	0.72	6.12	5.53	1.47	4.35	3.13	5.44	1.56	4.76	3.43
9.5	.08	5.50	0.40	3.80	6.18	0.82	2.27	0.91	6.08	0.92	2.51	1.00
10.5	.06	5.50	0.33	3.47	6.83	0.17	1.19	0.39	6.72	0.28	1.32	0.44
11.5	.06	2.50	0.15	1.73	7.48	-0.48	0.62	0.09	7.36	-0.36	0.70	0.10
12.5	.06	2.50	0.15	1.88	8.13	-1.13	0.32	0.05	8.00	-1.00	0.37	0.06
					Total			1048.33	Total			1099.93

$R_o = 21.08$

$r_m = 0.6406$

$T = 4.76$

$\lambda = 1.90$

Table 40(a): Life table data for *A. brassicae* females reared on young leaves of Mustard at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.40				0.39			
x	lx	m_x	lxm_x	$xlxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} lxm_x$
7.5	1	4.17	4.17	31.28	3.00	4.00	54.60	227.67	2.93	4.07	58.56	244.18
8.5	1	7.59	7.59	64.52	3.40	3.60	36.60	277.78	3.32	3.68	39.65	300.92
9.5	1	6.85	6.85	65.08	3.80	3.20	24.53	168.05	3.71	3.29	26.84	183.87
10.5	1	8.91	8.91	93.56	4.20	2.80	16.44	146.52	4.10	2.90	18.17	161.93
11.5	1	6.83	6.83	78.55	4.60	2.40	11.02	75.29	4.49	2.51	12.30	84.04
12.5	1	7.66	7.66	95.75	5.00	2.00	7.39	56.60	4.88	2.12	8.33	63.82
13.5	1	6.50	6.50	87.75	5.40	1.60	4.95	32.19	5.27	1.73	5.64	36.66
14.5	1	5.24	5.24	75.98	5.80	1.20	3.32	17.40	5.66	1.34	3.82	20.01
15.5	1	6.17	6.17	95.64	6.20	0.80	2.23	13.73	6.05	0.95	2.59	15.95
16.5	1	3.91	3.91	64.52	6.60	0.40	1.49	5.83	6.44	0.56	1.75	6.85
17.5	.83	4.20	3.49	61.01	7.00	0	1.00	3.49	6.83	0.17	1.19	4.14
18.5	.83	5.30	4.40	81.38	7.40	-0.40	0.67	2.95	7.22	-0.22	0.80	3.53
19.5	.83	5.00	4.15	80.93	7.80	-0.80	0.45	1.86	7.61	-0.61	0.54	2.25
20.5	.83	5.90	4.90	100.39	8.20	-1.20	0.30	1.48	8.00	-1.00	0.37	1.80
21.5	.81	7.36	5.96	128.18	8.60	-1.60	0.20	1.20	8.39	-1.39	0.25	1.48

Table 40(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.40				0.39			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
22.5	.67	8.90	5.96	134.17	9.00	-2.00	0.14	0.81	8.78	-1.78	0.17	1.01
23.5	.67	8.01	5.37	126.12	9.40	-2.40	0.09	0.49	9.17	-2.17	0.11	0.61
24.5	.67	8.01	5.37	131.57	9.80	-2.80	0.06	0.33	9.56	-2.56	0.08	0.42
25.5	.67	7.40	4.96	126.43	10.20	-3.20	0.04	0.20	9.95	-2.95	0.05	0.26
26.5	.67	4.65	3.12	82.56	10.60	-3.60	0.03	0.09	10.34	-3.34	0.04	0.11
27.5	.60	5.88	3.53	97.02	11.00	-4.00	0.02	0.06	10.73	-3.73	0.02	0.08
28.5	.50	6.32	3.16	90.06	11.40	-4.40	0.01	0.04	11.12	-4.12	0.02	0.05
29.5	.40	8.34	3.34	98.41	11.80	-4.80	0.01	0.03	11.51	-4.51	0.01	0.04
30.5	.33	6.25	2.06	62.91	12.20	-5.20	0.01	0.01	11.90	-4.90	0.01	0.02
31.5	.33	6.75	2.23	70.25	12.60	-5.60	0	0	12.29	-5.29	0.01	0.01
32.5	.33	8.25	2.72	88.40	-	-	-	-	-	-	-	-
33.5	.33	12.25	4.04	135.34	-	-	-	-	-	-	-	-
34.5	.33	13.25	4.37	150.77	-	-	-	-	-	-	-	-
35.5	.33	10.08	3.33	118.22	-	-	-	-	-	-	-	-

Table 40(a): Continued

R_o = 140.29 r_m = 0.394 T = 12.55 λ = 1.48	Total	1034.1	Total	1134.04

Figure 14: Longevity and age-specific fecundity of <u>A. brassicae</u> females reared on young and mature leaves of Mustard at 15°C.

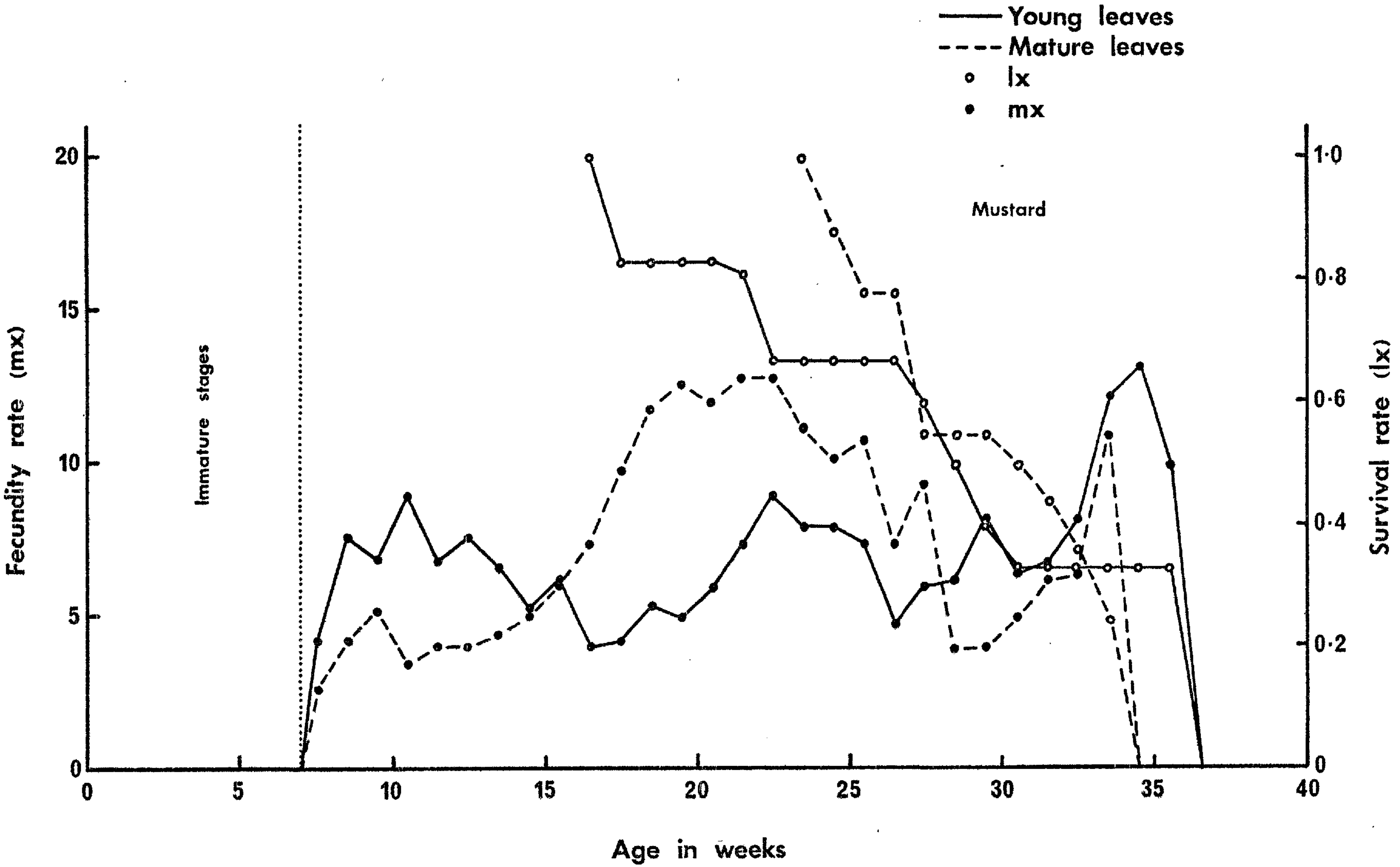

Young leaves
Mature leaves
lx
mx
Mustard
Immature stages
Fecundity rate (mx)
Survival rate (lx)
Age in weeks
0
5
10
15
20
25
30
35
40
0·2
0·4
0·6
0·8
1·0

Table 40(b): Life table data for A. brassicae females reared on mature leaves of Mustard at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.35				0.34			
x	lx	mx	lxmx	xlxmx	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
7.5	1	2.50	2.50	18.75	2.63	4.37	79.04	197.61	2.55	4.45	85.63	214.07
8.5	1	4.18	4.18	35.53	2.98	4.02	55.70	232.83	2.89	4.11	60.95	254.76
9.5	1	5.28	5.28	50.16	3.33	3.67	39.25	207.25	3.23	3.77	43.38	229.05
10.5	1	3.33	3.33	34.97	3.68	3.32	27.66	92.11	3.57	3.43	30.88	102.82
11.5	1	3.95	3.95	45.43	4.03	2.97	19.49	76.99	3.91	3.09	21.98	86.81
12.5	1	4.11	4.11	51.38	4.38	2.62	13.74	56.45	4.25	2.75	15.64	64.29
13.5	1	4.28	4.28	57.78	4.73	2.27	9.68	41.43	4.59	2.41	11.13	47.65
14.5	1	4.88	4.88	70.76	5.08	1.92	6.82	33.29	4.93	2.07	7.92	38.67
15.5	1	6.06	6.06	93.93	5.43	1.57	4.81	29.13	5.27	1.73	5.64	34.18
16.5	1	7.39	7.39	121.94	5.78	1.22	3.39	25.03	5.61	1.39	4.01	29.67
17.5	1	9.66	9.66	169.05	6.13	0.87	2.39	23.06	5.95	1.05	2.86	27.60
18.5	1	11.83	11.83	218.86	6.48	0.52	1.68	19.90	6.29	0.71	2.03	24.06
19.5	1	12.56	12.56	244.92	6.83	0.17	1.19	14.89	6.63	0.37	1.45	18.18
20.5	1	11.85	11.85	242.93	7.18	-0.18	0.84	9.98	6.97	0.03	1.03	12.21
21.5	1	12.78	12.78	273.27	7.53	-0.53	0.59	7.48	7.31	-0.31	0.73	9.32

Table 40(b): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.35				0.34			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
22.5	1	12.78	12.78	287.55	7.88	-0.88	0.44	5.30	7.65	-0.65	0.52	6.67
23.5	1	11.16	11.16	262.26	8.23	-1.23	0.29	3.26	7.99	-0.99	0.37	4.15
24.5	.88	10.23	9.00	220.56	8.58	-1.58	0.21	1.85	8.33	-1.33	0.26	2.38
25.5	.78	10.65	8.31	211.83	8.93	-1.93	0.15	1.21	8.67	-1.67	0.19	1.56
26.5	.78	7.43	5.80	153.58	9.28	-2.28	0.10	0.59	9.01	-2.01	0.13	0.78
27.5	.55	9.40	5.17	142.18	9.63	-2.63	0.07	0.37	9.35	-2.35	0.10	0.55
28.5	.55	4.10	2.26	66.52	9.98	-2.98	0.05	0.11	9.69	-2.69	0.07	0.15
29.5	.55	3.90	2.15	63.43	10.33	-3.33	0.04	0.08	10.03	-3.03	0.05	0.10
30.5	.50	5.03	2.52	76.86	10.68	-3.68	0.03	0.06	10.37	-3.37	0.03	0.09
31.5	.44	6.27	2.76	86.94	11.03	-4.03	0.02	0.05	10.71	-3.71	0.02	0.07
32.5	.36	6.42	2.31	75.08	11.38	-4.38	0.01	0.03	11.05	-4.05	0.02	0.04
33.5	.25	11.08	2.77	92.80	11.73	-4.73	0.01	0.02	11.39	-4.39	0.01	0.03

Table 40(b): Continued

Ro = 171.56 r_m = 0.349 T = 14.74 λ = 1.42	Total 1080.36	Total 1209.91

Table 41(a): Life table data for A. brassicae females reared on young leaves of Purple Sprout at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.38				0.39			
x	lx	mx	lxmx	xlxmx	rmx	7-rmx	e^{7-rmx}	e^{7-rmx}lxmx	rmx	7-rmx	e^{7-rmx}	e^{7-rmx}lxmx
7.5	1	3.21	3.21	24.08	2.93	4.07	58.56	187.97	2.85	4.15	63.43	203.62
8.5	1	7.78	7.78	66.13	3.32	3.68	39.65	308.45	3.23	3.77	43.38	337.50
9.5	1	7.29	7.29	69.26	3.71	3.29	26.84	195.68	3.61	3.39	29.67	216.26
10.5	1	7.93	7.93	83.27	4.10	2.90	18.17	144.12	3.99	3.01	20.29	160.88
11.5	1	7.93	7.93	91.20	4.49	2.51	12.30	97.58	4.37	2.63	13.87	110.02
12.5	1	5.01	5.01	62.63	4.88	2.12	8.33	41.74	4.75	2.25	9.49	47.53
13.5	1	5.29	5.29	71.42	5.27	1.73	5.64	29.84	5.13	1.87	6.49	34.32
14.5	1	5.29	5.29	76.71	5.66	1.34	3.82	20.20	5.51	1.49	4.44	23.47
15.5	.86	5.75	4.95	76.73	6.05	0.95	2.59	12.80	5.89	1.11	3.03	15.02
16.5	.84	5.63	4.73	78.05	6.44	0.56	1.75	8.28	6.27	0.73	2.08	9.82
17.5	.71	7.20	5.11	89.43	6.83	0.17	1.19	6.06	6.65	0.35	1.42	7.25
18.5	.71	6.50	4.62	85.47	7.22	-0.22	0.80	3.71	7.03	-0.03	0.97	4.48
19.5	.71	5.80	4.12	80.34	7.61	-0.61	0.54	2.24	7.41	-0.41	0.66	2.73
20.5	.71	5.50	3.91	80.16	8.00	-1.00	0.37	1.44	7.79	-0.79	0.45	1.77
21.5	.63	3.86	2.43	52.25	8.39	-1.39	0.25	0.61	8.17	-1.17	0.31	0.75

Table 41(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.38				0.39			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
22.5	.57	4.76	2.71	60.98	8.78	-1.87	0.15	0.42	8.55	-1.55	0.21	0.58
23.5	.51	5.63	2.87	67.45	9.17	-2.17	0.11	0.33	8.93	-1.93	0.15	0.42
24.5	.43	4.82	2.07	50.72	9.56	-2.56	0.08	0.16	9.31	-2.31	0.10	0.21
25.5	.29	6.75	1.96	49.98	9.95	-2.95	0.05	0.10	9.69	-2.69	0.07	0.13
26.5	.20	3.20	0.64	16.96	10.34	-3.34	0.04	0.02	10.07	-3.07	0.05	0.03
27.5	.14	6.00	0.84	23.10	10.73	-3.73	0.02	0.02	10.45	-3.45	0.03	0.03
28.5	.14	5.50	0.77	21.95	11.12	-4.12	0.02	0.01	10.83	-3.83	0.02	0.02
29.5	.14	8.50	1.19	35.11	11.51	-4.51	0.01	0.01	11.21	-4.21	0.01	0.02
30.5	.14	6.00	0.84	25.62	11.90	-4.90	0.01	0.01	11.59	-4.59	0.01	0.01
31.5	.14	5.00	0.70	22.05	12.29	-5.29	0.01	0	11.97	-4.97	0.01	0
32.5	.14	1.00	0.14	4.55	-	-	-	-	-	-	-	-
	Ro = 94.33				Total			1061.80	Total			1176.84
	r_m = 0.386											
	T = 11.78											
	λ = 1.47											

Table 41(b): Life table data for A. brassicae females reared on mature leaves of Purple Sprout at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.33				0.32			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	3.16	3.16	23.70	2.48	4.52	91.84	290.20	2.40	4.60	99.48	314.37
8.5	1	3.59	3.59	30.52	2.81	4.19	66.02	237.02	2.72	4.28	72.24	259.34
9.5	1	5.24	5.24	47.78	3.14	3.86	47.47	248.72	3.04	3.96	52.46	274.88
10.5	.95	3.74	3.56	37.38	3.47	3.53	34.12	121.48	3.36	3.64	38.09	135.61
11.5	.76	3.66	2.78	31.97	3.80	3.20	24.53	68.20	3.68	3.32	27.66	76.90
12.5	.75	3.50	2.63	32.88	4.13	2.87	17.64	46.39	4.00	3.00	20.09	52.82
13.5	.75	2.34	1.76	23.76	4.46	2.54	12.68	22.32	4.32	2.68	14.59	25.67
14.5	.69	2.34	1.61	23.35	4.79	2.21	9.12	14.68	4.64	2.36	10.59	17.05
15.5	.65	2.00	1.30	20.15	5.12	1.88	6.55	8.52	4.96	2.04	7.69	10.00
16.5	.65	3.34	2.17	35.81	5.45	1.55	4.71	10.22	5.28	1.72	5.58	12.12
17.5	.65	2.50	1.63	28.53	5.78	1.22	3.39	5.52	5.60	1.40	4.06	6.61
18.5	.56	3.75	2.10	38.85	6.11	0.89	2.44	5.11	5.92	1.08	2.94	6.18
19.5	.56	2.50	1.40	27.30	6.44	0.56	1.75	2.45	6.24	0.76	2.14	2.99
20.5	.56	2.00	1.12	22.96	6.77	0.23	1.26	1.41	6.56	0.44	1.55	1.74
21.5	.50	4.25	2.13	45.80	7.10	-0.10	0.90	1.93	6.88	0.12	1.13	2.40

Table 41(b): Continued

Pivotal age (weeks) x	lx	m_x	lxm_x	$xlxm_x$	Provisional r_m's							
					0.33				0.32			
					r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
22.5	.45	4.00	1.80	40.50	7.43	-0.43	0.65	1.17	7.20	-0.20	0.82	1.47
23.5	.33	2.25	0.74	17.39	7.76	-0.76	0.47	0.35	7.52	-0.52	0.59	0.44
24.5	.33	2.75	0.91	22.30	8.09	-1.09	0.34	0.31	7.84	-0.84	0.43	0.39
25.5	.33	4.75	1.57	40.04	8.42	-1.42	0.24	0.38	8.16	-1.16	0.31	0.49
26.5	.33	1.50	0.50	13.25	8.75	-1.75	0.17	0.09	8.48	-1.48	0.23	0.11
27.5	.33	3.00	0.99	27.23	9.08	-2.08	0.12	0.12	8.80	-1.80	0.17	0.16
28.5	.28	2.50	0.70	19.95	9.41	-2.41	0.09	0.06	9.12	-2.12	0.12	0.08
29.5	.05	2.00	0.10	2.95	9.74	-2.74	0.06	0.01	9.44	-2.44	0.09	0.01
	Ro = 43.49				Total			1086.66	Total			1201.79
	r_m = 0.3291											
	T = 11.46											
	λ = 1.39											

Figure 15: Longevity and age-specific fecundity of _A. brassicae_ females reared on young and mature leaves of (a) Purple Sprout, (b) Turnip at 15°C.

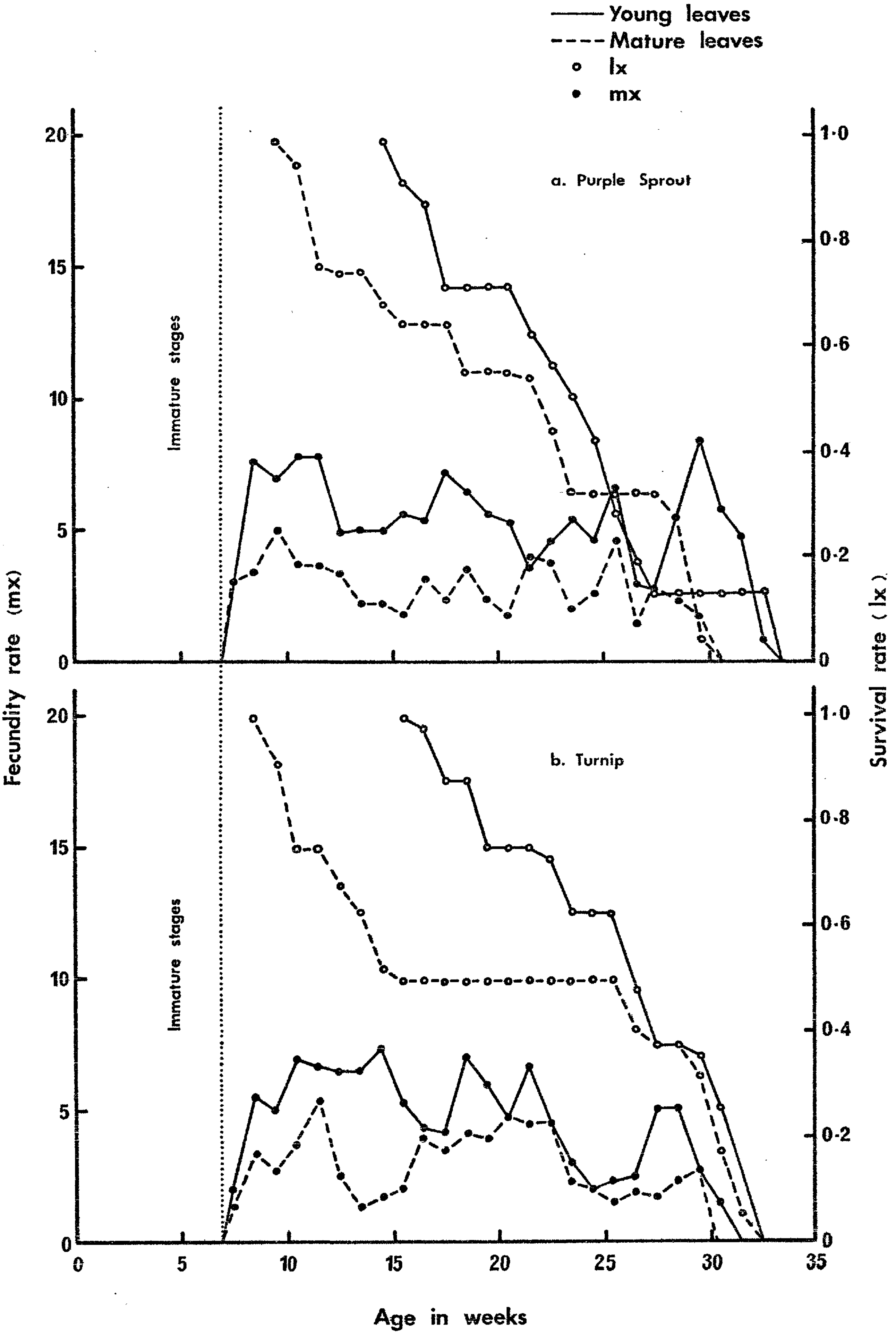

——— Young leaves
- - - - Mature leaves
○ lx
● mx
a. Purple Sprout
b. Turnip
Immature stages
Immature stages
Fecundity rate (mx)
0
5
10
15
20
Survival rate (lx)
0
0·2
0·4
0·6
0·8
1·0
Age in weeks
0
5
10
15
20
25
30
35

Table 42(a): Life table data for A. brassicae females reared on young leaves of Turnip at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.37				0.36			
x	lx	m_x	l_xm_x	xl_xm_x	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}l_xm_x$
7.5	1	2.06	2.06	15.45	2.78	4.22	68.03	140.15	2.70	4.30	73.70	151.82
8.5	1	5.64	5.64	47.94	3.15	3.85	46.99	265.04	3.06	3.94	51.42	290.00
9.5	1	5.01	5.01	47.60	3.52	3.48	32.46	162.62	3.42	3.58	35.87	179.73
10.5	1	7.31	7.31	76.76	3.89	3.11	22.42	163.90	3.78	3.22	25.03	182.96
11.5	1	6.75	6.75	77.63	4.26	2.74	15.49	104.54	4.14	2.86	17.46	117.87
12.5	1	6.38	6.38	79.75	4.63	2.37	10.70	68.25	4.50	2.50	12.18	77.72
13.5	1	6.58	6.58	88.83	5.00	2.00	7.39	48.62	4.86	2.14	8.50	55.93
14.5	1	7.44	7.44	107.88	5.37	1.63	5.10	37.97	5.22	1.78	5.93	44.12
15.5	1	5.24	5.24	81.22	5.74	1.26	3.53	18.47	5.58	1.42	4.14	21.68
16.5	.98	4.32	4.23	69.80	6.11	0.89	2.44	10.30	5.94	1.06	2.89	12.21
17.5	.88	4.07	3.58	62.65	6.48	0.52	1.68	6.02	6.30	0.70	2.01	7.21
18.5	.88	6.86	6.04	111.74	6.85	0.15	1.16	7.02	6.66	0.34	1.40	8.49
19.5	.75	6.00	4.50	87.75	7.22	-0.22	0.80	3.61	7.02	-0.02	0.98	4.41
20.5	.75	4.66	3.50	71.75	7.59	-0.59	0.55	1.94	7.38	-0.38	0.68	2.39
21.5	.75	6.57	4.93	106.00	7.96	-0.96	0.38	1.89	7.74	-0.74	0.48	2.35

Table 42(a): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.37				0.36			
x	lx	mx	$lxmx$	$xlxmx$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxmx$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxmx$
22.5	.73	4.42	3.23	72.68	8.33	-1.33	0.26	0.85	8.10	-1.10	0.33	1.08
23.5	.63	3.00	1.89	44.42	8.70	-1.70	0.18	0.35	8.46	-1.46	0.23	0.44
24.5	.63	1.90	1.20	29.40	9.07	-2.07	0.13	0.15	8.82	-1.82	0.16	0.19
25.5	.63	2.10	1.32	33.66	9.44	-2.44	0.09	0.12	9.18	-2.18	0.11	0.15
26.5	.48	2.45	1.18	31.27	9.81	-2.81	0.06	0.07	9.54	-2.54	0.08	0.09
27.5	.38	5.16	1.96	53.90	10.18	-3.18	0.04	0.08	9.90	-2.90	0.06	0.11
28.5	.38	5.18	1.97	56.15	10.55	-3.55	0.03	0.06	10.26	-3.26	0.04	0.08
29.5	.36	2.82	1.02	30.09	10.92	-3.92	0.02	0.02	10.62	-3.62	0.03	0.03
30.5	.25	1.50	0.38	11.59	11.29	-4.29	0.01	0.01	10.98	-3.98	0.02	0.01
	Ro	=	93.34		Total			1042.05	Total			1163.46
	r_m	=	0.365									
	T	=	12.43									
	λ	=	1.44									

Table 42(b): Life table data for A. brassicae females reared on mature leaves of Turnip at 15°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.29			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
7.5	1	1.39	1.39	10.43	2.25	4.75	115.58	160.66	2.18	4.82	123.97	172.31
8.5	1	3.45	3.45	29.33	2.55	4.45	85.63	295.41	2.47	4.53	92.76	320.02
9.5	.91	2.75	2.50	23.75	2.85	4.15	63.43	158.59	2.76	4.24	69.41	173.52
10.5	.75	3.91	2.93	30.77	3.15	3.85	46.99	137.69	3.05	3.95	51.94	152.17
11.5	.75	5.41	4.06	46.69	3.45	3.55	34.81	141.34	3.34	3.66	38.86	157.78
12.5	.68	2.62	1.78	22.25	3.75	3.25	25.79	45.91	3.63	3.37	29.08	51.76
13.5	.63	1.40	0.88	11.88	4.05	2.95	19.11	16.81	3.92	3.08	21.76	19.15
14.5	.52	1.67	0.87	12.62	4.35	2.65	14.15	12.31	4.21	2.79	16.28	14.16
15.5	.50	2.02	1.01	15.66	4.65	2.35	10.49	10.59	4.50	2.50	12.18	12.30
16.5	.50	3.97	1.99	32.84	4.95	2.05	7.77	15.46	4.79	2.21	9.12	18.14
17.5	.50	3.59	1.80	31.50	5.25	1.75	5.75	10.36	5.08	1.92	6.82	12.28
18.5	.50	4.15	2.08	38.48	5.55	1.45	4.26	8.87	5.37	1.63	5.10	10.62
19.5	.50	4.14	2.07	40.37	5.85	1.15	3.16	6.54	5.66	1.34	3.82	7.91
20.5	.50	4.76	2.38	48.79	6.15	0.85	2.34	5.57	5.95	1.05	2.86	6.80
21.5	.50	4.64	2.32	49.88	6.45	0.55	1.73	4.02	6.24	0.76	2.14	4.96

Table 42(b): Continued

Pivotal age (weeks)					Provisional r_m's							
					0.30				0.29			
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
22.5	.50	4.65	2.33	52.43	6.75	0.25	1.28	2.99	6.53	0.47	1.60	3.73
23.5	.50	2.27	1.14	26.79	7.05	-0.05	0.95	1.08	6.82	0.18	1.20	1.36
24.5	.50	4.02	2.01	49.25	7.35	-0.35	0.70	1.42	7.11	-0.11	0.90	1.80
25.5	.50	1.64	0.82	20.91	7.65	-0.65	0.52	0.43	7.40	-0.40	0.67	0.55
26.5	.41	2.04	0.84	22.26	7.95	-0.95	0.39	0.32	7.69	-0.69	0.50	0.42
27.5	.38	1.83	0.70	19.12	8.25	-1.25	0.29	0.20	7.98	-0.98	0.38	0.26
28.5	.38	2.32	0.88	25.13	8.55	-1.55	0.21	0.19	8.27	-1.27	0.28	0.25
29.5	.32	2.84	0.91	26.81	8.85	-1.85	0.16	0.14	8.56	-1.56	0.21	0.19
30.5	.18	0	0	0	-	-	-	-	-	-	-	-
31.5	.06	0	0	0	-	-	-	-	-	-	-	-
	R_o = 41.14 r_m = 0.294 T = 12.64 λ = 1.34				Total			1036.90	Total			1142.44

Table 43: Population statistics of A. brassicae females reared on young and mature leaves of three species of Cruciferacae at 25°, 20°, and 15°C.

Population statistics	Host plants species	25°C		20°C		15°C	
		Leaf types					
		Young	Mature	Young	Mature	Young	Mature
G.R.R. (♀/♀)	Mustard	188.82	157.57	342.23	302.47	205.93	203.02
	Purple Sprout	84.38	69.67	144.72	79.27	147.13	70.66
	Turnip	73.48	49.14	135.74	65.88	113.42	71.48
Ro (♀/♀)	Mustard	147.55	141.23	249.87	235.71	140.29	171.56
	Purple Sprout	60.77	44.64	85.28	45.47	94.33	43.49
	Turnip	32.00	17.79	55.01	21.08	93.34	41.14
r_m (♀/♀/week)	Mustard	1.445	1.436	1.005	0.992	0.394	0.349
	Purple Sprout	1.201	1.188	0.861	0.743	0.386	0.329
	Turnip	1.030	0.920	0.762	0.641	0.365	0.294
T (weeks)	Mustard	3.45	3.45	5.47	5.50	12.55	14.74
	Purple Sprout	3.42	3.20	5.16	5.14	11.78	11.46
	Turnip	3.37	3.13	5.26	4.76	12.43	12.64
λ (♀/♀/week)	Mustard	4.24	4.20	2.73	2.70	1.48	1.42
	Purple Sprout	3.32	3.28	2.37	2.10	1.47	1.39
	Turnip	2.80	2.51	2.14	1.90	1.44	1.34

Table 44: The contribution of each age group to the value of r_m when r_m = 1.04 on young leaves of Earliest at 25°C.

Pivotal age (x)	$e^{7-r_m x} l_x m_x$	Percentage contribution of each age group
2.5	699.54	66.52
3.5	279.37	26.57
4.5	54.88	5.22
5.5	14.67	1.40
6.5	2.94	0.28
7.5	0.21	0.02
	1051.61	100.00

Figure 16: Relationship between the finite rate of increase (λ), net reproductive rate (Ro), generation time (T), and temperature.

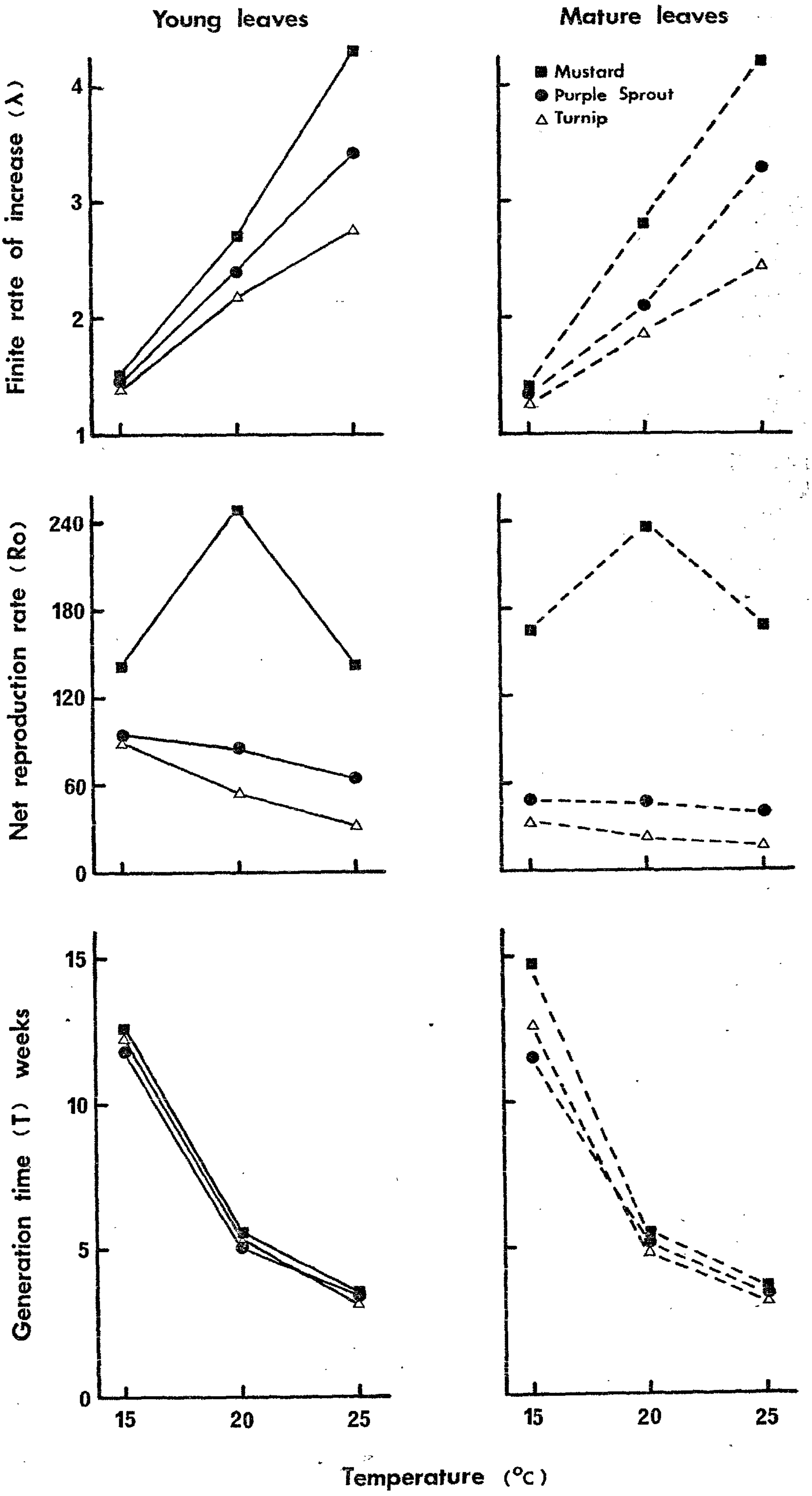
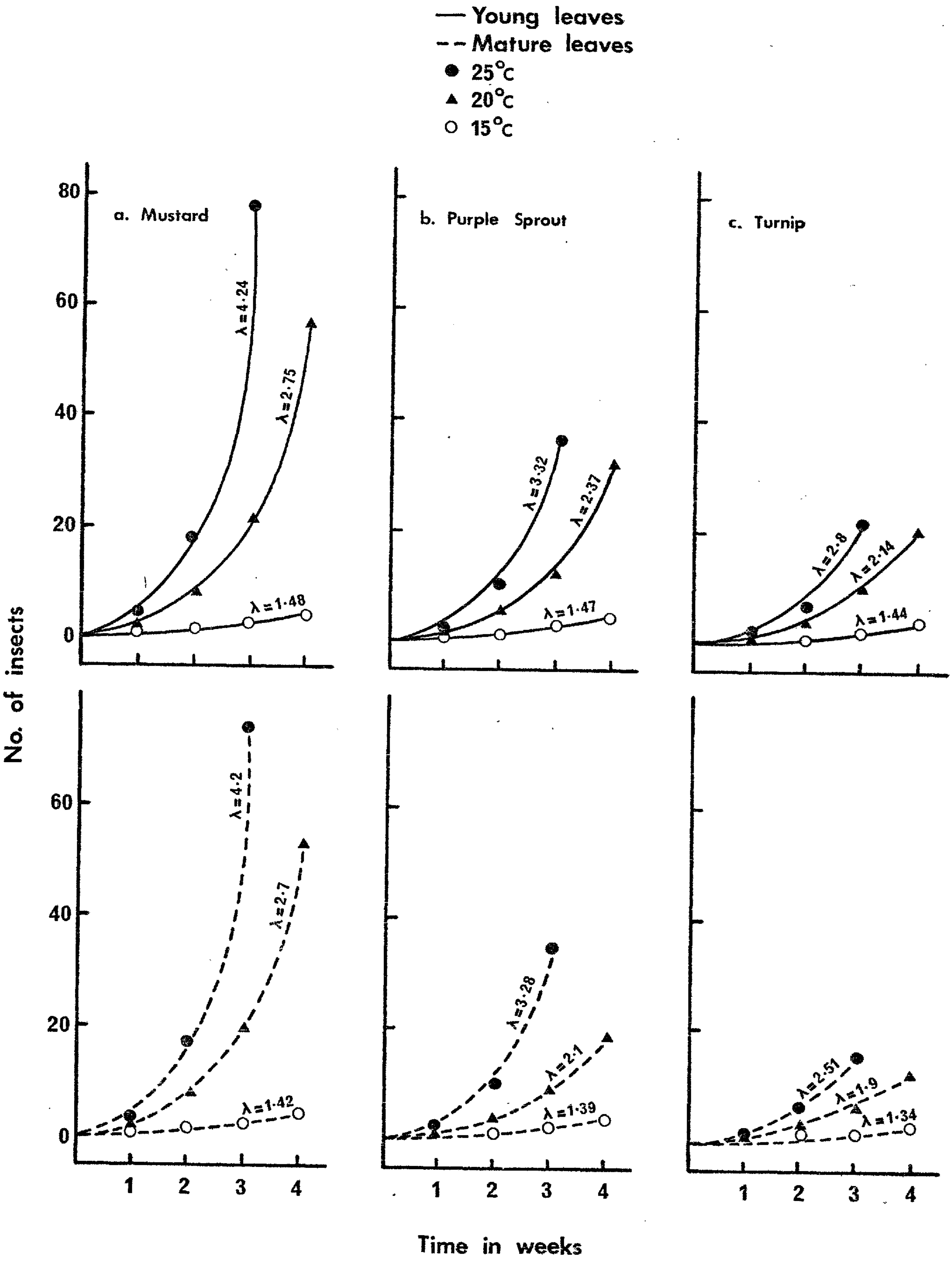

Young leaves
Mature leaves
■ Mustard
● Purple Sprout
△ Turnip
Finite rate of increase (λ)
1
2
3
4
Net reproduction rate (Ro)
0
60
120
180
240
Generation time (T) weeks
0
5
10
15
15
20
25
15
20
25
Temperature (°c)

Figure 17: Curves for various values of λ/♀/week, showing population growth of *A. brassicae* on young (———) and mature (-----) leaves of (a) Mustard, (b) Purple Sprout, (c) Turnip at 25°, 20°, and 15°C.


— Young leaves
-- Mature leaves
● 25°c
▲ 20°c
○ 15°c
a. Mustard
b. Purple Sprout
c. Turnip
No. of insects
80
60
40
20
0
λ=4·24
λ=2·75
λ=1·48
λ=3·32
λ=2·37
λ=1·47
λ=2·8
λ=2·14
λ=1·44
λ=4·2
λ=2·7
λ=1·42
λ=3·28
λ=2·1
λ=1·39
λ=2·51
λ=1·9
λ=1·34
1
2
3
4
Time in weeks

D. DISCUSSION

Population changes occur because of interactions of many factors e.g. parasitism, predation, food shortage, and disease. When some of the factors are excluded, it becomes possible to evaluate the effects of any introduced variable such as leaf age, host plant, and temperature on the population growth. This can only be achieved under laboratory conditions.

The effect of leaf age on longevity of the cabbage whitefly, A. brassicae, when reared on different varieties and species of Brassica, was compared as mean longevity as well as the time required for the populations to reach 50% mortality (LT_{50}).

The mean longevities on young leaves were generally higher than on mature leaves. The differences were significant for the varieties ($p < .01$, $p = .05$, $p = .01$ at 25°, 20°, and 15°C respectively); whereas the differences were not significant for the species. Because arithmetic means are subject to influence by extreme values, the time required for the populations to reach 50% mortality was considered a more rational approach. LT_{50} was in most cases longer on young leaves than on mature leaves. The differences were, however, not significant for all plant types. Henderson and Holloway (1942) and Watson (1964) had similar conclusion in their studies on leaf age effect on mites. Bernays et al (1975) reported lower survival of nymphs of Locusta migratoria migratorioides (R. & F.) on seedling leaves than on mature leaves. Thus the effect of leaf age on survival varies with different insects and their host plants.

Ranges of LT_{50} on the varieties (young and mature leaves combined) were 1-3 weeks, 1-4 weeks, and 8-12 weeks at 25°, 20°, and 15°C respectively. The differences within each temperature regime were not significant. The conclusion was that survival was not affected by the varieties. Dahms et al (1936) found significant differences in the varietal effects of sorghum on the longevity of the chinch bug, Blissus leucopterus.

Among the host plant species, LT50 ranged from 2-6 weeks at 25°, 3-12 weeks at 20°, and 15-23 weeks at 15°C. The differences were significant (p = .05) at the two higher temperatures respectively. At 15°C, survival on Mustard (22 weeks) and Turnip (19.5 weeks) were not significantly different but both differed significantly (p = .05) from Purple Sprout (16 weeks). Generally, the species had profound effect on survival. Brown (1972) observed that the survival of the wheat aphid, Schizaphis graminum (Rond.), on wheat, rye, and oats differed significantly.

Comparison of the survival values on the varieties and species at 25°C showed the longest on Mustard (6 weeks), followed by Purple Sprout (4.5 weeks). Earliest (3.0 weeks), June Star (2.5 weeks), Turnip (2.5 weeks), and Large Blood Red (2.5 weeks) did not differ significantly. Golden Acre (1.5 weeks) had the shortest value.

Chemical synthesis varies inherently between species and also differs within the same species. Total protein content of some species is consistently higher than that of other species (Boyd, 1968, 1970a). The differences in longevity of the cabbage whitefly, A. brassicae, could be attributed to differences in quantity/quality of such chemicals that promote survival.

Leaf age had remarkable effect on fecundity, more eggs being always laid on young leaves than on mature leaves. Hussey and Gurney (1959) reported a marked decline in the oviposition rate of the greenhouse whitefly, T. vaporariorum, with leaf age. Trehan (1944) showed that the cotton whitefly, Bemisia gossypiperda, laid 51.5%, 46.7%, and 1.8% of the total eggs on the top, middle, and bottom leaves respectively. Southwood and

Reader (1976) found that only 20% of the eggs of the viburnum whitefly, *A. jelinekii*, were laid on leaves more than one year old. Henderson and Holloway (1942) found no significant difference in the number of eggs laid on young leaves and medium (mature) leaves by the citrus red mite, *Panonychus citri*. Henneberry (1962) and Watson (1964) observed a significant difference in the fecundity of the two spotted spider mite, *Tetranychus telarius*, on young and mature leaves. Van Emden (1969b) showed the different response of two aphid species: *B. brassicae* and *M. persicae* to leaf age; the former showed reduced fecundity on old leaves whereas the latter showed an increase. Brown (1972) reported that the mean fecundity of the wheat aphid, *S. graminum*, on young and mature leaves did not differ significantly. Thus the effect of leaf age on fecundity of phytophagous insects/arthropods seems variable.

Other effects of leaf age have been reported. For example, Grison (1947) was able to obtain extra generations of the browntail moth, *Euprotis phaerrhoea*, when first instar larvae were fed on young apple sprouts while senescent leaves promoted diapause. Lees (1953a) showed that senescent apple leaves led to the production of 'winter females' which laid diapausing eggs. Grison (1956) found that the females of the Colorado beetle, *L. decemlineata*, stopped egg laying when fed with senescent leaves of potato.

The fact that leaf age had no significant effect on longevity would mean that the differences observed in the mean fecundity and age specific fecundity data could not have resulted from differences in longevity. The differences could be a reflection of the physical and chemical properties of the leaves.

Plant tissues such as endodermis and schlerenchyma are known to impede or deflect the penetrating stylets of Aphidoidea and Coccoidea (Arnaud, 1918; Staniland, 1924; Entwistle and Longworth, 1963). Tanton (1962) showed that mustard beetles, Phaedon cochleariae Fab., reared on the leaves of kale, turnip, and Brussels sprout suffered great larval and pupal mortality as the toughness of the leaves increased. Feeny (1970) implicated leaf toughness as the main factor preventing late larval feeding by the winter moth. Iheagwam (1974) recorded a significant negative correlation between leaf toughness of some varieties of cabbage and fecundity of the cabbage whitefly, A. brassicae. Moran (1975) considered leaf hardness as the overriding factor involved in ovipositional preferences for young flush leaves in the citrus psylla, Trioza eryteae. However, Pollard (1971) remarked that studies on the relationship between the physical properties of plants and the feeding of insects are complicated by other properties such as elasticity, plasticity, toughness and tenacity, as well as hardness.

Chemical properties of leaves are often considered of greater importance to insects than the physical properties with respect to feeding and consequently, reproduction. This statement is supported by the results of Iheagwam (1974) who found that the partial correlation coefficient for fecundity and nitrogen to be significant while that for fecundity and leaf toughness, though high, was not significant. Evans (1938) reported that the higher the percentage total nitrogen in cabbage leaves the greater the number of nymphs produced by B. brassicae. Henneberry (1962) observed that more progeny were produced by mites on plants supplied high nitrogen than were produced by those on plants supplied low nitrogen. Kennedy and Booth (1951) noticed that the growing and senescing leaves of certain plants were more susceptible to M. persicae and A. fabae than mature green leaves of the same plants. The explanation for the leaf age effect was that the aphids' food would be especially rich in soluble organic nitrogen where growth, and hence protein synthesis, takes place, and where senescence with attendant protein breakdown occurs, but low where neither growth nor senescence was in progress as in mature leaves. Van Emden and Bashford (1969) reported a significant decrease in soluble nitrogen in three leaf ages of Brussels sprout: 1.046% in young leaves, 0.865% in medium (mature) leaves, and 0.690% in old leaves. The difference in the nitrogen content of young and mature leaves seems the proximate, but by no means the only cause of the difference in fecundity on both leaf types.

Fraenkel (1953) postulated that the insects nutritional requirements could not be a factor in determining host plant specificity. Host specificity was attributed to the presence of "secondary" biochemicals such as essential oils, alkaloids and glycosides within the plant tissues.

Gupta and Thorsteinson (1960) showed that the diamond black moth, Plutella maculipennis, laid eggs on rough plastic surfaces but the addition of allyl isothiocyanate generally increased the number of eggs laid. The extensive work of Straatman (1962) with Papilionacea indicated the role of specific volatile attractants in oviposition. Mustard oil glucoside sinigrin is present in the crucifers - the host plants of the cabbage whitefly, A. brassicae. Wensler (1962) showed that the cabbage aphid, B. brassicae, did not feed on young leaves of the broad bean, Vicia faba L., except when the leaves were treated with sinigrin. These observations prove that oviposition can be regulated and stimulated by chemical attractants. Since the concentration of allyl isothiocyanate is higher in young leaves than in mature leaves of Brussels sprout (Van Emden and Bashford, 1969), this could be regarded as one of the several possible factors accounting for higher fecundity of the cabbage whitefly, A. brassicae, on young leaves than on mature leaves.

The age specific fecundity rate (m_x) on all plant types reached a peak early in the reproductive periods, generally within the first three weeks, but usually in the second week. At lower temperatures, however, the occurrence was rather erratic.

Provision of new food in oviposition experiments is known to cause a stimulation of egg production. In the experiments described in this section, insects were regularly being moved to new leaves of the same physiological age to ensure accurate counting of eggs and also to reduce any repressive effect of high egg density on oviposition. This may have given rise to the bimodal and multimodal nature of some of the age specific fecundity curves.

When maximum fecundity rate (m_x) is related to the survival rate (lx) of the populations (Figs. 2-6 and 10-15) it becomes quite evident that maximum m_x occurred when a high proportion of the females was still alive. Both the maximum m_x and the age at which it is attained are more important factors in determining the intrinsic rate of increase (r_m) than the total number of individuals produced through the whole life of the insect. Only individuals produced in the first few weeks have a significant effect on the size of the intrinsic rate of increase (r_m) and the net reproductive rate (Ro). This fact is clearly illustrated in Table 44. For $r_m = 1.04$ (on young leaves of Earliest at 25°C), 66.5% of it was accounted for by the first week of adult life. The first two weeks combined contributed 93.1% towards the final value. On the other hand, 1.4% was contributed in the fourth week and 0.02% in the sixth week. These results support the fact that r_m is determined to a much greater extent by the rate of oviposition in the first few weeks of adult life than by the total number of eggs laid in the life span of the adult. Thus with each successive week, eggs laid made a lessened contribution to the value of r_m.

The gross reproductive rate (G.R.R.) and the net reproductive rate (Ro) generally increased with decreasing temperature reaching a maximum at 15°C except on Mustard where the maximum values were reached at 20°C. From Table 43 it is clear that although Ro at 15°C was higher than either at 20° or 25°C, yet the values of r_m at the two latter temperatures were higher.

Temperature exerts a profound effect on r_m through its influence on all the main components of r_m: survival rate, fecundity rate, and development time. As was pointed out above, total fecundity is not as important in the growth of populations as is the age at which the maximum fecundity rate occurs. At 25°C, development time was short and maximum fecundity rate was reached quite early in the reproductive life. Though Ro at 15°C was higher than at 25°C or 20°C, the value of r_m was quite low. The major factor in reducing the rate of population growth at 15°C was the lengthened development time coupled with the fact that eggs were laid more slowly early in life.

The values of r_m at 15°C appear to have been underestimated because of the exaggerated generation times (T). This was probably because the eggs were assumed laid at the mid-point of the oviposition period. As Howe (1953b) pointed out, the mid-point method cannot be used with confidence if oviposition period is longer than four weeks.

The value of r_m increased 2.87 times for a rise of 10°C (from 15° to 25°C) on young leaves of the varieties and 3.20 times on the young leaves of the species. In general, results obtained in this investigation showed considerable shortening of the development time with increasing temperature. This supports the conclusion of Birch (1948) and Howe (1953a) that this is one of the major effects of temperature upon r_m.

The significance of the data on the population growth rate of the cabbage whitefly, *A. brassicae*, will be more apparent if they are considered in relation to the habitat of the insect.

Habitat is the template against which evolutionary pressures fashion the ecological strategy of a species. The instability-stability habitat spectrum gives rise to the r-K selection continuum (Southwood *et al*, 1974). Southwood (1968, 1971) pointed out that the stability of a habitat for a particular animal depends upon the relationship between the animals generation time (τ) and the length of time the habitat remains favourable (H). When the ratio τ/H approaches unity, the evolutionary pressures on animals with this type of habitat will be toward an r- strategy.

The cabbage whitefly, *A. brassicae*, feeds and breeds on leaves of cabbage, Brussels sprouts, Broccoli, cauliflower, Savoy, etc. Most of these vegetables mature soon after planting and are harvested. For example, Golden Acre is sown in January/February for late May/June harvesting. Similarly, for summer and autumn harvesting, spring sowing varieties of cabbage are sown in March/April and planted outdoors during June/July. Thus the habitat of the cabbage whitefly, *A. brassicae*, is transient.

The spectrum of r- to K- strategies is correlated with a range of habitat stabilities. MacArthur (1960) pointed out that the relationship is a general one between "opportunist" species (r- strategists) in unpredictable environments and "equilibrium" species (K- strategists) in predictable ones. Since the habitat of the cabbage whitefly, *A. brassicae*, is unpredictable, the insect possesses one of the attributes of r-strategists.

An r- strategist operates where the niche hypervolume is frequently empty and the premium is on the ability to exploit this opportunity rapidly.

From the population statistics recorded in this investigation, it is evident that the cabbage whitefly, A. brassicae, has a high population growth rate. This allows the insect to compete successfully against other species in exploiting the habitat and/or to use up the available resource before it deteriorates.

Considering the size (.012 mg - .144 mg on emergence) and the short generation time of the cabbage whitefly, A. brassicae, the high reproductive ability is hardly surprising since there is usually a close association between small size and a large reproductive rate. Bonner (1965) showed strong correlation between body size and generation time among organisms.

The high population growth rate and small size of the cabbage whitefly, A. brassicae, are adaptations to its ephemeral habitat. These two features qualify the insect as a typical r- strategist.

SECTION Ib: STUDIES ON THE POPULATION DYNAMICS OF THE GREENHOUSE WHITEFLY, *TRIALEURODES VAPORARIORUM*, ON DIFFERENT HOST PLANTS

A. MATERIALS AND METHODS

1. Plant types

The following experimental plants were used:

(a) Mustard

(b) Tomato

The plants were grown as described in Section Ia.

Experiments on fecundity and longevity were carried out on young leaves only and at one constant temperature (25°C).

2. Whitefly culture

Laboratory cultures of the greenhouse whitefly were maintained on tomato plants at 25°C. Other conditions were similar to those already described for the cabbage whitefly.

3. Construction of life tables and calculation of population parameters

The methods were similar to those already outlined in Section Ia.

B. RESULTS

1. Longevity and fecundity

(a) Longevity and age-specific survival rates (l_x)

Longevity of *T. vaporariorum* on young leaves of mustard and tomato is shown in Table 45 as mean longevity and as age-specific survival rates in Tables 47 and 48 and Figs. 19(a) and (b). Time for the population to reach 50% mortality (LT_{50}) was shorter (1½ weeks) on mustard and longer (3 weeks) on tomato.

(b) Fecundity and age-specific fecundity rates (m_x)

More eggs were laid on tomato leaves (73.5) than on mustard leaves (42.23) (Table 45). From the mean cumulative fecundity per female plotted in Fig. 20, fecundity was higher on tomato early in the adult life. However, towards the end of adult life, fecundity curves for both plants levelled off with that for mustard being superior.

The age-specific fecundity rates (m_x) are presented in Tables 47 and 48 and illustrated graphically in Figs. 19(a) and (b).

On mustard leaves, maximum fecundity was reached in the second week of the reproductive life (Fig. 19(a)) whereas on tomato leaves it was attained in the first week (Fig. 19(b)).

2. Population growth statistics

(a) Gross reproductive rate (G.R.R.)

The G.R.R. was higher on mustard leaves (8.29) than on tomato leaves (5.81) (Table 46).

On tomato leaves, the maximum fecundity rate (m_x) was reached in the first week of adult life. The value was higher than that reached on mustard in the first week of adult life. But from the second week of adult life, m_x was consistently higher on mustard than on tomato. Since G.R.R. $= \sum m_x$, the value on mustard was higher than that on tomato (Tables 47 and 48 and Figs. 19 and 20).

(b) Net reproductive rate (Ro)

The value of Ro was higher on tomato leaves (5.22) than on mustard (3.68) (Table 46).

(c) Intrinsic rate of increase (r_m)

r_m was higher on tomato leaves (0.550) than on mustard (0.409) (Table 46).

Figs. 18(a) and (b) illustrate the graphical determination of the true r_m values of the cabbage whitefly, *A. brassicae*, and the greenhouse whitefly, *T. vaporariorum*, when both species were reared on young leaves of mustard.

(d) Generation time (T)

The generation times were approximately equal (3 weeks) on both plant types (Table 46).

(e) Finite rate of increase (λ)

Since λ was derived from r_m, the value obtained on tomato leaves (1.73) was higher than that on mustard (1.51) (Table 46)

Table 45: Mean fecundity and longevity of *T. vaporariorum* females when reared on young leaves of Mustard and Tomato at 25°C.

	Mustard	Tomato
$\bar{x}$ no. eggs/♀	42.23 ± 6.76	73.50 ± 4.29
Range	1 - 153	38 - 101
$\bar{x}$ longevity (days)	10.30 ± 2.56	20.0 ± 2.35
Range	2 - 23	11 - 27
LT_{50} (weeks)	1.5	3.0

Table 46: Population statistics of *T. vaporariorum* females when reared on young leaves of mustard and tomato at 25°C.

Population statistics	Mustard	Tomato
G.R.R.	8.29	5.81
Ro	3.68	5.22
r_m	0.409	0.550
T	3.27	3.13
λ	1.51	1.73

Figure 18: Graphical calculations of true r_m's from two trial values for (a) *A. brassicae*, and (b) *T. vaporariorum*, when both were reared on young leaves of mustard at 25°C.

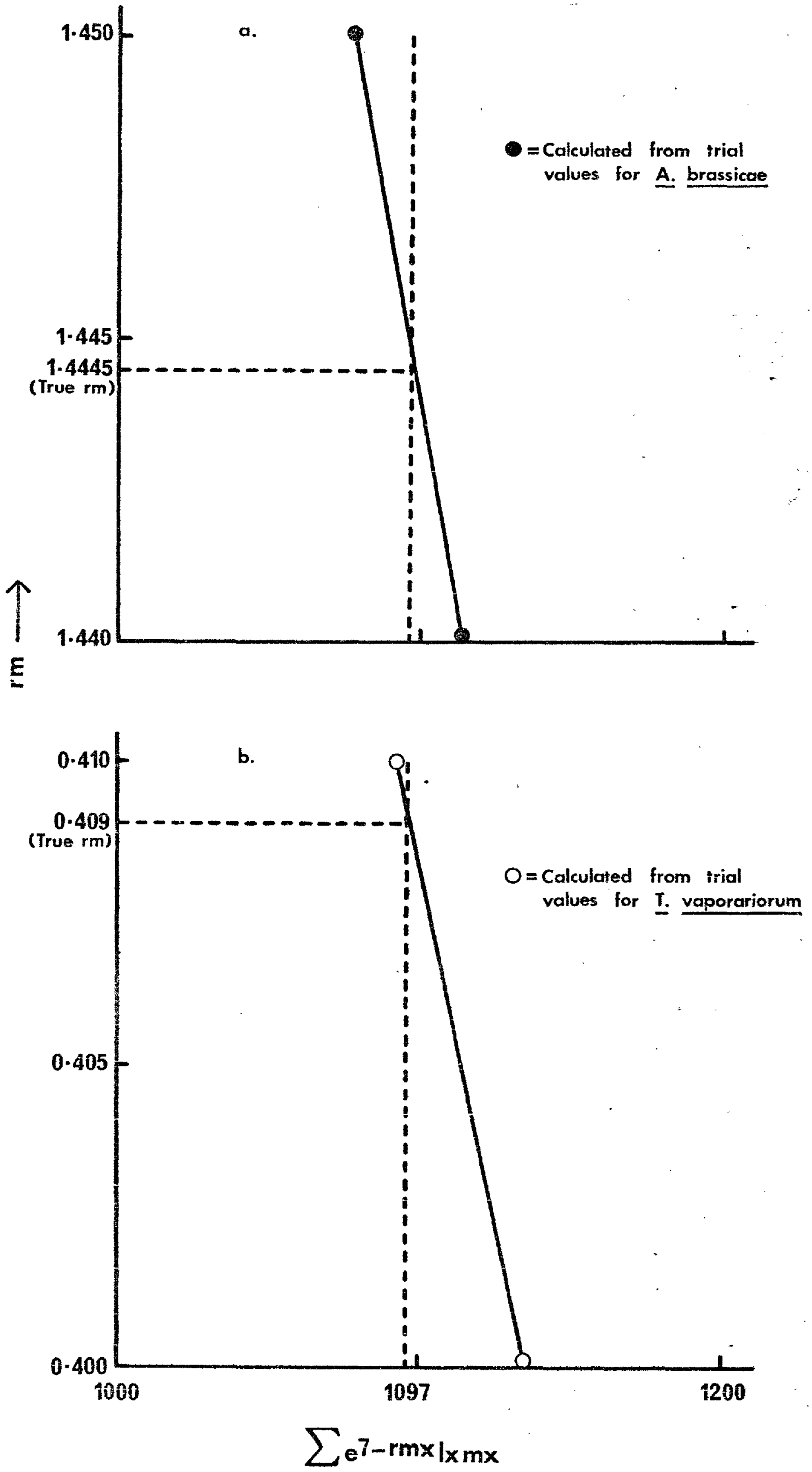

a.
1·450
1·445
1·4445
(True rm)
1·440
● = Calculated from trial values for A. brassicae
rm →
b.
0·410
0·409
(True rm)
0·405
0·400
○ = Calculated from trial values for T. vaporariorum
1000
1097
1200
$\sum e^{7-rmx} l_x m_x$

Table 47: Life table data for T. vaporariorum females reared on young leaves of Mustard at 25°C and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.41				0.40			
x	lx	m_x	lxm_x	$xlxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$	r_mx	$7-r_mx$	e^{7-r_mx}	$e^{7-r_mx}lxm_x$
2.5	.88	1.72	1.51	3.78	1.03	5.97	391.51	591.18	1.00	6.00	403.43	609.18
3.5	.45	3.30	1.49	5.20	1.44	5.56	259.82	387.13	1.40	5.60	270.43	402.94
4.5	.23	2.77	0.64	2.87	1.85	5.15	172.43	110.36	1.80	5.20	181.27	116.01
5.5	.07	0.50	0.04	0.19	2.26	4.74	114.43	4.58	2.20	4.80	121.51	4.86
	Ro	=	3.68		Total			1093.25	Total			1132.99
	r_m	=	0.409									
	T	=	3.27									
	λ	=	1.51									

Table 48: Life table data for T. vaporariorum females reared on young leaves of Tomato at 25°C, and table showing calculations of r_m with two provisional r_m's.

Pivotal age (weeks)					Provisional r_m's							
					0.55							
x	l_x	m_x	$l_x m_x$	$x l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$r_m x$	$7-r_m x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
2.5	1	2.69	2.69	6.73	1.38	5.62	275.89	742.14				
3.5	.91	2.05	1.87	6.55	1.93	5.07	159.17	297.65				
4.5	.73	0.79	0.58	2.61	2.48	4.52	91.84	53.27				
5.5	.28	0.28	0.08	0.44	3.03	3.97	52.98	4.24				
	Ro = 5.22				Total			1097.3				
	r_m = 0.55											
	T = 3.13											
	λ = 1.73											

Figure 19: Longevity and age-specific fecundity of adult *T. vaporariorum* females when reared on young leaves of (a) Mustard, and (b) Tomato at 25°C.

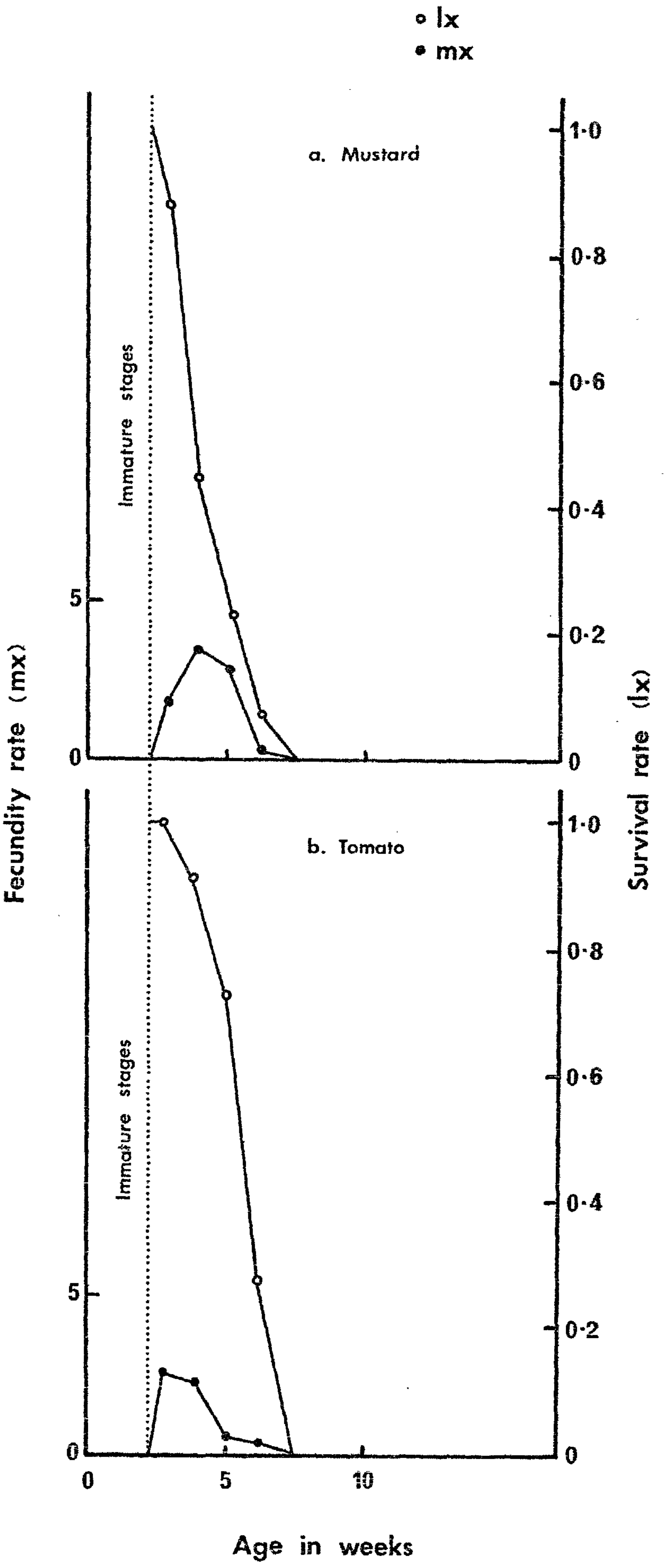
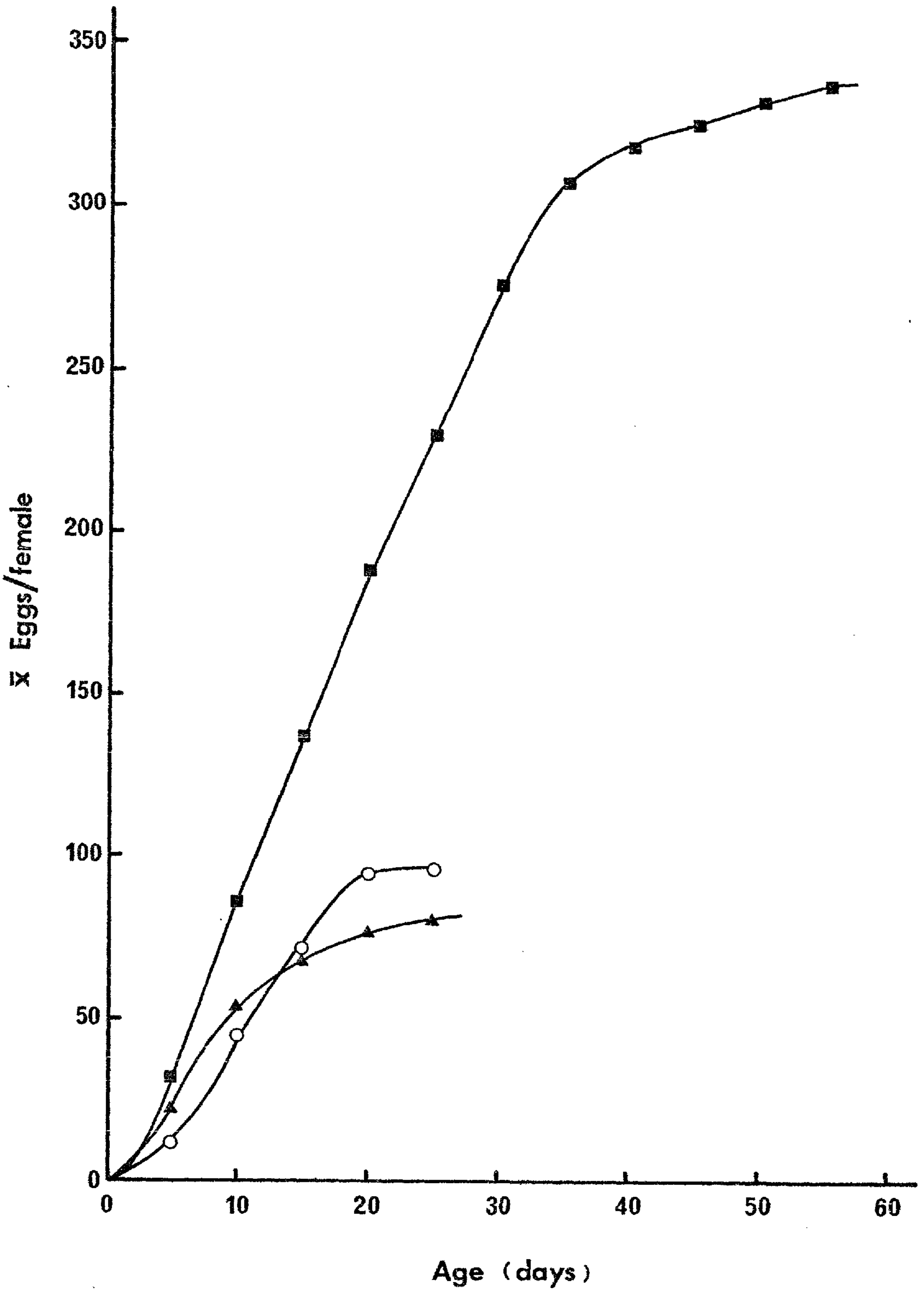

○ lx
● mx
a. Mustard
b. Tomato
Immature stages
Immature stages
Fecundity rate (mx)
0
5
0
5
Survival rate (lx)
0
0·2
0·4
0·6
0·8
1·0
0
0·2
0·4
0·6
0·8
1·0
Age in weeks
0
5
10

Figure 20: Cumulative total number of eggs laid per female *A. brassicae* on young leaves of mustard (■——■), and *T. vaporariorum* on young leaves of mustard (O——O) and young leaves of tomato (▲——▲) at 25°C.


x̄ Eggs/female
350
300
250
200
150
100
50
0
0
10
20
30
40
50
60
Age (days)

C. DISCUSSION

Phytophagous insects have been classified according to their feeding habits as monophagous, oligophagous, and polyphagous. These terms refer to the number of plant species accepted as food by the insect species concerned. Thorsteinson (1960) remarked that the above classification does not seem to be quite clear on whether the food plants should be enumerated by species, genera, or families.

Dethier (1947) suggested that oligophagy would be best defined in terms of attractance of several different chemicals, as in Papilio ajax larvae. Attractance to one chemical, or to a group of chemicals confused by the insect as one, would constitute monophagy, and an insect specific to the large group of cruciferous plants and other plant families that contain mustard-oil glucosides would be regarded as monophagous. On this basis, the cabbage whitefly, A. brassicae, could be classified as monophagous.

Thorsteinson (1960) pointed out that the oligophagous habit in L. decemlineata larvae may not be based on a restricted distribution of feeding stimulants, but on the absence of feeding inhibitors in the food plants and the presence of inhibitors in all other plants. If this view is applied to the cabbage whitefly, A. brassicae, it will explain its occurrence on non-cruciferous plants (Butler, 1938). It seems more appropriate to classify it as oligophagous.

Insects that feed on any plant free of feeding inhibitors were classified as polyphagous (Dethier, 1947). Since the greenhouse whitefly, T. vaporariorum, feeds on a wide range of taxonomically different plants, it is definitely polyphagous.

The fecundity of phytophagous insects varies with host plant species.

One of the crops on which the greenhouse whitefly, T. vaporariorum, causes great economic damage is tomato. It is, therefore, not surprising that its r_m was higher on the young leaves of tomato than on the young leaves of mustard on which it also feeds in the greenhouse. From the results of the cumulative fecundity (Fig. 20), it was higher on tomato leaves in the first two weeks of reproductive life but thereafter became higher on mustard leaves.

When the cabbage whitefly, A. brassicae, and the greenhouse whitefly, T. vaporariorum, were reared on young leaves of mustard, and their fecundities plotted as mean cumulative number of eggs per female (Fig. 20), the curve for A. brassicae increased sharply and continued for several days before levelling off. That for T. vaporariorum increased gradually and levelled off while that of A. brassicae was still increasing. The difference in the reproductive ability of the two species could be related to their different feeding habits.

Hussey (1965) pointed out that a form of stability similar to that found in tropical rain-forests could be introduced into glasshouses by a succession of crops in the same greenhouse, thus creating 'perennial' conditions. Since the greenhouse whitefly, T. vaporariorum, dwells mainly in greenhouses which may contain many different plants all the year round, it could be argued that its habitat is fairly stable when compared with that of the cabbage whitefly, A. brassicae. But because this stability is under man's control, a knowledge of the nature of the original habitat would be most helpful in this discussion. Unfortunately, there seems to be no published work on this aspect of the ecology.

Because of this possible difference in the relative stability of the habitats, it will be expected that the species that lives in a more unstable habitat will possess a higher intrinsic rate of increase for maximum exploitation of the habitat than the species that lives in a more stable habitat. This supposition is supported by the results obtained in this experiment in which the value of r_m was higher in the cabbage whitefly (1.45 on young leaves of mustard at 25°C) than in the greenhouse whitefly (0.55 on young leaves of tomato at 25°C).

At the present time one can only speculate as to the immediate causes (differences in feeding?) or ultimate factors (evolutionary pressures due to habitat stability?) responsible for this difference.

SECTION II: EFFECTS OF TEMPERATURE AND POPULATION DENSITY ON POPULATION PARAMETERS OF THE CABBAGE WHITEFLY, *A. BRASSICAE*

A. INTRODUCTION

The durations of growth and development of insects are influenced by temperature. The reciprocal of the developmental period at constant temperatures is often regarded as the speed of development (Davidson, 1944).

The term 'threshold of development' is usually taken to mean a point on the temperature scale at or below which development ceases. This view stems from the belief that the relationship between rate of insect development and temperature can be expressed as a straight line. However, experiments have shown that a non-linear relationship between temperature and the rate of development is the general rule.

Threshold of development has also been used to designate the minimum temperature at which some particular stage of development could be completed. Hodson and Al Rawy (1956) point out that this concept accords little recognition to the possibility that some development, though short of the completion of a process, might take place below the calculated threshold. Johnson (1940) emphasized the need for determining thresholds for the particular processes being studied.

In some insects development is arrested at certain stages of development. It seems obvious that the temperature relations of the resting stages (quiescence or diapause) will be different from the active stages and the pre- and post- diapause periods. Howe (1967) remarks that the concept of rate of development for a whole life cycle may be useful even when the various instars are known to differ, but it breaks down when development cannot be completed at any constant temperature.

Development in insects is a complex process with many temperature thresholds. The temperature threshold most commonly obtained in constant temperature experiments is that for complete development and hatching while that for the various larval stages has not received much attention. El-Khidir (1963) studied the effect of constant temperatures on egg development and duration of development from egg to adult in the cabbage whitefly, A. brassicae. No work seems to have been reported on the developmental rate and temperature thresholds of the larval instars.

Development periods are influenced by a number of factors. High larval density slows down the rate of development in some insects thereby prolonging the duration of development.

Pearl and Parker (1922) were the first to study the effect of density on the reproductive rate of laboratory insect populations of Drosophila. The variables they measured were "mean population average" and "imagoes per mated female per day". Watt (1960) commented that since the dependent variable Pearl and Parker counted was the number of imagoes, rather than the number of eggs, they were prone to the criticism that the effect of density on fecundity was confounded with the effect of density on pre-imaginal survival. The shape of the curve they obtained was termed "Drosophila-type" by Fujita (1954).

Allee (1931) showed that the effect of density on reproduction rate could be different from the "Drosophila-type". He found that the rate of increase of population per female Tribolium per day was greatest (after 11 days) not at the lowest density but at the second lowest. Fujita (1954) labelled the curve the "Allee-type".

Kirchner (1939) observed that the "Drosophila-type" and "Allee-type" curves were not each peculiar to certain species. He obtained both curves in experimental populations of the stick-insect Dixippus (Carausius) morosus

(Brunn. and Redt.). The Allee-type curve occurred in the largest universe while the Drosophila-type occurred in the smallest universe.

Utida (1941a) obtained an intermediate type of curve - "intermediate-type" (Fujita, 1954). Crombie (1942) studying laboratory populations of the beetle _Rhyzopertha_ _dominica_ (Fab.) also obtained an intermediate-type curve.

The aims of the investigation on the cabbage whitefly, _A._ _brassicae_, described in this section were to determine

i. the durations, rates, and temperature thresholds of development of the immature stages;

ii. the effect of larval density on duration of development;

iii. the effect of adult density on fecundity and longevity; and

iv. the pre-oviposition periods, fecundity, and longevity of the mated and virgin females.

B. MATERIALS AND METHODS

1. Duration, rates, and thresholds of development

The durations of development of the 5 immature stages (egg - instar IV) were determined at 25°, 20°, 15°C, and 10°C.

Whitefly cultures were maintained at each constant temperature with a photoperiod of LD 16:8.

At each constant temperature, young adults (males and females) from the culture were caged on young leaves of Brussels Sprout for 24 hours during which eggs were laid. Eggs thus laid were assumed to be of the same age. To avoid the retarding effect of high larval density on rate of development, the number of eggs on each leaf was between 10 and 30.

All immature stages were allowed to develop on intact leaves. The duration of development for each stage was taken as the mean number of days before the last individual in a particular stage completed its development. It was easy to know when the eggs hatched. For the larval stages, the presence of exuviae was used as an index to determine when development in one stage was completed and that for another stage started. Since each stage is morphologically different from the others, the general structure was also used as a criterion for determining the end of development at each stage.

The observed times for development were plotted against temperature to obtain the course of the temperature-time curve. The reciprocals for time were plotted against temperature. Each of the reciprocals was multiplied by 100, so that values on the ordinate represent the average percentage development made by each immature stage at the given temperature.

The temperature threshold of development was estimated graphically by extending the regression line until it intercepts the temperature axis. The point of interception was taken to represent the threshold.

2. Effect of larval density on development

The first larval instar of the cabbage whitefly is about .33 mm x .16 mm in size (Desphande, 1933). Because of their small size and difficulty in handling, it was more convenient to start with the egg stage. Eggs were obtained as described above.

The experiment was conducted at one constant temperature (20°C), and the host plant used was Earliest.

The range of densities investigated was 5-228. Only those larvae that hatched out within 24 hours of commencement of hatching were considered in the experiment.

The area of the leaf surface on which the larvae were confined was 3.14 cm^2, being the area of the leaf cage used. Individuals at each density level were observed until they all emerged as adults and the average duration of development was calculated. Reciprocals of the development times were used as points for the regression line.

A little difficulty was encountered with the very high density groups as some of the fourth instars did not emerge before the leaves on which they were being reared dried up.

3. Larval density and population growth curves (theoretical consideration)

The fecundity of the females resulting from the larval density experiments was not determined. However, results obtained from other experiments were used.

Since the larvae were reared on young leaves of Earliest at 20°C, the net reproductive rate (Ro) obtained in the population growth experiments at 20°C (see Section Ia) was assigned to the low (10) and high (110) density levels. The generation times (T) were obtained from the results of the duration of development described above. With Ro and T known, r_m and λ were calculated for the two density levels and curves for values of λ/♀/week were drawn as described in Section Ia.

4. Effect of adult density on fecundity and longevity

Virgin females were used for this study since male insects are often reported to interfere with oviposition. This approach, therefore, specifically excludes any possible depression in fecundity level due to males.

Virgin females were obtained by isolating the pupal stages singly. On emergence they were caged on young leaves of Mustard at 25°C. The densities (numbers/3.14 cm^2 of leaf surface) investigated were 1, 2, 3, and 4. The number of eggs laid was counted daily until the females died. Insects were frequently moved to new leaves for the same reasons given in Section Ia.

5. Fecundity and longevity of virgin females

Virgin females were obtained as described above and caged singly on young leaves of Mustard at 25°C. These were observed 24 hourly until the first eggs were laid. The time between emergence and first oviposition was the pre-oviposition period. Data for fecundity and longevity were obtained as described for mated females in Section Ia.

C. RESULTS

1. Development

(a) Developmental period

Durations of development of the egg and larval stages at 25°, 20°, and 15°C are presented in Table 49. Table 50 shows the percentage of the total duration of development (egg-adult) occupied by each stage. The temperature - time curves are illustrated in Figs. 23, 24, and 25.

The duration of development for each stage increased with decreasing temperature, being shortest at 25° and longest at 15°C.

On the average, 35% of the development time from egg to adult was occupied by the embryonic stage, 30% by instar IV, 13% by instar I, 12% by instar III, and 10% by instar II.

(b) Rates of development

The rate of development for each stage was determined as reciprocal of time for development multiplied by 100 to give the average percentage development in one day. Since the speed of development was derived from the duration of development described above, the trends were similar; speed of development being fastest in instar II and slowest in the egg stage at each constant temperature.

The rates of development are presented in Fig. 21.

(c) Developmental thresholds

Temperature thresholds of development were obtained by extrapolation from the regression lines of speed of development on temperature (Figs. 23-25).

Table 49: Duration of development (days) of immature stages of A. brassicae at constant temperatures (males and females not distinguished).

Temp.	Rep.	Egg	Av. duration	Instar I	Av. duration	Instar II	Av. duration	Instar III	Av. duration	Instar IV	Av. duration	Duration (egg-adult)	$\bar{x}$ duration (egg-adult)
25°C	i	6.2 ±.07 (30)*	6.2	2.9 ±.06 (22)	2.75	1.91±.09 (22)	2.14	2.16±.07 (31)	2.42	5.43±.12 (23)	5.49	18.6	19.01
	ii	6.3 ±.09 (24)		2.6 ±.08 (36)		2.33±.098 (36)		2.25±.09 (24)		5.65±.18 (23)		19.13	
	iii	6.1 ±.05 (35)		2.75±.14 (24)		2.19±.07 (32)		2.86±.08 (36)		5.40±.1 (24)		19.30	
20°C	i	8.67±.14 (18)	8.64	3.6 ±.13 (25)	3.48	2.54±.11 (28)	2.59	2.96±.09 (26)	3.00	7.78±.15 (22)	7.61	25.55	25.32
	ii	8.40±.17 (17)		3.6 ±.14 (25)		2.63±.10 (27)		3.08±.05 (26)		7.63±.16 (19)		25.34	
	iii	8.86±.14 (22)		3.24±.09 (25)		2.59±.11 (27)		2.96±.13 (23)		7.43±.13 (21)		25.08	
15°C	i	18.36±.12 (12)	18.76	6.2 ±.13 (10)	6.30	4.2 ±.13 (17)	4.33	5.5 ±.15 (12)	5.67	17.17±.38 (12)	16.97	51.43	52.1
	ii	18.84±.14 (16)		6.5 ±.22 (10)		4.31±.15 (16)		5.9 ±.07 (14)		16.88±.18 (16)		52.43	
	iii	19.09±.17 (11)		6.2 ±.13 (10)		4.47±.12 (17)		5.9 ±.1 (10)		16.77±.17 (13)		52.43	

* Figures in parentheses indicate number of observations.

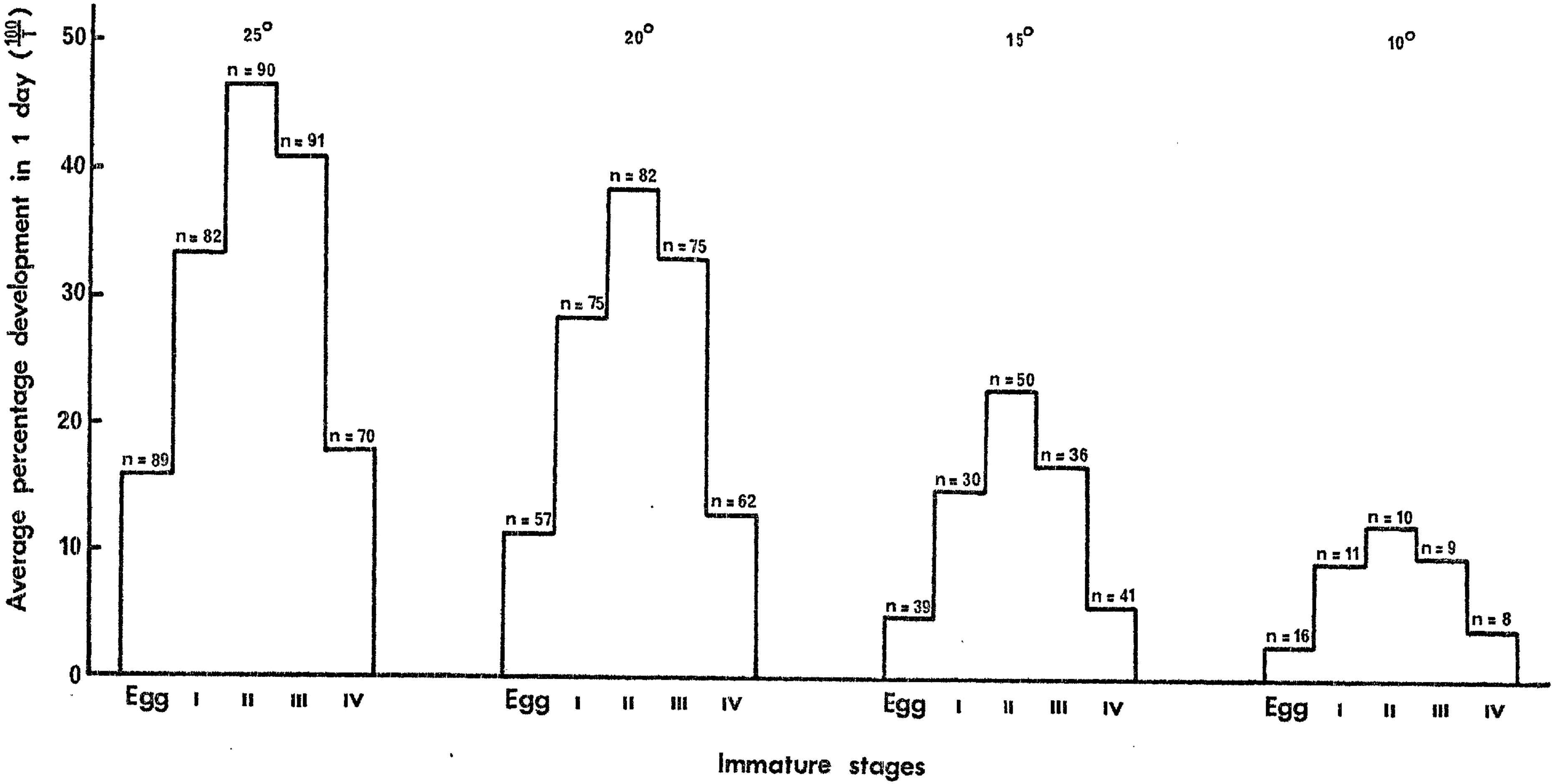
Table 50: Percentage of total duration of development (egg-adult) occupied by each immature stage at constant temperatures.

Stages	25°	20°	15°
Egg	33	34	37
Instar I	14	13	12
Instar II	11	10	8
Instar III	13	11	11
Instar IV	29	30	32

Table 51: Regression equations and temperature thresholds of development for immature stages of *A. brassicae*.

Immature stage	Regression equation	Temperature threshold
Egg	$y = -9.94 + 1.014x$	10°C
Instar I	$y = -15.00 + 2.04x$	7.3°C
Instar II	$y = -11.75 + 2.41x$	5.0°C
Instar III	$y = -16.60 + 2.37x$	6.5°C
Instar IV	$y = -14.00 + 1.32x$	10.4°C

Figure 21: Rates of development of immature stages of the cabbage whitefly <u>A. brassicae</u> at 25°, 20°, 15°, and 10°C. (n = number of observations)



Average percentage development in 1 day ($\frac{100}{T}$)
50
40
30
20
10
0
25°
n = 89
n = 82
n = 90
n = 91
n = 70
20°
n = 57
n = 75
n = 82
n = 75
n = 62
15°
n = 39
n = 30
n = 50
n = 36
n = 41
10°
n = 16
n = 11
n = 10
n = 9
n = 8
Egg I II III IV
Egg I II III IV
Egg I II III IV
Egg I II III IV
Immature stages

Figure 22: Temperature threshold of development for immature stages of *A. brassicae*.

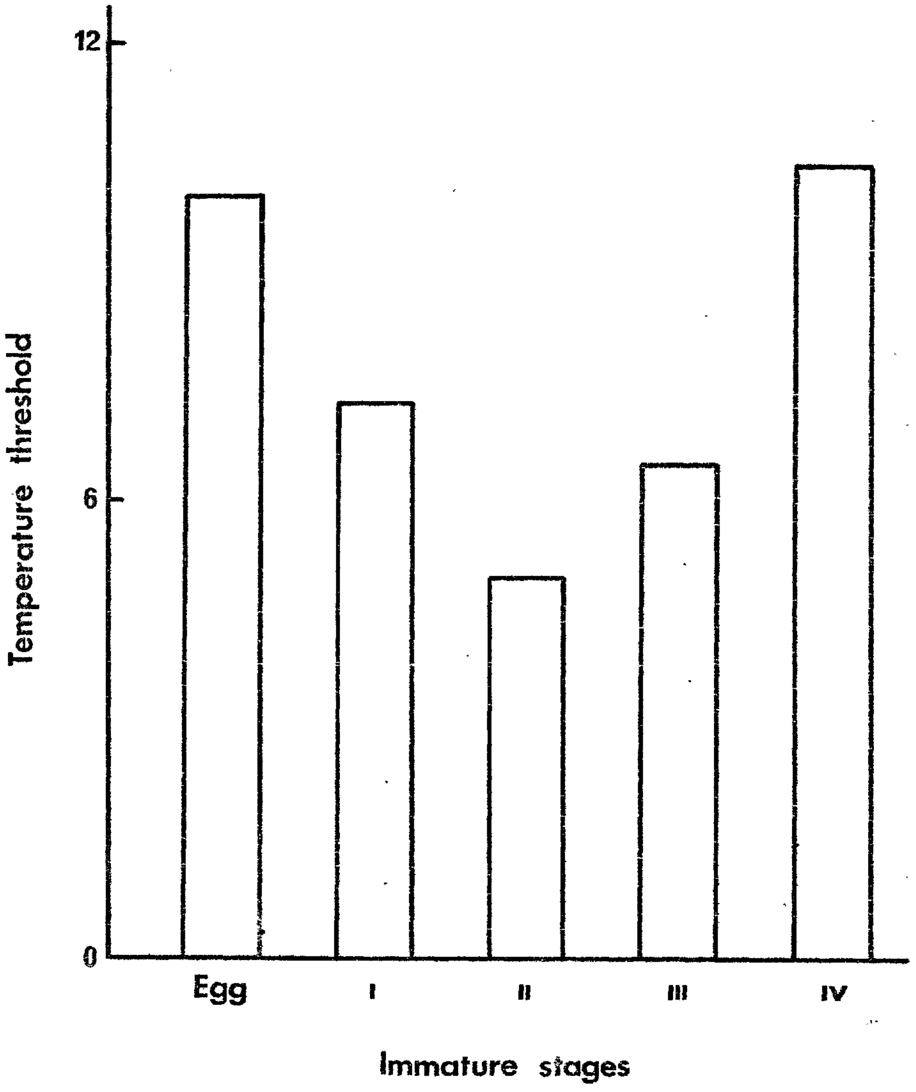

Temperature threshold
12
6
0
Egg
I
II
III
IV
Immature stages

Figure 23: Temperature-time curves (O———O) and graphical determination of temperature thresholds (●———●) for egg stage and first instar of the cabbage whitefly, *A. brassicae*.

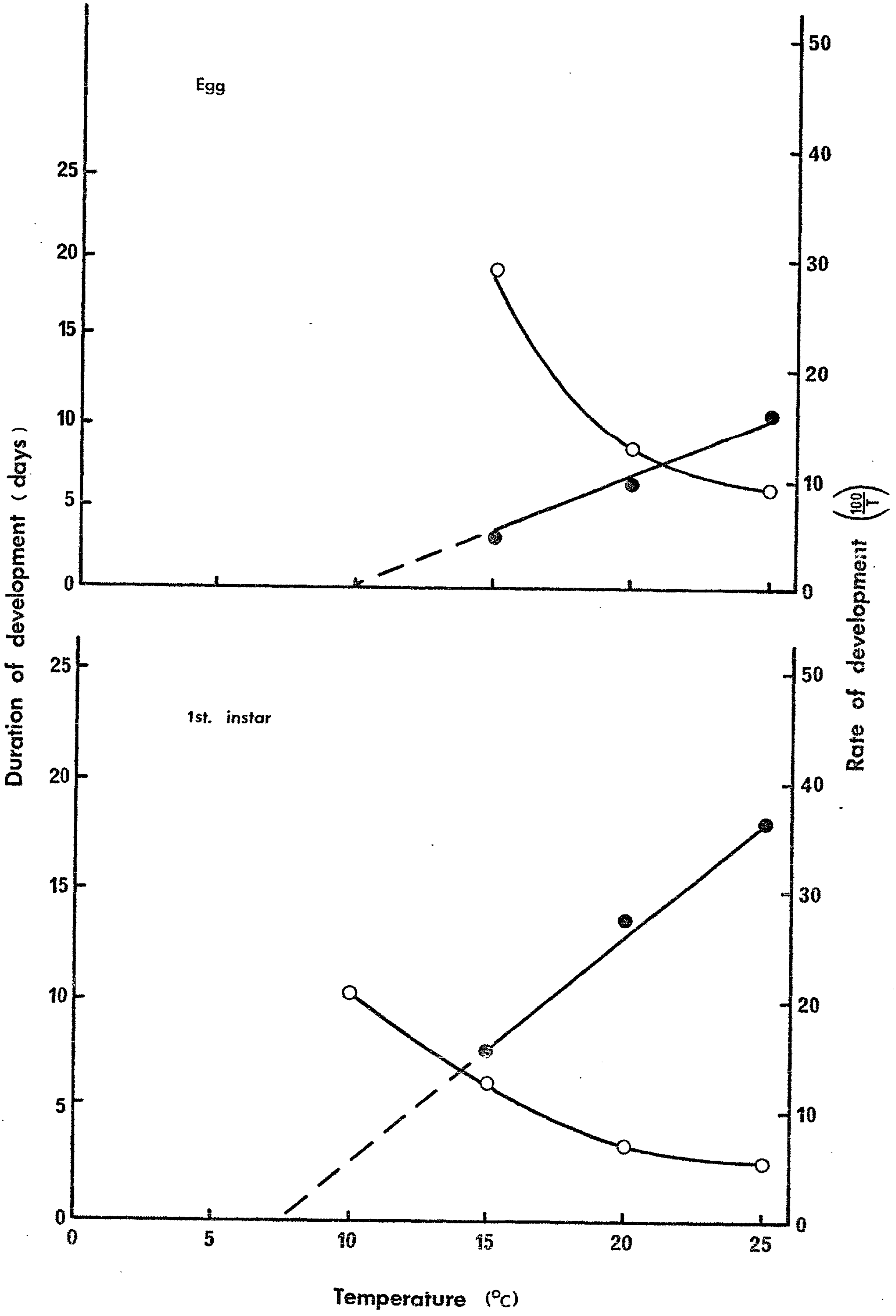

Egg
1st. instar
Duration of development (days)
Rate of development $\left(\frac{100}{T}\right)$
Temperature (°C)
0
5
10
15
20
25
30
40
50

Figure 24: Temperature-time curves (O———O) and graphical determination of temperature thresholds (●———●) for (a) second and (b) third instars of the cabbage whitefly, *A. brassicae*.

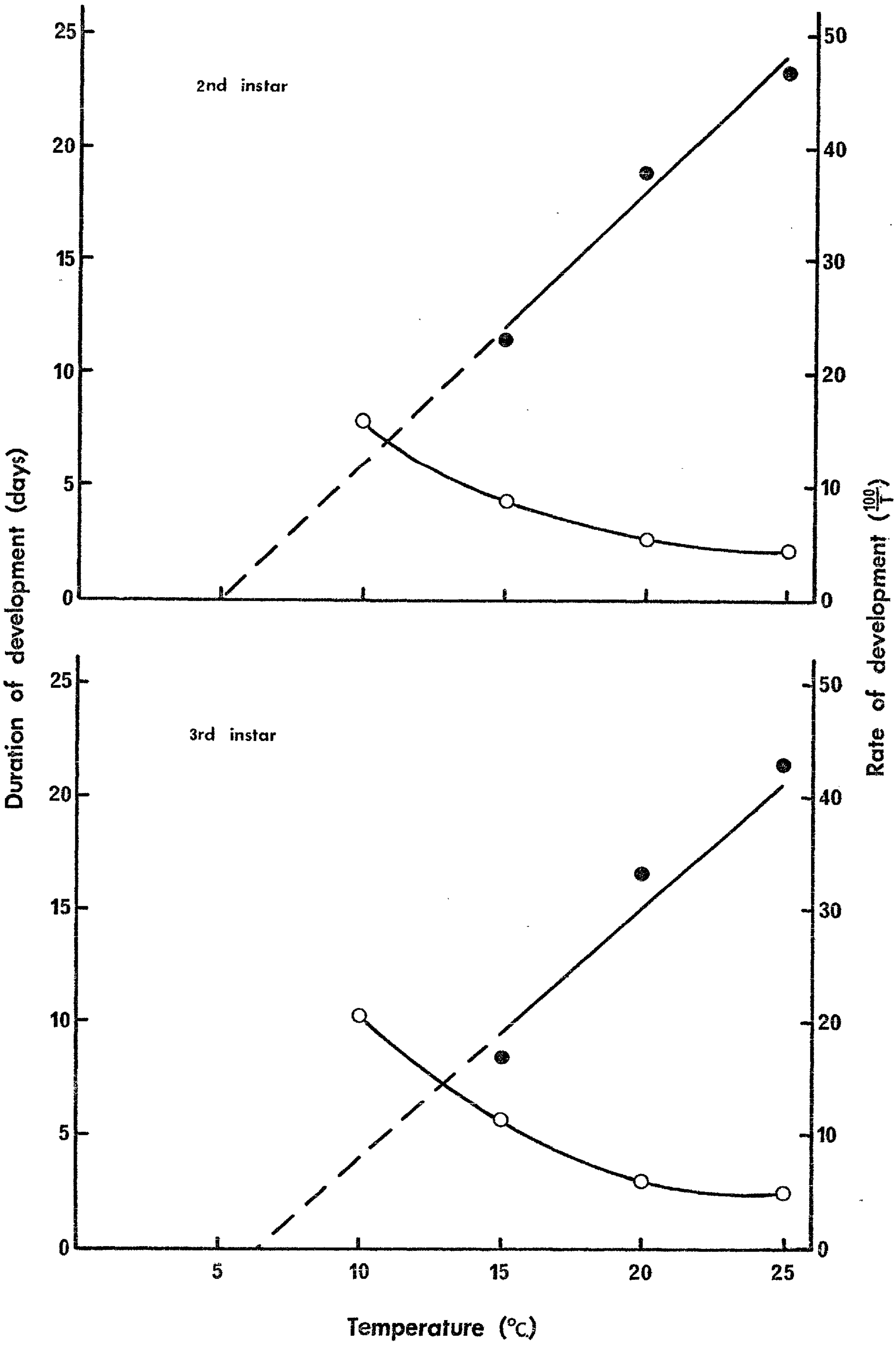
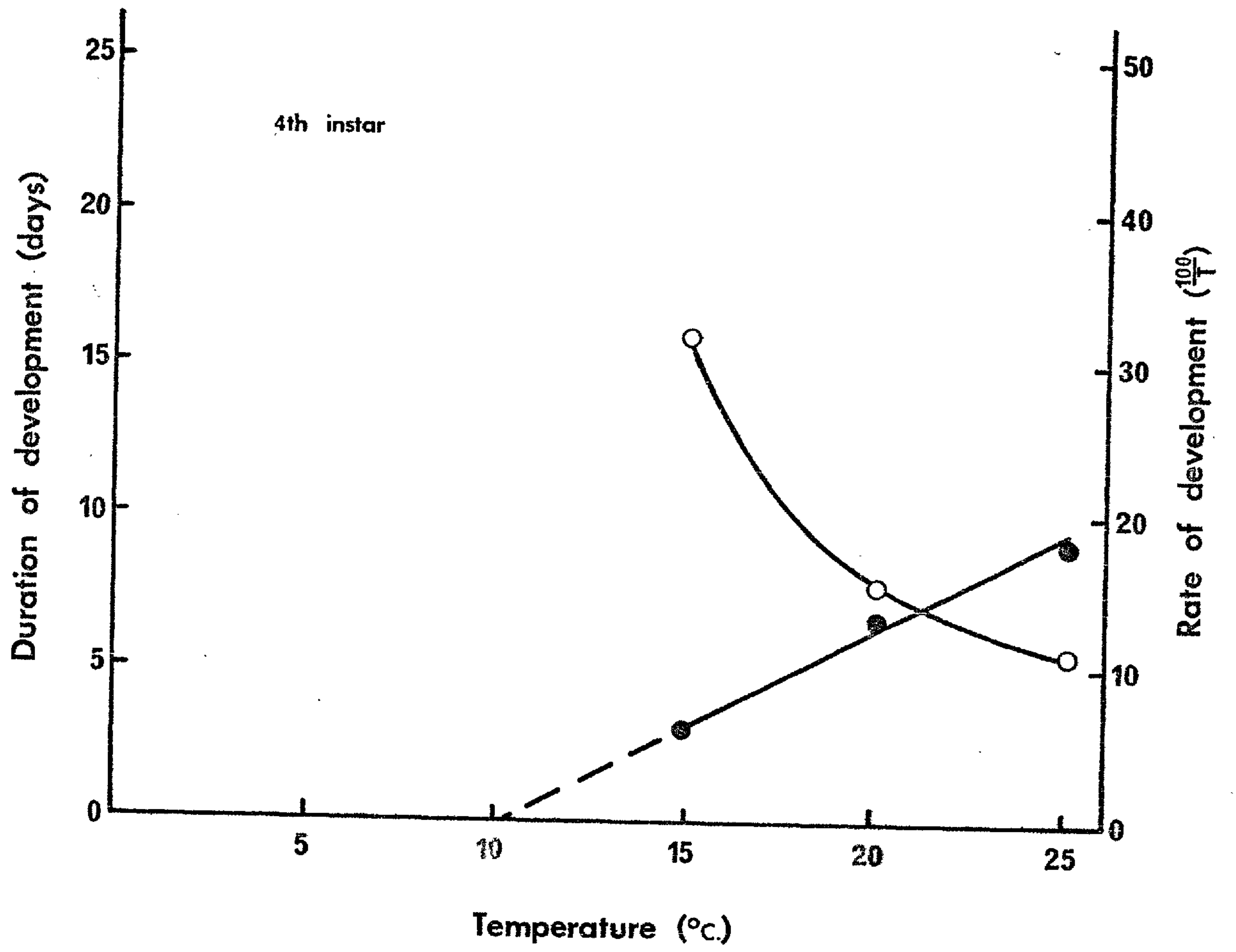

2nd instar
3rd instar
Duration of development (days)
Rate of development ($\frac{100}{T}$)
0
5
10
15
20
25
0
10
20
30
40
50
5
10
15
20
25
Temperature (°C)

Figure 25: Temperature-time curves (O———O) and graphical determination of temperature thresholds (●———●) for fourth instar of the cabbage whitefly, A. brassicae.


4th instar
Duration of development (days)
0
5
10
15
20
25
Rate of development ($\frac{100}{T}$)
0
10
20
30
40
50
Temperature (°c.)
5
10
15
20
25

The regression equations and temperature thresholds for the immature stages are presented in Table 51.

Temperature thresholds were highest and approximately equal in the egg stage and instar IV, being 10° and 10.4°C respectively. These were followed by instar I (7.3°), instar III (6.5°), and instar II (5°C) (Fig. 22).

2. Density effects

(a) Effect of larval density on duration of development

Results of the effect of larval density on duration of development are shown in Table 52. Fig. 26 illustrates the relationship between larval density and the rate of development.

The correlation coefficient (r) between larval density and duration of development was very high ($r = .879$; $p < .1$) and the slope of the regression line (b) was $- .006$.

The mean rate of development decreased with increased density up to 130 larvae per 3.14 cm^2 leaf surface. Further increase in density did not seem to have had much effect on the rate of development.

(b) Population growth curve (theoretical consideration)

At very high densities, the mean duration of development was increased by about one week. Thus, while the generation time (T) was 4 weeks for low density group it was 5 weeks for high density group with consequent lowering of the intrinsic rate of increase (r_m) and the finite rate of increase (λ).

For the calculation of the population parameters r_m and λ, Ro was assumed equal for both density levels. The values obtained are

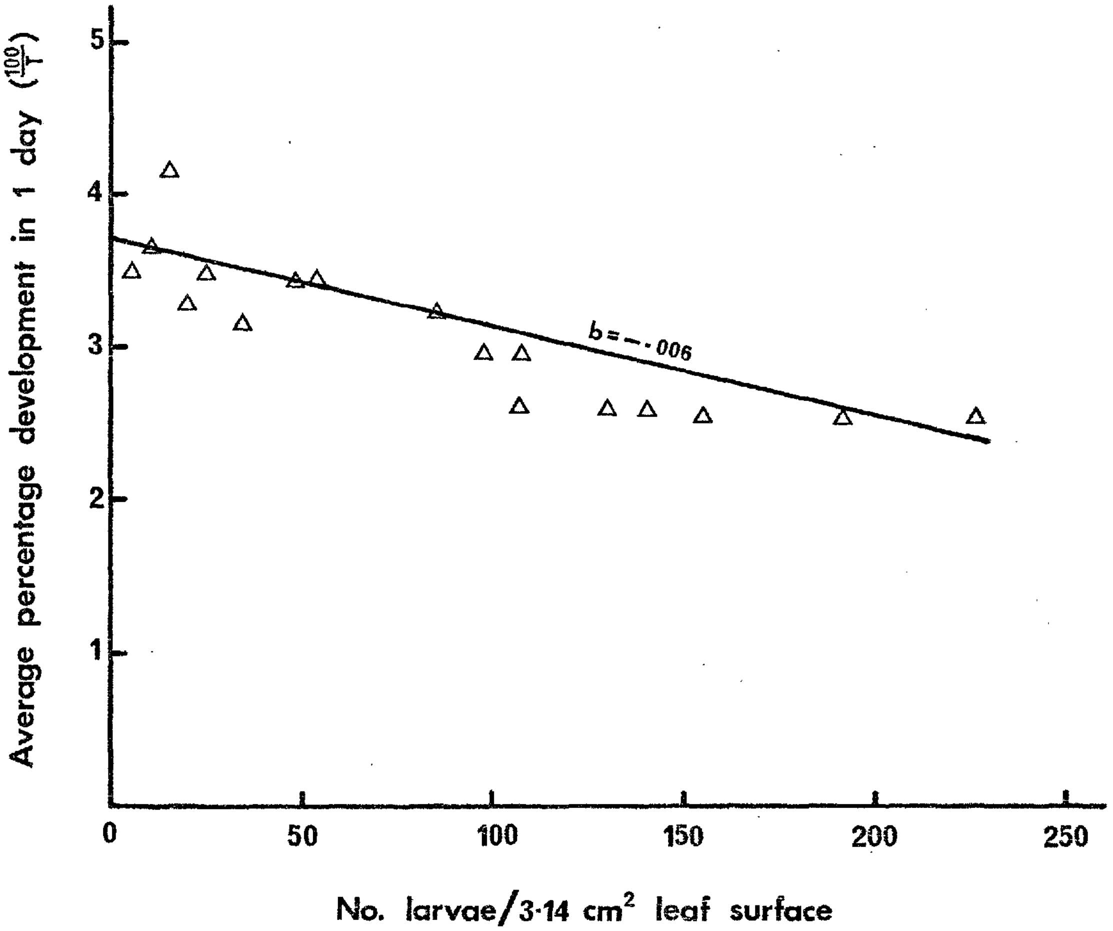
Table 52: Effect of larval density of *A. brassicae* on duration of development at 20°C.

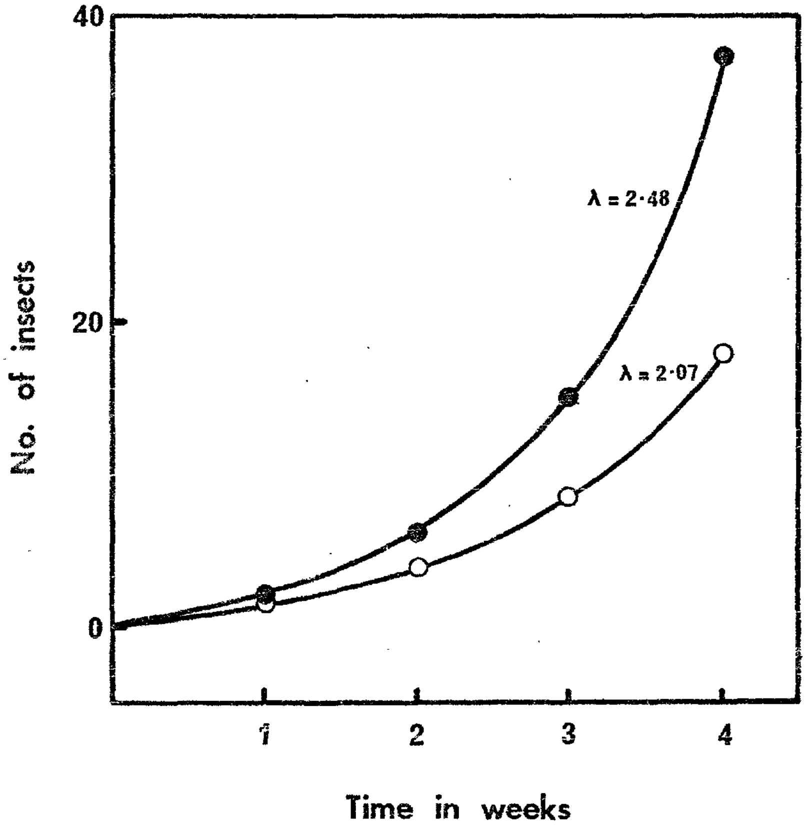
No. of larvae	Duration of development (days)
5	28
10	27
15	24
20	30
25	29
35	31
47	29
60	29
85	30
97	33
117	33
117	39
130	39
150	38
156	38
192	38
228	38

Correlation coefficient (r) = .879; $p < .1$

Figure 26: The relationship between larval density of the cabbage whitefly, *A. brassicae*, and the rate of development to adult stage.

Figure 27: Curves for various values of λ/♀/week, showing population growth of *A. brassicae* females reared from low (●——●) and high (○——○) larval densities.


Average percentage development in 1 day (100/T)
5
4
3
2
1
0
50
100
150
200
250
b = −.006
No. larvae/3·14 cm² leaf surface


40
20
0
No. of insects
λ = 2·48
λ = 2·07
1
2
3
4
Time in weeks

presented in Table 53. But since most workers have shown that very crowded individuals have low fecundity, these estimates will be too high for crowded situations.

Table 53: Ro, T, rm, and λ calculated for low and high density levels.

Population parameters	Low density	High density
Ro	37.8	37.8
T	4 weeks	5 weeks
rm	0.91	0.73
λ	2.48	2.07

The theoretical curves of population growth at both densities (Fig. 27) show that the population reached in 4 weeks time by one female from the low density group would be 38 while that of a single female from the high density group would be 18. Therefore, population levels reached by females are influenced by the larval density in which they developed.

(c) Effect of adult density on fecundity and longevity

Results on fecundity and longevity are summarized in Tables 54 and 55 respectively and illustrated in Fig. 28.

Both fecundity and longevity decreased with increased density. Insects caged singly laid most and lived longest.

3. Virgin and mated females

Results were obtained from females reared on young leaves of Mustard at 25°C.

Figure 28: Effect of density ~~of~~ on fecundity and longevity of virgin *A. brassicae* females.

(regression line for fecundity)

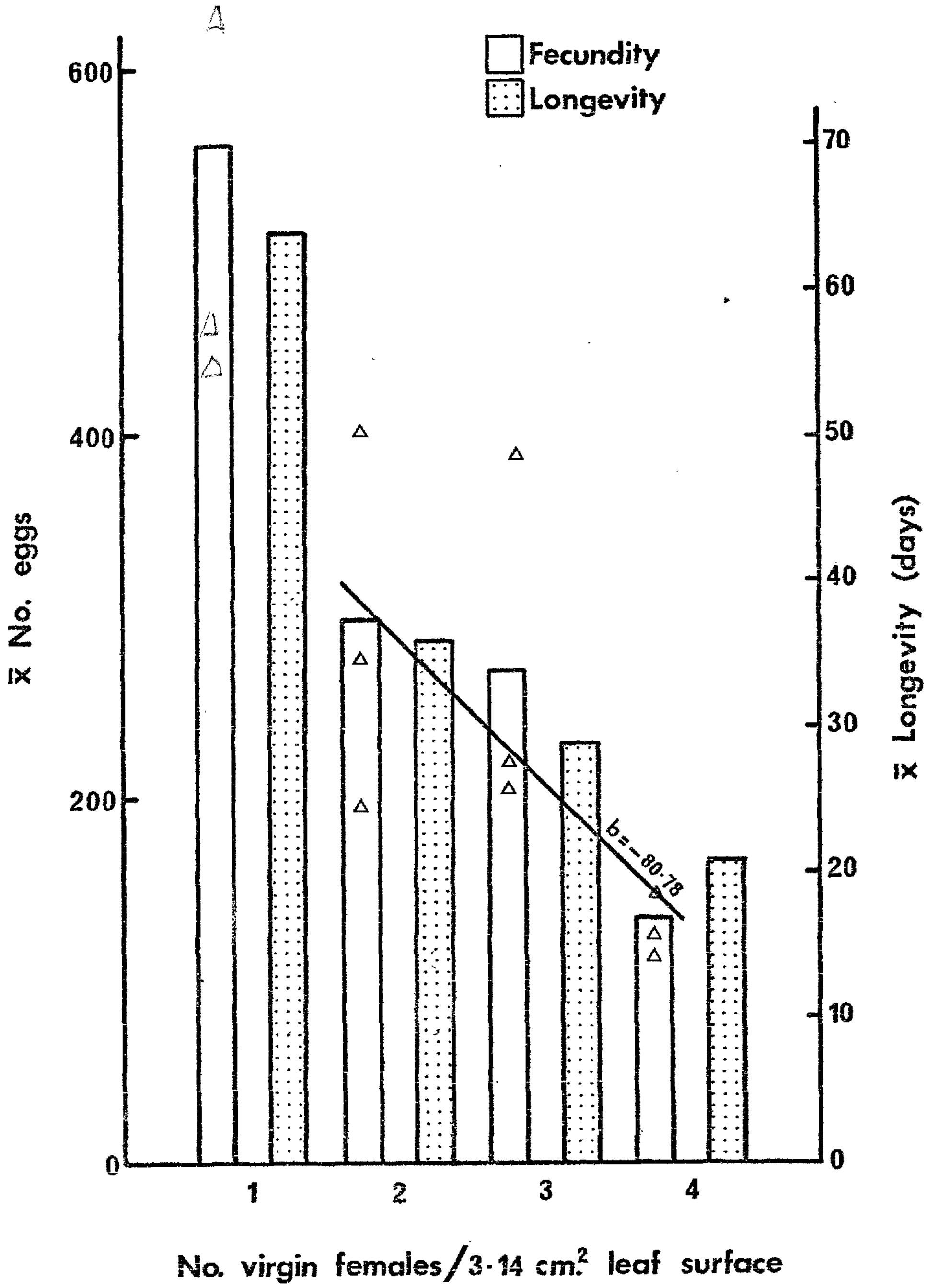

Fecundity
Longevity
600
400
200
0
x̄ No. eggs
70
60
50
40
30
20
10
0
x̄ Longevity (days)
b=−80·78
1
2
3
4
No. virgin females/3·14 cm.² leaf surface

Table 54: Effect of adult density on fecundity of A. brassicae when reared on young leaves of Mustard at 25°C.

No. females	Total eggs laid	No. eggs/♀	$\bar{x}$ eggs/♀
1	476	476	508.3
1	612	612	
1	437	437	
2	570	283.5	297.8
2	412	206.0	
2	805	402.0	
3	689	229.7	274.1
3	1134	378.0	
3	644	214.7	
4	614	153.6	135.6
4	473	118.3	
4	540	135.0	

Table 55: Effect of adult density on longevity of A. brassicae females when reared on young leaves of Mustard at 25°C.

No. females	Total longevity (days)	$\bar{x}$ longevity/♀
1	73	64
1	49	
1	70	
2	34	36
2	25	
2	50	
3	28	29
3	38	
3	21	
4	16	21
4	26	
4	20	

(a) Pre-oviposition period

The mean pre-oviposition period was shorter in the virgin females (1.45 days) than in the mated ones (1.75 days) (Table 56). However, the difference was not significant.

(b) Fecundity

Virgin females laid more eggs than the mated females (Fig. 29). The mean number of eggs per female was 561.1 (virgin) and 318.9 (mated) (Table 56). The difference between the mean fecundity was highly significant ($p < .001$).

(c) Longevity

Virgin females lived longer than mated ones (Fig. 30). The mean longevity in days was 61.6 for virgins and 42.6 for mated females (Table 56). The difference between the means was highly significant ($p < .001$).

Table 56: Summary of data on fecundity and longevity of mated and virgin females of *A. brassicae* on young leaves of Mustard (white) at 25°C.

	Mated	Virgin
No. of females	19	20
$\bar{x}$ pre-oviposition period (days)	1.75 ± 0.18	1.45 ± 0.15
$\bar{x}$ no. of eggs per female	318.9 ± 23.62	561.1 ± 25.7
$\bar{x}$ longevity (days) per female	42.6 ± 1.88	61.6 ± 2.36

Figure 29: Mean fecundity per female cabbage whitefly, _A_. _brassicae_, (mated and virgin) per week.

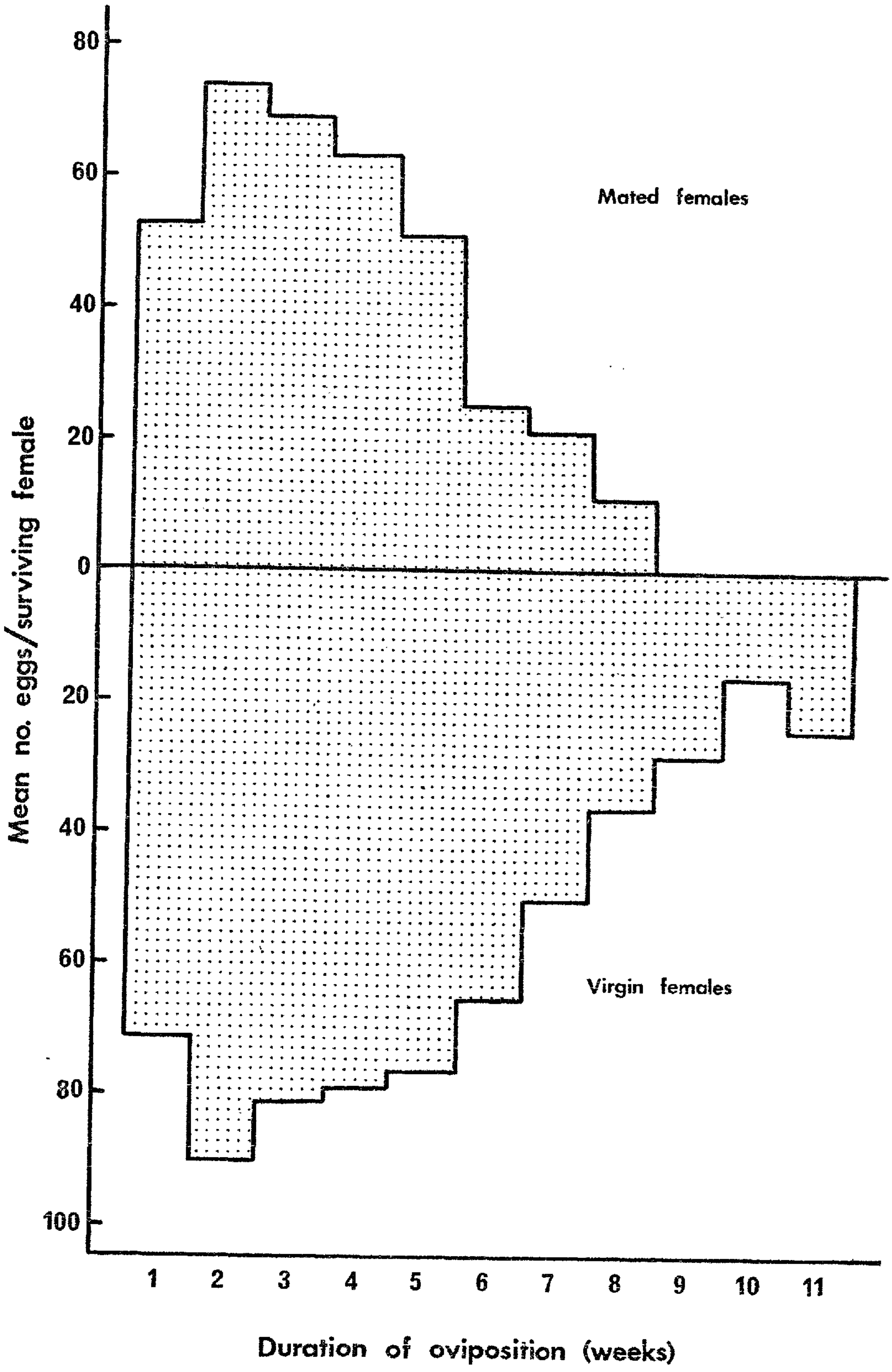
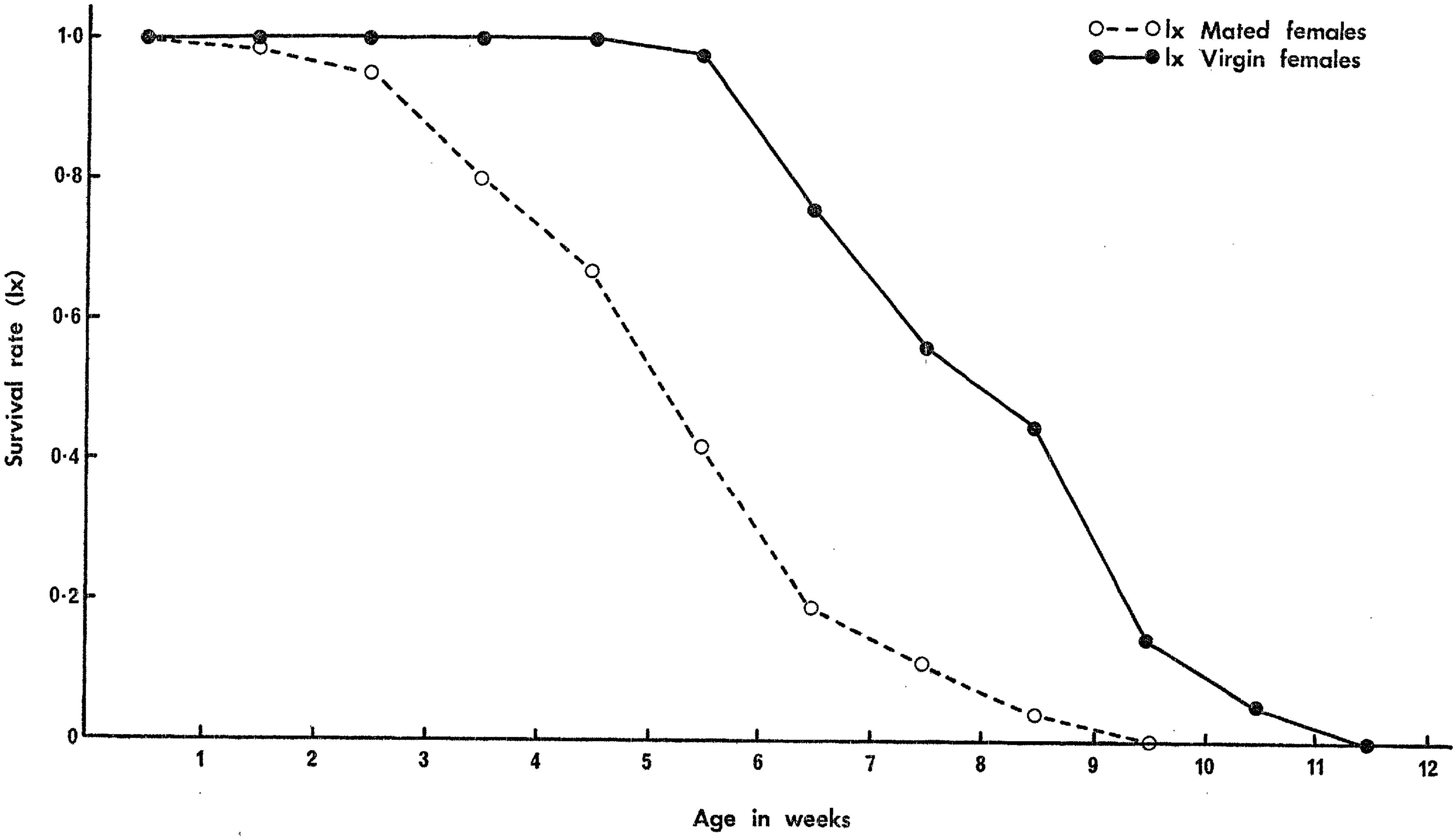

80
60
40
20
0
20
40
60
80
100
Mean no. eggs/surviving female
Mated females
Virgin females
1
2
3
4
5
6
7
8
9
10
11
Duration of oviposition (weeks)

Figure 30: Survival rates of mated and virgin females of the cabbage whitefly, _A._ _brassicae_.


○- - -○ lx Mated females
●——● lx Virgin females
Survival rate (lx)
1·0
0·8
0·6
0·4
0·2
0
1
2
3
4
5
6
7
8
9
10
11
12
Age in weeks

D. DISCUSSION

Cold blooded animals complete their development more rapidly in warm weather than in cool (Andrewartha and Birch, 1954). Davidson (1944) pointed out that a particular species of insect has an inherent power of attaining the average speed of development which may be different for different stages of the life cycle of the same species.

The actual speed of development of each immature stage of the cabbage whitefly, A. brassicae, was different from the others. It was fastest in the second instar, followed by the third, first, and fourth instars and slowest in the embryonic stage. However, the developmental rates for the fourth instar and the embryonic stage were approximately equal. This trend was observed at each constant temperature. In the pea aphid, Acyrthosiphon pisum, the rate of development was faster and equal in the first three nymphal stages but slowed down in the fourth apteriform and alatiform (Campbell and Mackauer, 1975).

Each immature stage of the cabbage whitefly, A. brassicae, had a different temperature threshold of development with the exception of the embryonic and fourth instar stages in which the thresholds were approximately equal (10° and 10.4°C respectively). The thresholds for the rest of the stages were 7.3° (first instar), 5° (second instar), and 6.5°C (third instar). The thresholds, therefore, declined with age but rose again in the last two instars.

In the alfalfa weevil, Hypera postica, the developmental threshold for larvae varied between instars (Guppy and Mukerji, 1974). In the cabbage white butterfly, Pieris rapae, the threshold at Vancouver is remarkably high in the first and second instars, but declines as the larva grows older (Campbell et al, 1974). In England, temperature threshold for P. rapae is highest in the egg (8.3°). All the larval stages have the same threshold (7.7°), while the pupa has the lowest threshold (2.8°) (Richards, 1940; Baker, 1968). However, in the pea aphid, *A. pisum*, and the cabbage aphid, *B. brassicae*, all instars had the same thresholds (Campbell *et al*, 1974).

The temperature thresholds of the immature stages of the cabbage whitefly, *A. brassicae*, are not particularly important in summer when the temperature is generally high and favours continuous development. They are, however, important in relation to development of immature stages produced by non-diapausing females either late in the summer or early in the autumn.

The decline in temperature threshold of the early stages of development ensures that development continues in autumn and winter while the sudden rise in the fourth instar arrests its development until temperature rises in spring. This explains the occurrence of fourth instars in the field during winter and the absence of adult emergence late in the winter. The nature of the developmental arrest is discussed in Section III of this thesis.

Some of the resting fourth instars retain their viability and emerge in spring provided the host plant leaves do not wither. The values of the temperature thresholds of development obtained in this investigation explain, therefore, why some immature stages of the cabbage whitefly, *A. brassicae*, persist in nature under autumn and winter conditions.

The use of immobile insects in the study of density effects provides a more realistic information than mobile ones which, in nature, seldom crowd because of their ability to walk off or fly away thereby averting the consequences of crowding.

In summer, the cabbage whitefly, *A. brassicae*, lays many eggs. Since the females are negatively phototactic and unable to fly persistently (see Section IV) they tend to remain on a leaf and lay as many eggs as possible. With many females feeding and ovipositing on the same leaf, many eggs occur on a leaf. Hargreaves (1914) reported that in the greenhouse whitefly, *T. vaporariorum*, the first instar wanders about for about three days before settling while in some other species, the larvae simply get clear of the egg shells and settle. In the cabbage whitefly, *A. brassicae*, the first instar crawls a few millimetres from the hatching point and fixes itself by means of the stylet. Subsequent immature stages develop in the same position until adults emerge. Thus the immature stages are often close together in nature.

Results of my laboratory experiments showed a high correlation ($r = .879$; $p < .1$) between larval density and duration of development. Development to adult stage was prolonged in individuals that emerged from the high density group. Miller (1964) had similar results for two species of *Drosophila*. The reduced rate of development with increased larval density in the cabbage whitefly, *A. brassicae*, could be due to semistarvation resulting from limited space and food resources.

High larval density could have far reaching consequences on the population growth of a species. Since high larval density slows down the rate of development, the mean generation time (T) is increased which in turn reduces the number of generations produced in a year.

Crowding is one of the factors which reduce the body size of insects e.g. Miller (1964) with *Drosophila*. From observations made on laboratory cultures of the cabbage whitefly, *A. brassicae*, crowding also reduces their body size. Since fecundity of the female cabbage whitefly, *A.*

brassicae, is proportional to her weight on emergence (Iheagwam, 1974), females emerging from the high larval density group will be expected to lay fewer eggs than those from low density group. Thus with the observed prolonged mean generation time (T) and the expected lower net reproductive rate (Ro), both the intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) of females from the high larval density group will be expected to be lower than those of the other group. Consequently, the rate of growth of the population is bound to be slower than in the other group.

In the cabbage whitefly, *A. brassicae*, increased adult density resulted in reduced fecundity and longevity. In *Cardiaspina albitextura* the mean number of eggs laid per female was reduced by crowding (Clark, 1963). In the cotton stainer, *D. fasciatus*, both fecundity and longevity decreased with increased adult density (Hodjat, 1968). In the African migratory locust, *Locusta migratoria migratorioides*, crowding increased adult longevity whereas in adult Red Locust, *Nomadacris septemfasciata*, and the Desert Locust, *Schistocerca gregaria*, it was reduced (Norris, 1950, 1952).

Reduced fecundity with increased density in experiments involving both male and female insects has been attributed to 'fighting' (Crombie, 1942) or "pestering effects" of males (Valentine, 1952; Hodjat, 1968). Clark (1963) reported that the mean number of eggs laid by 12 batches of 8 females of *Cardiaspina albitextura* when kept alone was 242.7; in the presence of 8 males, 238; and in the presence of 32 males, 171.8. These results show that the pestering effect of males was only evident when they were in excess of females. Richards (1927) has already pointed out that reduction in fecundity will occur in some insects as the number of excess males increases.

In my experiment, effects of males were specifically excluded by using only virgin females and yet fecundity was reduced. The cause may be due to competition for oviposition sites. Interference among the females themselves is another possible factor.

The influence of mating on egg production has been determined in many insects. When virgin females of the cabbage whitefly, A. brassicae, were reared on young leaves of Mustard, the pre-oviposition period was shorter than that of mated females reared under the same conditions. The difference was, however, not significant. Thus mating is not a precondition for commencement of oviposition in the cabbage whitefly. In the cotton stainer, D. fasciatus, there is no significant difference in the pre-oviposition periods of virgin and mated females (Odhiambo, 1968). Virgin females of the blow-fly, Lucilia cuprina, have well developed ovaries but do not lay any eggs (Mackerras, 1933); virgin tsetse-fly females on the other hand, have very much delayed ovulation time (Mellanby, 1937; Vanderplank, 1947).

Virgin females of the cabbage whitefly, A. brassicae, laid more eggs than mated females and the difference was very highly significant ($p < .001$). It is pertinent to point out that while virgin females were caged singly, mated ones were caged in bisexual pairs. Because of this difference in density levels, it is doubtful whether the two fecundity results are strictly comparable. However, when the mean fecundity of the mated females was compared with that of virgin females reared in unisexual pairs, the values were 318.9 and 300 respectively. From the regression analysis of fecundity on density of virgin females at three density levels (2, 3, and 4), the mean fecundity when the density was two females was 315.5 - very close to that of mated females. Perhaps it is more accurate to conclude that fecundity of virgin and mated females of the cabbage whitefly, A.

brassicae, does not differ significantly. In the cotton stainer, *D. fasciatus*, virgin females produced more egg batches than mated ones but the mean total egg production of the two groups was not significantly different (Odhiambo, 1968). In *Rhodnius prolixus*, mated females lay twice as many eggs as virgin females (Davey, 1965).

Thomsen (1927) showed that the unfertilised eggs of the cabbage whitefly, *A. brassicae*, develop into haploid males. Butler (1938) also made a similar observation. Morrill (1903) reported that in America, unfertilised eggs of the greenhouse whitefly, *T. vaporariorum*, always give rise to males (arrhenotoky) while Hargreaves (1914) and Williams (1917) showed that in England nearly all give rise to females (thelytoky). Though these observations seem contradictory, Wigglesworth (1965) has pointed out that geographical or local races of insects may be characterized by their mode of reproduction. Thomsen (1927) confirmed that in the greenhouse whitefly, *T. vaporariorum*, there is a race that shows arrhenotokous parthenogenesis; fertilised eggs producing females, unfertilised producing males; and a race consisting almost exclusively of females. Thomsen further pointed out that in the latter race the diploid constitution is restored by autoregulation - probably through splitting of chromosomes without nuclear division. In the coccids *Lecanium hesperidum* and *L. hemisphaericum*, Thomsen also reported that there are parthenogenetic races producing only females, and bisexual races with a minority of males. The bisexual races show facultative thelytoky: unfertilised eggs develop into females, fertilised eggs into either sex. In the unfertilised eggs of this race the diploid chromosome number is restored at the outset of development by fusion between the second polar body and the egg nucleus, while in the parthenogenetic races, the reduction division is omitted, so that the oocytes are always diploid.

The difference in the observations of Morrill in America and Hargreaves and Williams in England on the sexes resulting from unfertilised eggs of *T. vaporariorum* could be attributed to the fact that different geographical races were studied.

The virgin females of the cabbage whitefly, *A. brassicae*, lived significantly longer ($p < .001$) than mated females. The longevity data were obtained from females used for fecundity experiments and therefore have similar limitations as already discussed. In the cotton stainer, *D. fasciatus*, the difference in longevity of virgin and mated females is not significant (Odhiambo, 1968). The prolonged longevity in the virgin females of the cabbage whitefly, *A. brassicae*, increases their chances of encountering males before they die.

SECTION III: PHOTOPERIODISM IN THE CABBAGE WHITEFLY, *A. BRASSICAE*.

A. INTRODUCTION

Variations in weather often create a short-term deviation from the optimum ecological factors such as temperature, food and humidity, while seasonal and climatic changes of cyclic nature such as winter or summer cause great and prolonged deviation of temperature and associated factors. Insects are subject to all these environmental changes.

Insects inhabiting areas of extreme ecological inconsistences are characterized by various degrees of arrested growth and development (dormancy). Unfavourable weather changes are often overcome by retarded but continued growth whereas seasonal and long-term extremes of cold have induced a characteristic period of dormancy.

The intensity of dormancy varies with the geographical locations of the insect. For example, in the tropics most insects such as the cotton whitefly, Bemisia tabaci, continue development uninterruptedly, while in the temperate region other species such as the viburnum whitefly, Aleurotrachelus jelinekii (Frauenf.), enter long periods of suspended growth (Southwood and Reader, 1976). An intermediate situation with varied degree of dormancy depending, however, on the nature and severity of environmental stresses, occurs among species inhabiting the middle zones of the two extreme regions. Examples of such gradation include the sugar cane stem borer, Chilo infuscatellas (Snell.), which develops continuously in South India but enters larval dormancy of varied duration in North India (Pradhan and Bhatia, 1956). Several species of mosquito in America have uninterrupted development in the southern United States while entering diapause in the northern States and Canada (Clements, 1963; Danilevsky, 1965; Harward and Takata, 1965). The differences in the environmental stress may be manifested in the number of generations produced in a year.

The term diapause was coined by Wheeler (1893) to describe the stage between anatrepsis and catatrepsis during blastokinesis when growth of the embryo of the grasshopper Xiphidium ensiferum (L.) was arrested. Henneguy (1904) used the term to apply to the physiological state of arrest or dormancy which is known to occur in many insects. Ecologists have since used the term, rather loosely, to include almost any sort of arrested development. Thus, the term diapause needed a more precise definition and restricted application.

Shelford (1929) introduced the term "quiescence" for instances of growth interruptions due to the direct effect of unfavourable environment and restricted the use of the term "diapause" to cases where development is arrested 'spontaneously' and does not respond immediately to any ordinary amelioration of the external environment. Roubaud (1930) proposed the terms 'pseudodiapause' for quiescence and 'diapause vrai' for diapause. Lees (1955) considered the immediacy of response to environmental factors as a valid basis for distinction between spontaneous and delayed termination of dormancy. Muller (1965) classified dormancy on the basis of immediacy of termination, differences in the nature of ecological stimuli required for induction and termination, and the differences in the intensity of ecological stimuli. Mansingh (1971) proposed a system of classification based on evolutionary, ecological and phenological factors associated with dormancy.

Various factors that regularly change during the course of the season may serve as signals for diapause initiation. These include temperature, humidity, and the nutritive status of the food source.

Temperature has often been regarded as a major environmental factor inducing diapause. Yet in some insects, diapause sets in at temperatures higher than those at which active development begins in spring. Bodenheimer (1951) implied that in Carpocapsa pomenella progressive trend of lower night maxima, in nature expressed as the turning point of the annual temperature curve, determined diapause induction. Temperature shocks in the laboratory may have a similar effect.

The food of most phytophagous species varies in quality and moisture content with the season. Lees (1953a) showed that senescing leaves strongly induced diapause in the fruit tree spider mite, Metatetranycus ulmi. Grison (1947) showed that diapause was promoted by feeding larvae of the browntail moth, Euproctis phaeorrhoea (L.), on senescent leaves of apple. Among parasitic insects, many hymenopterous and tachinid parasitoids possess a specialized stage, often the first instar larva, which lies dormant until the host terminates its dormancy. Hymenopterous parasites of the wheat-blossom midge have been found in their hosts seven years after the host had ceased feeding (Barnes, 1952). However, food and other components of the environment such as humidity, are not very regular in their seasonal occurrence.

Of all components of the environment, solar photoperiod has the advantage of being an immediate expression of the astronomical factors determining the daily and seasonal rhythms of weather and climate. Photoperiod changes with mathematical precision in the course of the year.

Marcovitch (1924) was the first to describe the effect of daylength on the occurrence of sexual forms in aphids. Kogure (1933) analysed photoperiodism in the commercial silkworm and its relation to temperature and light quality. Elaborate work has since been done (e.g. Danilevsky, 1948, 1949, 1951; Dickson, 1949; and Lees, 1953a, b). The subject photoperiodism has been reviewed by a number of authorities (e.g. Andrewartha, 1952; Danilevsky, 1956; Lees, 1954, 1955, 1959a; Muller, 1957).

Insect reaction to photoperiod is displayed in very different forms. Two types are usually distinguished; the long-day types in which long-day prevents diapause and the short-day in which it facilitates its initiation (Danilevsky et al, 1970).

The incidence of diapause may be highly variable not only from species to species but also between different populations of the same species. In some there is only one generation each year (univoltine) and every individual in the generation enters diapause irrespective of any possible variations in the environment (obligatory diapause). An example of this among the aleyrodids may be the viburnum whitefly, A. jelinekii, in which a prolonged developmental arrest occurs in the fourth instar (Korobitzin, 1967; Southwood and Reader, 1976). On the other hand, some species have several generations in one year (multivoltine) of which generations that do not diapause alternate with a generation in which all the individuals enter diapause (facultative diapause). The cabbage whitefly, A. brassicae, illustrates this phenomenon.

Facultative diapause is induced in all cases by environmental factors. In the majority of cases of obligatory diapause, it is induced by external factors which may have affected an earlier sensitive stage of development of the current generation, or even of its parent generation.

The stage of the insect sensitive to the photoperiodic induction of diapause, and the photoperiodic regimen which induces diapause vary from species to species. Sensitivity to photoperiod is not usually extended to the whole life cycle. In most cases it is intensified in a limited number of stages or instars. Moreover sensitive and responsive stages are mostly different (de Wilde, 1962a).

The threshold of the photoperiodic response, in particular the critical photoperiod causing diapause in 50% of the population is of most ecological importance as it determines the calendar time of diapause initiation in nature. The exact duration of the critical photoperiod and the proportion of the population entering diapause frequently vary with temperature and over the geographical range of the species (Danilevsky, 1965; Beck, 1968; Danilevsky et al, 1970; Tauber and Tauber, 1972).

Since Duclaux (1869) reported the effect of prolonged chilling on the termination of embryonic diapause in silkworm, and Williams (1946) showed the effect of cold temperatures on the termination of pupal diapause of *Hyalophora cecropia*, prolonged exposure to cold temperature has been regarded as a prerequisite for the termination of diapause in most insects.

Since no detailed investigation of the environmental factors regulating diapause induction and termination in the cabbage whitefly, *A. brassicae*, has been published, the primary aims of the investigation described in this section were to determine:

i. the influence of photoperiod on diapause induction;
ii. the influence of photoperiod and temperature on incidence of diapause;
iii. the sensitive stages of development to photoperiod;
iv. the influence of food source on diapause; and
v. the factors that terminate diapause.

B. MATERIALS AND METHODS

1. Light-box

Wooden light boxes (60 cm x 60 cm x 60 cm) with perforated floors were used. Each box was equipped with a time-switch, two 45 cm long fluorescent tubes and an axial fan, and kept in a constant temperature room set at a temperature pertinent to each experiment.

2. Experimental plants

Brussels Sprout plants grown as described in Section I were used.

3. Whitefly culture

A culture of non-diapausing cabbage whitefly was maintained at 20°C and a light duration of 16 hours and 8 hours dark (LD16:8).

4. Criteria for diapause

The following were considered as possible criteria for diapause:

(a) The very dark pigmentation of the winter morphs since summer morphs are generally yellow with thin pigmentation. This criterion was not used because the dark pigmentation was not very apparent in laboratory bred winter morphs.

(b) Absence of oviposition. The fact that oviposition occurred meant that this criterion was inappropriate.

(c) The age at first oviposition. This was found very easy to monitor and was therefore used as the criterion for diapause.

(d) For the immature stages, induction of diapause was considered as failure to develop beyond the 4th instar. This was based on the fact that in the field, some 3rd and 4th instar larvae are found on the middle and lower leaves of host plants in winter. But since such larvae develop to the adult stage when brought into the laboratory and since development was not arrested in the laboratory bred winter morphs, the criterion was not a useful one.

Females that oviposited within 21, 14, and 6 days on emergence at 15°, 20°, and 25°C respectively were regarded as non-diapausing while females whose ages at first oviposition fell outside these ranges were said to have diapaused. The demarcation between non-diapausing and diapausing forms was chosen with reference to the mean pre-oviposition periods for non-diapausing females: 3.2, 1.4, and 0.8 days at 15°, 20°, and 25°C respectively with LD16:8 (El-Khidir, 1963).

5. Diapause response at different light regimens

Non-diapausing females from the culture were caged on leaves of Brussels Sprout at 15°C and kept at 8 different light regimens: LD12:12; LD13:11; LD14:10; LD15:9; LD15½:8½; LD15¾:8¼; LD16:8; LD24:0, until eggs were laid. The eggs were allowed to develop to adult stage at the photoperiod in which they were laid. On emergence each female was caged with one male on young leaves of Brussels Sprout and retained at the same photoperiod. Males were obtained from the main culture to avoid any possible influence of male reproductive diapause on the initiation of oviposition by the female. Insects were moved on to new leaves, and plants changed at first signs of deterioration. Diapause termination was assumed with the oviposition of the first egg. Records of ages at first oviposition were kept.

6. Sensitive stages of development to photoperiod

Experiments on the sensitive stages were carried out at 20°C. Non-diapausing females from the main culture were caged on leaves of Brussels

Sprout at LD16:8 for about 24 hours during which eggs were laid. Insects were transferred from LD16:8 to LD12:12 at the following stages of development:

i. eggs less than 24 hrs old
ii. early instar I
iii. early instar II
iv. early instar III
v. late instar III
vi. early instar IV
vii. teneral adults

Adult females resulting from each group of immature stage were caged on emergence in pairs (male + female) on young leaves of Brussels Sprout and retained at LD12:12 and 20°C until eggs were laid. Ages at first oviposition were noted and each female was discarded as soon as it laid the first egg.

7. Influence of temperature and photoperiod on the incidence of diapause

Females were reared from egg to adult stages at the following photoperiods: LD12:12; LD14:10; LD16:8; LD24:0 at 25° and 20°C respectively. At 15°C, the results of the diapause response at different light regimens were used. On emergence the females were treated as described for diapause response at different photoperiods.

8. Effect of food source on diapause

Laboratory bred 'summer' females of the cabbage whitefly, *A. brassicae*, were, on emergence, reared in pairs (male + female) on the top leaves of overwintering Brussels Sprout collected from the field in early December 1975. Each pair of insects was caged on leaves with petioles dipping in water. The mean age at first oviposition was obtained. The experiments were carried out at LD16:8 and 15°C.

For control experiment, some of the laboratory bred 'summer' females were, on emergence, caged in pairs (male + female) on young leaves of potted Brussels sprout grown at LD16:8 and 20°C (i.e. summer condition) and kept at LD16:8 and 15°C. The mean ages at first oviposition under the two treatments were compared by the t-test.

Remark: It would have been ideal to use field collected summer females for this experiment. This was, however, not possible because by the time the first generation of the cabbage whitefly appeared in May or June, the Brussels sprout plants in the field had produced new summer foliage.

9. Diapause development

(a) By chilling

Diapausing females were collected from the field on 28.ix.75. These were caged on young leaves of Brussels sprout. One half of the insects was kept at a low temperature (5°C) and a short photoperiod (LD12:12) for 5 days and thereafter transferred to LD16:8 and 15°C.

(b) By exposure to long photoperiod (LD16:8)

The second half of the diapausing insects was kept at LD16:8 and 15°C.

The means of the number of days from time of field collection to first oviposition (termination of diapause) for the two groups of insects were compared by the t-test.

10. Field collections

During the autumn/winter of 1975/76, overwintering females of the cabbage whitefly, *A. brassicae*, were collected from a field plot of Brussels Sprout plants from 28.ix.75 to 22.ii.76. Collections were made once in

September and twice in the subsequent months except February with three collections.

The field collected females were subjected to the following temperature treatments and light regimens:

Date of collection	Temperature	Photoperiod
September to November	20°C	LD16:8
	20°C	LD12:12
	15°C	LD16:8
	15°C	LD12:12
December to February	10°C	LD16:8
(7.xii.75 to 15.ii.76)	10°C	LD12:12
	in addition to the other treatments	

All females field collected on 22.ii.76 were subjected to only one light regimen (LD16:8) but three temperatures (20°, 15°, and 10°).

In all cases, females were caged singly and the time from field collection to first oviposition in the laboratory was recorded.

Field temperature records for the duration of collection were obtained from the meterological unit in the Field Station.

11. Comparison of fecundity of 'summer' and 'winter' females

Summer females were collected as pupae from the field and kept in the laboratory at 25°C until adults emerged. On emergence, adults were caged in bisexual pairs on young leaves of Brussels Sprout and the number of eggs laid each day was counted until the female died.

Overwintering females were collected from the field on 22.ii.76, paired with males and kept at 25°C and LD16:8. Records were kept of the number of eggs laid each day by each female.

Data from the two groups of insects were compared assuming that the first eggs were laid on day 1. Thus the chronological ages of the insects were ignored.

C. RESULTS

1. Photoperiod

The incidence of diapause at 15°C and with different photoperiods of constant duration is presented in Table 57 and Fig. 31. Distribution of ages at first oviposition in each photoperiod is illustrated in Figs. 32(a) and (b).

With photoperiods lasting from LD12:12 to LD15$\frac{3}{4}$:8$\frac{1}{4}$, high incidence of diapause occurred. As the photoperiod extended to LD16:8, the incidence dropped abruptly to zero. Thus the critical photoperiod was LD15$\frac{3}{4}$:8$\frac{1}{4}$.

No diapause was observed at LD16:8 and continuous light (LD24:0) respectively.

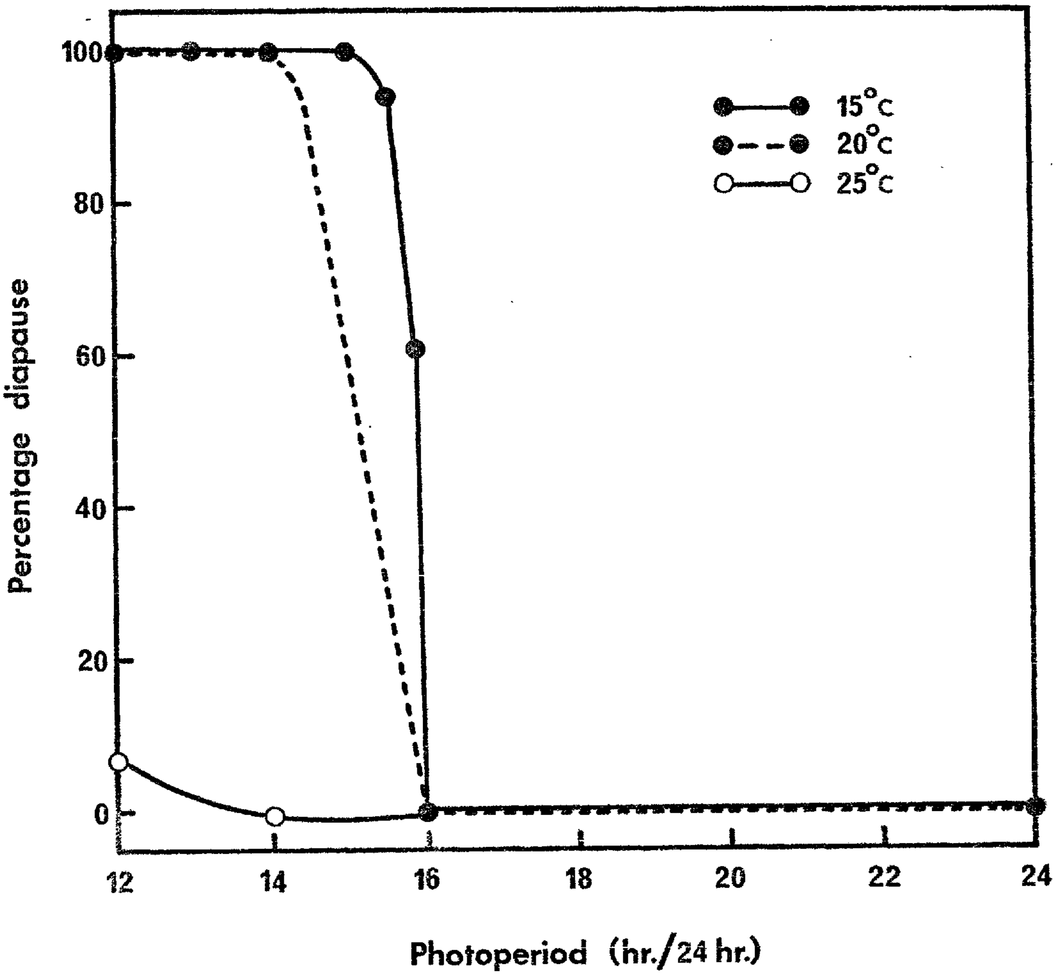
Table 57: Induction of diapause by photoperiod in *A. brassicae* females at 15°C.

Photoperiod	% Diapause
LD 12 :12	100
LD 13 :11	100
LD 14 :10	100
LD 15 : 9	100
LD 15$\frac{1}{2}$: 8$\frac{1}{2}$	94.7
LD 15$\frac{3}{4}$: 8$\frac{1}{4}$	60.0
LD 16 : 8	0
LD 24 : 0	0

2. Temperature and photoperiod

The results obtained when insects were reared at constant temperatures

Figure 31: Influence of photoperiod on diapause in A. brassicae females at constant temperatures of 15°, 20°, and 25°C.


100
80
60
40
20
0
Percentage diapause
12
14
16
18
20
22
24
Photoperiod (hr./24 hr.)
15°C
20°C
25°C

of 15°, 20°, and 25°C, and with different photoperiods are presented in Table 58. The respective curves are shown in Fig. 31.

The distribution of ages at first oviposition is illustrated in Figs. 32-34.

Table 58: The influence of temperature and photoperiod on the incidence of diapause (% diapause) in *A. brassicae* females.

Temperature (°C)	Photoperiod			
	LD 12:12	LD 14:10	LD 16:8	LD 24:0
15	100	100	0	0
20	100	100	0	0
25	7	0	0	0

With photoperiods of LD12:12 and LD14:10, 100 percent diapause occurred at both 15° and 20°C. No case of diapause was observed when insects were reared in LD16:8 or LD24:0.

The ages at first oviposition of females reared at 25°C with photoperiods indicated above, were subjected to analysis of variance and the means were compared by Duncan's new multiple range test. The effect of different photoperiods on ages at first oviposition was significant ($p < .01$) but the means did not differ significantly. The preoviposition period ranged from 1-7 days. Females that laid eggs at LD12:12 after 6 days were regarded as showing intermediate diapause.

Thus, while short photoperiods favoured diapause at 15° and 20°C, they had no effect at 25°C.

Figure 32(a): Distribution of ages at first oviposition of *A. brassicae* females reared from egg to adult stage under different photoperiods at 15°C.

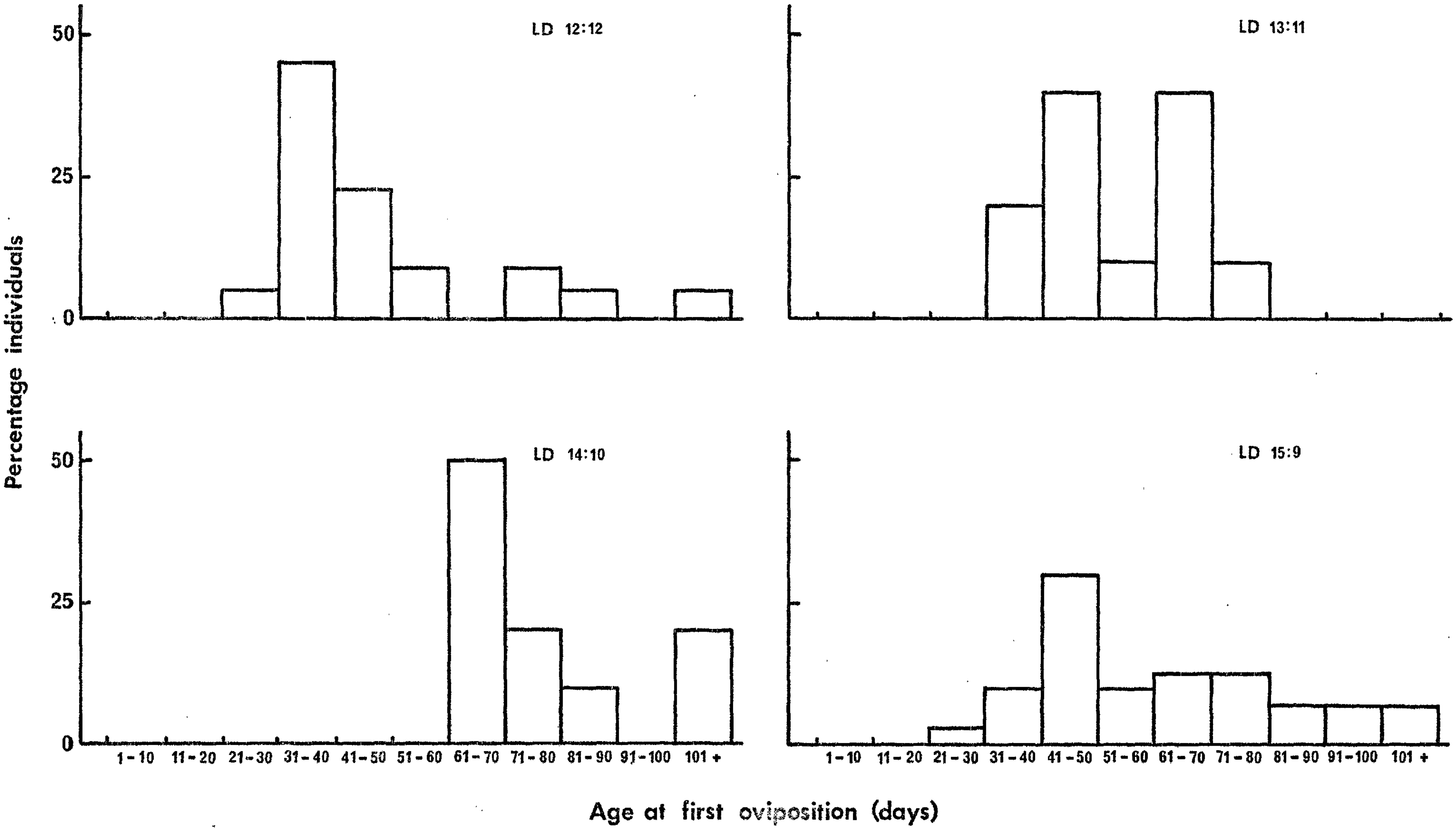

Percentage individuals
50
25
0
LD 12:12
LD 13:11
LD 14:10
LD 15:9
1-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101 +
Age at first oviposition (days)

Figure 32(b): Distribution of ages at first oviposition of *A. brassicae* females reared from egg to adult stage under different photoperiods at 15°C.

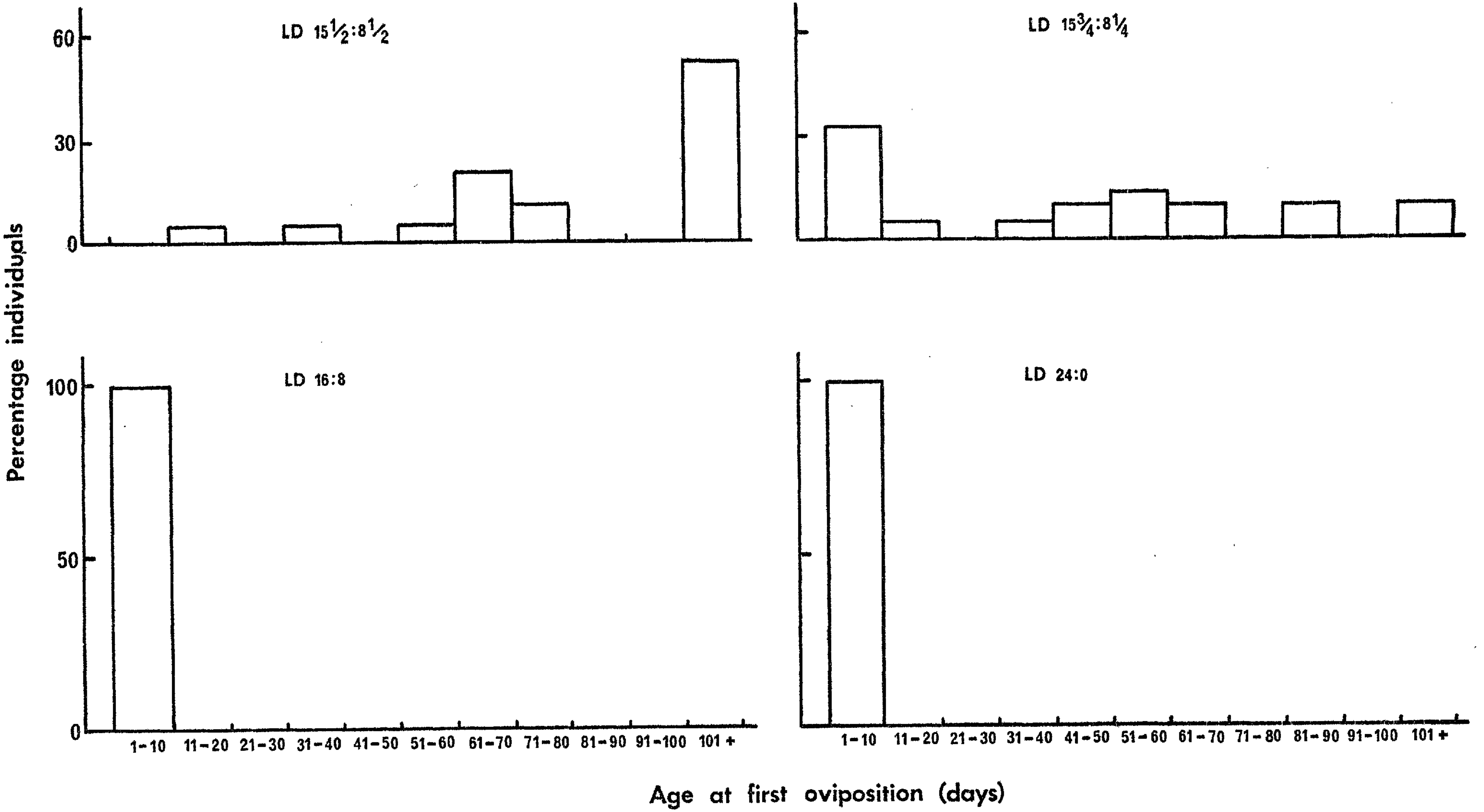

LD 15½:8½
LD 15¾:8¼
LD 16:8
LD 24:0
Percentage individuals
60
30
0
100
50
0
1-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101 +
Age at first oviposition (days)

Figure 33: Distribution of ages at first oviposition of *A. brassicae* females reared from egg to adult stage under different photoperiods at 20°C.

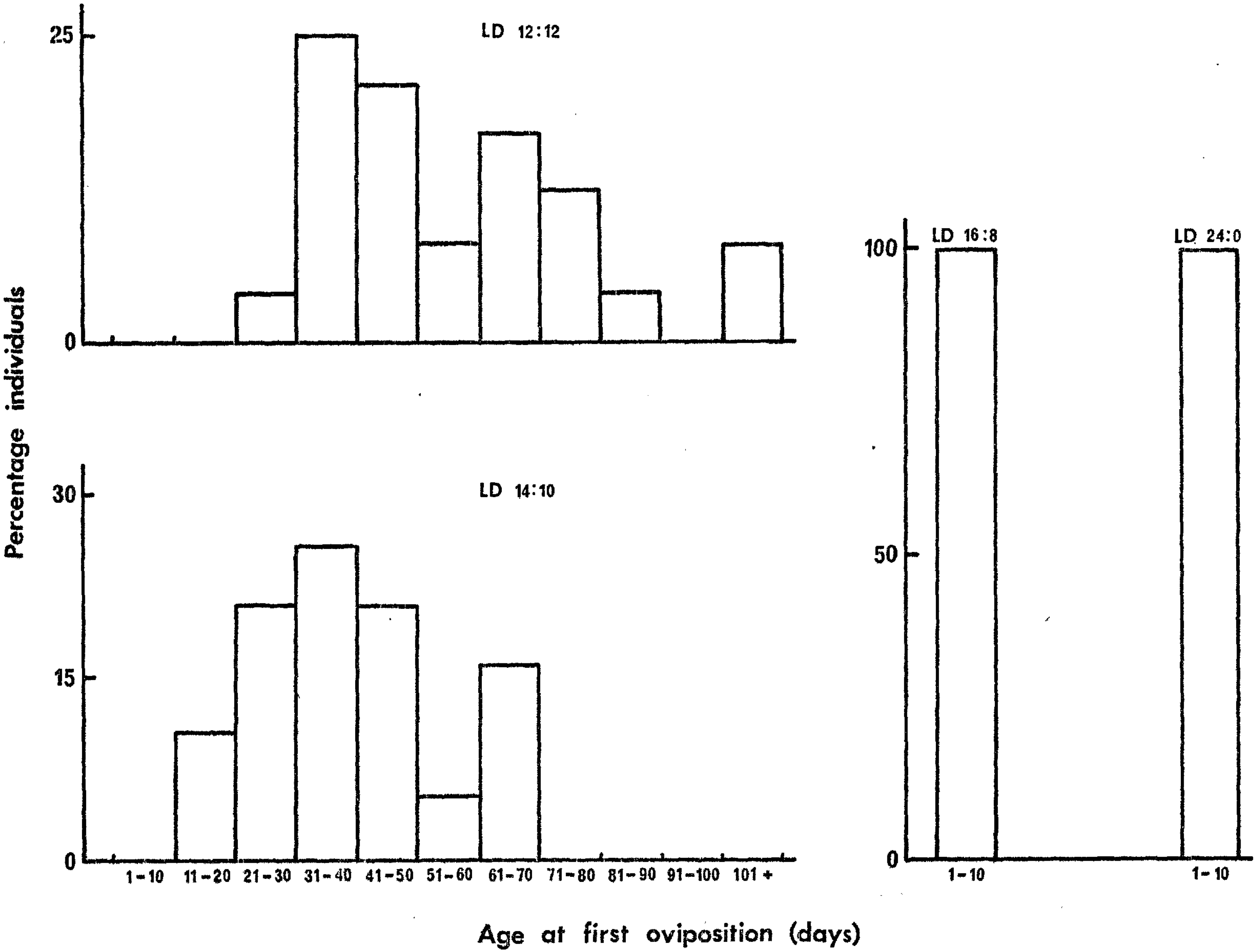
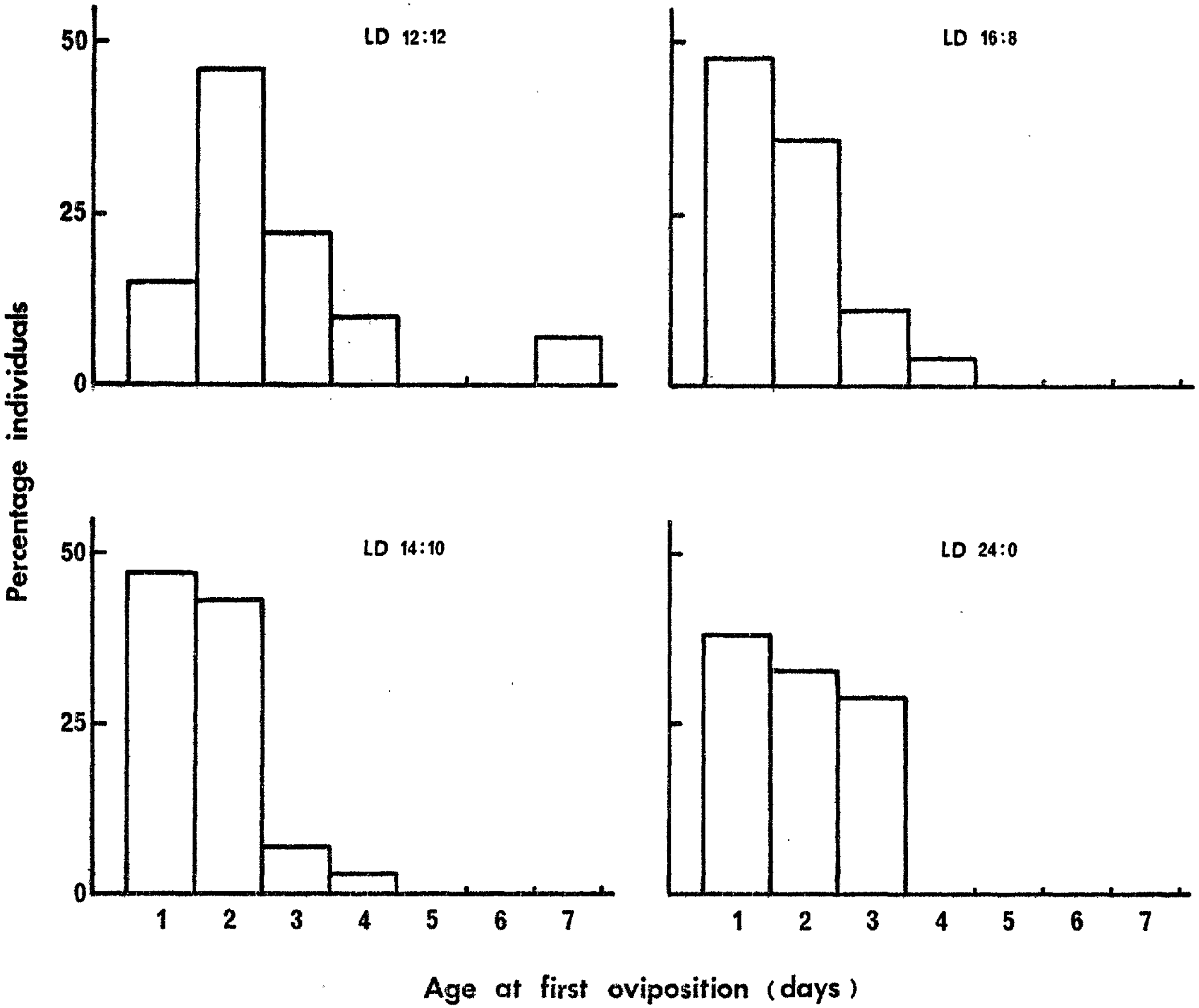

LD 12:12
25
0
Percentage individuals
LD 14:10
30
15
0
1-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101 +
LD 16:8
LD 24:0
100
50
0
1-10
1-10
Age at first oviposition (days)

Figure 34: Distribution of ages at first oviposition of _A. brassicae_ females reared from egg to adult stage under different photoperiods at 25°C.


LD 12:12
LD 16:8
LD 14:10
LD 24:0
50
25
0
Percentage individuals
1
2
3
4
5
6
7
Age at first oviposition (days)

3. Sensitive stages

Data on preoviposition time (days), range, and percentage diapause in the various developmental stages are compared in Table 59.

The percentage diapause in the different stages is illustrated in Fig. 35 while the mean preoviposition times and their comparison by Duncan's new multiple range test are graphically represented in Fig. 36. Calculations for the multiple range test are shown in Table 60.

The distribution of ages at first oviposition for each immature stage is presented in Fig. 37.

Females transferred as eggs, instar I, and instar II from LD16:8 to LD12:12 showed 100% diapause. A high incidence of diapause (86%) also occurred in the females transferred to LD12:12 in the early instar III but dropped sharply to 35% when transferred in the late instar III stage. Early instar IV and teneral adults were insensitive to short photoperiod. Thus, the main sensitive stages of development to photoperiod were found to be the eggs, instar I, instar II, and early instar III.

The mean preoviposition period in days was longest in instar II (78.32) and shortest in the early instar IV (2.87).

Comparison of means by Duncan's new multiple range test showed that the means for instar II (78.32), instar I (65.90), and egg (59.17), did not differ significantly. However, they were significantly different ($p = .05$) from the rest. The mean preoviposition time for early instar III (49.31) was significantly different while those for late instar III (18.35), teneral adults (3.00), and early instar IV (2.87) were not significant.

The first females from immature stages transferred from LD16:8 to LD12:12 as eggs and instar I laid eggs after 27 and 24 days respectively.

The age at first oviposition was remarkably longer in females transferred as instar II (43 days).

The age class intervals (in days) with the highest percentage of females were 31-40 for individuals transferred to LD12:12 at the egg stage, 51-60 and 61-70 for individuals transferred at instar I, and 51-60 for those transferred at instars II and III respectively.

Table 59: Mean preoviposition times (days), range, and percentage diapause.

Developmental stage	No. of observations	Mean preoviposition time	Range	% Diapause
Egg	24	59.17	27 - 141	100
Instar I	28	65.90	24 - 101	100
Instar II	22	78.32	43 - 126	100
Early instar III	29	49.31	7 - 91	86
Late instar III	17	18.35	2 - 69	35
Early instar IV	15	2.87	2 - 5	0
Teneral adult	22	3.00	1 - 7	0

4. Influence of food plant on diapause

The preoviposition periods of non-diapausing females reared on young leaves of summer and winter leaves of Brussels Sprout are presented in Table 61.

The difference between the means were not significant by t-test.

Table 60: Comparison of mean ages at first oviposition of female *A. brassicae* transferred at various developmental stages from LD16:8 to LD12:12 by Duncan's new multiple range test.

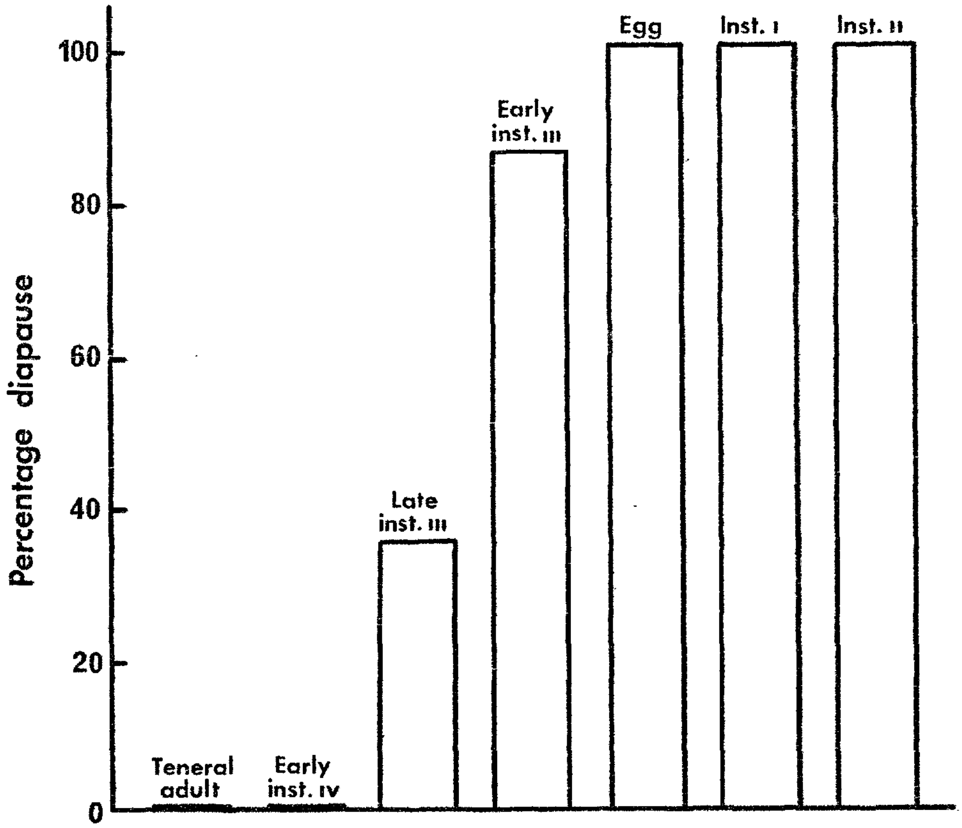
Value of p	2	3	4	5	6	7	8
Significant Studentized Range (SSR)	3.15	3.19	3.23	3.26	3.29	3.34	3.38
Least Significant Range (LSR)	25.17	25.49	25.81	26.05	26.29	26.69	27.01

Early instar IV	Teneral adults	Late instar III	Early instar III	Egg	Instar I	Instar II
2.87	3.0	18.35	49.31	59.17	65.9	78.32

Any two means not underscored by the same line are significantly different (p = .05) while any two means underscored by the same line are not significantly different.

Figure 35: Percentage diapause when *A. brassicae* females were transferred at the stages indicated from LD16:8 to LD12:12 at 20°C.

Figure 36: Mean preoviposition time of *A. brassicae* females transferred at the stages indicated from LD16:8 to LD12:12 at 20°C.


Percentage diapause
100
80
60
40
20
0
Teneral adult
Early inst. IV
Late inst. III
Early inst. III
Egg
Inst. I
Inst. II

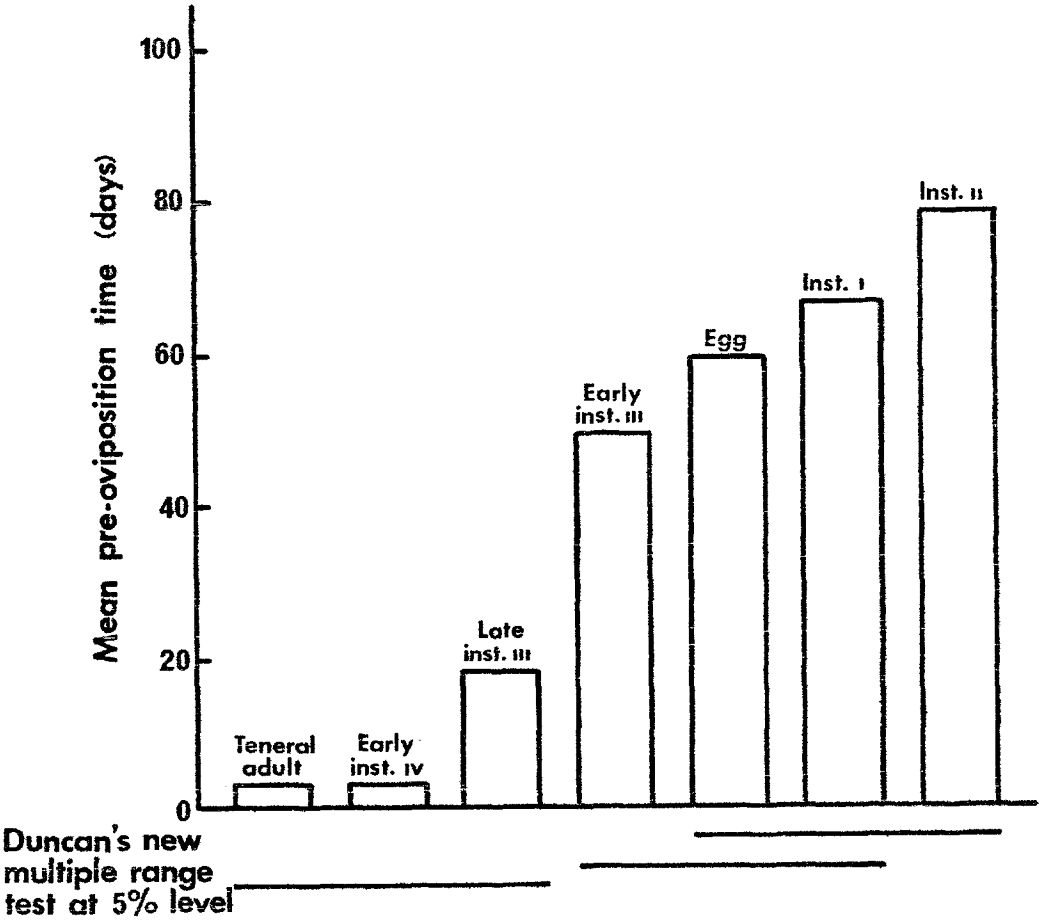

Mean pre-oviposition time (days)
100
80
60
40
20
0
Teneral adult
Early inst. IV
Late inst. III
Early inst. III
Egg
Inst. I
Inst. II
Duncan's new multiple range test at 5% level

Figure 37: Distribution of ages at first oviposition of A. brassicae females transferred from LD16:8 to LD12:12 at the various stages of development at 20°C.

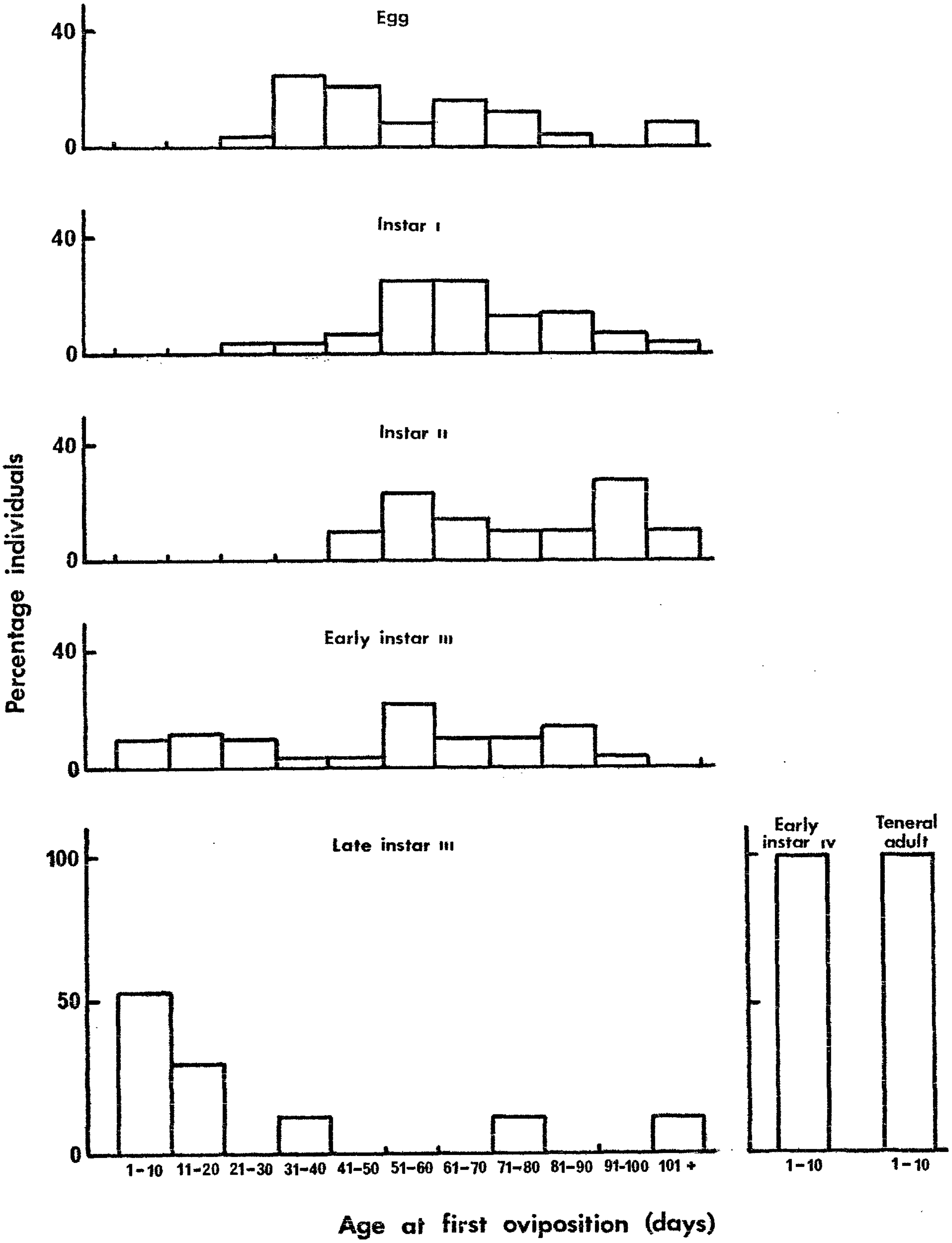

Egg
Instar I
Instar II
Early instar III
Late instar III
Early instar IV
Teneral adult
Percentage individuals
40
0
100
50
1-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101 +
Age at first oviposition (days)

Table 61: The influence of the food source on diapause induction (preoviposition period in days) in A. brassicae (summer morphs).

Young leaves (summer)	Young leaves (winter)
3	3
6	18
3	4
2	15
3	15
3	14
3	2
3	4

5. Effect of chilling on diapause development

Table 62 represents the preoviposition periods of chilled and unchilled diapausing females.

The two mean preoviposition periods were compared using the t-test.

With 17 degrees of freedom and a least significant difference of 2.11, there was a significant difference ($p = .05$) between the mean preoviposition periods of chilled (35.56 days) and unchilled (50.6 days) diapausing females kept at LD16:8.

Table 62: Preoviposition periods of chilled and unchilled diapausing females of *A. brassicae*.

Chilled females	Unchilled females
40	60
41	50
42	46
42	52
34	54
29	43
22	43
42	59
37	50
	49

6. Field collected females

Tables 63(a) and (b) show dates of field collection, mean durations and range (days) at first oviposition of females reared in LD16:8 and LD12:12 respectively at 20°C. Similar data for LD16:8 and LD12:12 at 15°C are presented in Tables 64(a) and (b) respectively. Results obtained at 10°C with LD16:8 and LD12:12 are summarized in Tables 65(a) and (b) respectively.

The mean durations before oviposition under different experimental conditions are graphically illustrated in Fig. 38.

Analysis of variance showed that the effect of dates of collection on the mean number of days at first oviposition was very highly significant ($p < .001$) (Tables 66(a), 67(a), 68(a), 69(a)).

The mean durations before oviposition occurred increased with decreasing temperature, being longest at 10° and shortest at 20°C. The durations were also longer at LD12:12 than at LD16:8 for each temperature treatment.

There was a progressive decrease in mean days at first oviposition as the mean weekly field temperature fell in autumn/winter.

The mean number of days before oviposition occurred was significantly longer ($p = .05$) in females field collected before December than in those field collected thereafter when they were reared at LD16:8 and 20°C. With LD12:12 and 20°C, the same trend as described above was followed though the durations were longer in the latter conditions. The results at 15°C with LD16:8 and LD12:12 were in general, of the pattern described above.

Comparisons of all mean durations by Duncan's new multiple range are presented in Tables 66(b), 67(b), 68(b), 69(b).

With LD12:12, the mean durations in days were 1.9 times as long as in LD16:8 at 20°C. At 15° and 10°C respectively, the durations were 1.7 times longer with LD12:12 than with LD16:8.

At 20°C, oviposition commenced within the first week when females were field collected in early December and early January and kept at LD16:8 and LD12:12 respectively. At 15°C, females field collected in mid January and reared at LD16:8 oviposited in the first week while those reared at LD12:12 did so when field collection was made in mid February.

7. Field collected pupae

Pupae field collected on 20.x.75 and kept at LD12:12 and 20°C emerged as adults. The adults had a mean preoviposition period of 23.3 days.

Pupae field collected on 13.ii.76 also emerged as adults, but the adults had a shorter mean preoviposition period of 4.1 days, under similar laboratory conditions as those collected earlier.

8. Fecundity of 'summer' and 'winter' females.

The mean fecundity per female was found to be 62.9 for summer females and 113.3 for winter females.

The mean cumulative fecundities of both morphs are plotted in Fig. 39. The fecundity of the diapause emerged winter females was consistently higher than that of the summer non-diapausing females.

Table 63(a): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD16:8 and 20°C.

Date field-collected	Number of insects	Mean	Range
28.ix.75	12	32.08	26 - 47
12.x.75	6	28.50	25 - 36
26.x.75	6	18.70	13 - 26
9.xi.75	11	12.30	7 - 19
23.xi.75	9	8.20	4 - 18
7.xii.75	12	7.17	5 - 13
21.xii.75	10	6.40	2 - 12
4.i.76	10	5.20	2 - 15
18.i.76	10	3.60	2 - 8
1.ii.76	10	3.00	2 - 4
15.ii.76	6	2.26	2 - 3
22.ii.76	10	1.95	1 - 4

Table 63(b): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD12:12 and 20°C.

Date field-collected	Number of insects	Mean	Range
28.ix.75	9	72.89	46 - 92
12.x.75	5	59.00	22 - 140
26.x.75	5	41.20	23 - 72
9.xi.75	6	19.57	10 - 31
23.xi.75	9	11.67	6 - 21
7.xii.75	11	10.10	4 - 15
21.xii.75	6	8.17	4 - 20
4.i.76	10	4.6	1 - 6
18.i.76	10	5.2	2 - 14
1.ii.76	10	2.9	1 - 6
15.ii.76	10	2.9	2 - 5

Table 64(a): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD16:8 and 15°C.

Date field-collected	Number of insects	Mean	Range
28.ix.75	10	49.7	44 - 61
12.x.75	6	34.0	23 - 51
26.x.75	5	25.2	15 - 37
9.xi.75	9	17.0	13 - 24
23.xi.75	9	15.33	8 - 24
7.xii.75	12	9.75	5 - 14
21.xii.75	10	6.60	4 - 12
4.i.76	10	8.00	4 - 11
18.i.76	10	6.10	2 - 11
1.ii.76	9	4.30	1 - 6
15.ii.76	10	3.90	1 - 6
22.ii.76	14	3.30	1 - 6

Table 64(b): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD12:12 and 15°C.

Date field-collected	Number of insects	Mean	Range
28.ix.75	14	81.43	41 - 152
12.x.75	3	68.67	65 - 76
26.x.75	6	46.17	25 - 79
9.xi.75	9	23.0	17 - 28
23.xi.75	12	22.83	8 - 51
7.xii.75	12	16.00	5 - 33
21.xii.75	10	18.50	9 - 27
4.i.76	10	12.00	5 - 57
18.i.76	10	6.20	4 - 11
1.ii.76	10	8.00	3 - 18
15.ii.76	10	7.40	1 - 11

Figure 38: Mean weekly temperatures and mean durations (days) at first oviposition of field collected A. brassicae females kept at three constant temperatures (20°, 15°, and 10°C) with two photoperiodic regimens (LD16:8 and LD12:12) for each constant temperature.

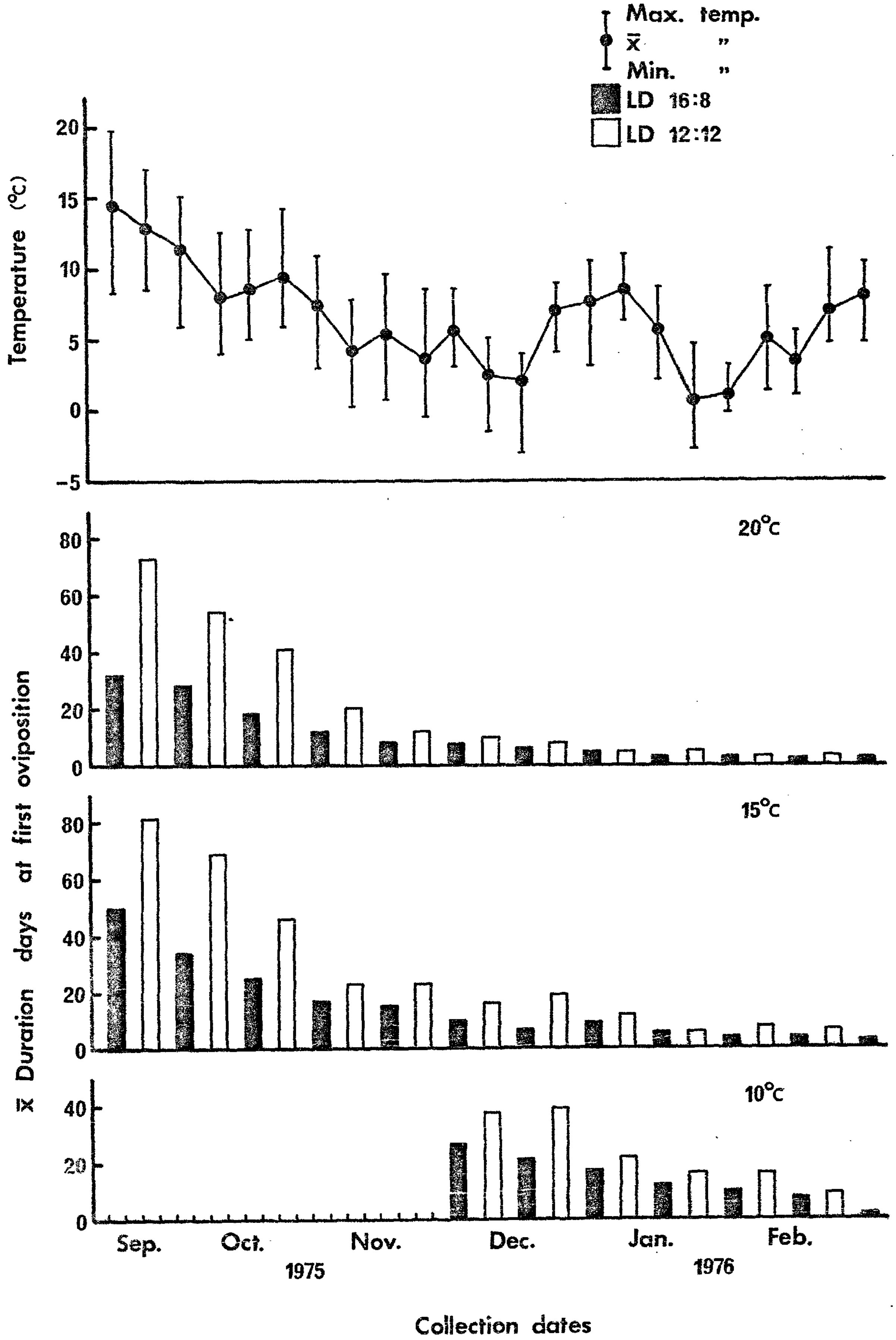

Max. temp.
x̄ "
Min. "
LD 16:8
LD 12:12
Temperature (°C)
20
15
10
5
0
-5
20°c
15°c
10°c
80
60
40
20
0
x̄ Duration days at first oviposition
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
1975
1976
Collection dates

Table 65(a): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD16:8 and 10°C.

Date field-collected	Number of insects	Mean	Range
7.xii.75	12	26.0	12 - 38
21.xii.75	9	21.2	9 - 30
4.i.76	8	17.3	14 - 23
18.i.76	10	11.7	1 - 19
1.ii.76	9	10.4	2 - 20
15.ii.76	5	6.8	6 - 8
22.ii.76	10	1.6	1 - 6

Table 65(b): Number of days to terminate diapause by *A. brassicae* females after transfer from outdoors to LD12:12 and 10°C.

Date field-collected	Number of insects	Mean	Range
7.xii.75	10	38.0	28 - 59
21.xii.75	8	39.3	37 - 45
4.i.76	10	21.9	4 - 56
18.i.76	10	15.6	2 - 42
1.ii.76	9	15.8	6 - 25
15.ii.76	6	9.0	4 - 11

Table 66(a): Analysis of variance for effect of dates of field collection on time before oviposition at 20°C with LD16:8.

Source of variation SV	Degree of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Date of collection	10	10098.07	100.981	6.17*
Residual	90	1472.09	16.36	
Total	100	11570.16		

* Denotes significance at $p < .001$

Table 66(b): Comparison of means by Duncan's new multiple range test

Value of p	2	3	4	5	6	7	8	9	10	11	12
Significant Studentized Range (SSR)	2.80	2.95	3.05	3.12	3.18	3.22	3.26	3.29	3.32	3.36	3.40
Least Significant Range (LSR)	3.42	3.60	3.72	3.81	3.88	3.93	3.98	4.01	4.05	4.10	4.15

2.0 2.3 3 3.6 5.2 6.4 7.2 8.2 12.3 18.7 28.5 32.1

Any two means not underscored by the same line are significantly different (p = .05).

Table 67(a): Analysis of variance for effect of dates of field collection on time before oviposition at 20°C with LD12:12.

Source of variation SV	Degree of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Date of collection	10	47814.21	4781.42	26.67*
Residual	81	14522.95	179.30	
Total	91	62337.16		

* Denotes significance at $p < .001$

Table 67(b): Comparison of means by Duncan's new multiple range test

Value of p	2	3	4	5	6	7	8	9	10	11	12
Significant Studentized Range (SSR)	2.80	2.95	3.05	3.12	3.18	3.22	3.26	3.29	3.32	3.36	3.40
Least Significant Range (LSR)	11.84	12.48	12.90	13.20	13.45	13.62	13.79	13.92	14.04	14.21	14.38

2.9 2.9 4.6 5.2 8.2 10.10 11.7 19.6 41.2 59.0 72.9

Any two means not underscored by the same line are significantly different (p = .05).

Table 68(a): Analysis of variance for effect of dates of field collection on time before oviposition commenced at 15°C with LD16:8.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Date of collection	11	20050.2	1822.75	107.47*
Residual	96	1626.21	16.96	
Total	107	21676.41		

* Denotes significance at $p < .001$

Table 68(b): Comparison of means by Duncan's new multiple range test

Value of p	2	3	4	5	6	7	8	9	10	11	12
Significant Studentized Range (SSR)	2.80	2.95	3.05	3.12	3.18	3.22	3.26	3.29	3.32	3.36	3.40
Least Significant Range (LSR)	3.33	3.51	3.63	3.71	3.78	3.83	3.88	3.92	3.95	4.00	4.04

3.3 3.9 4.3 6.1 6.6 8.0 9.8 15.3 17 25.2 34 49.7

Any two means not underscored by the same line are significantly different (p = .05).

Table 69(a): Analysis of variance for effect of dates of field collection on time before oviposition commenced at 15°C with LD12:12.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Date of collection	10	64984.97	6498.5	31.08*
Residual	95	19859.38	209.1	
Total	105	84844.35		

* Denotes significance at $p \leqslant .001$

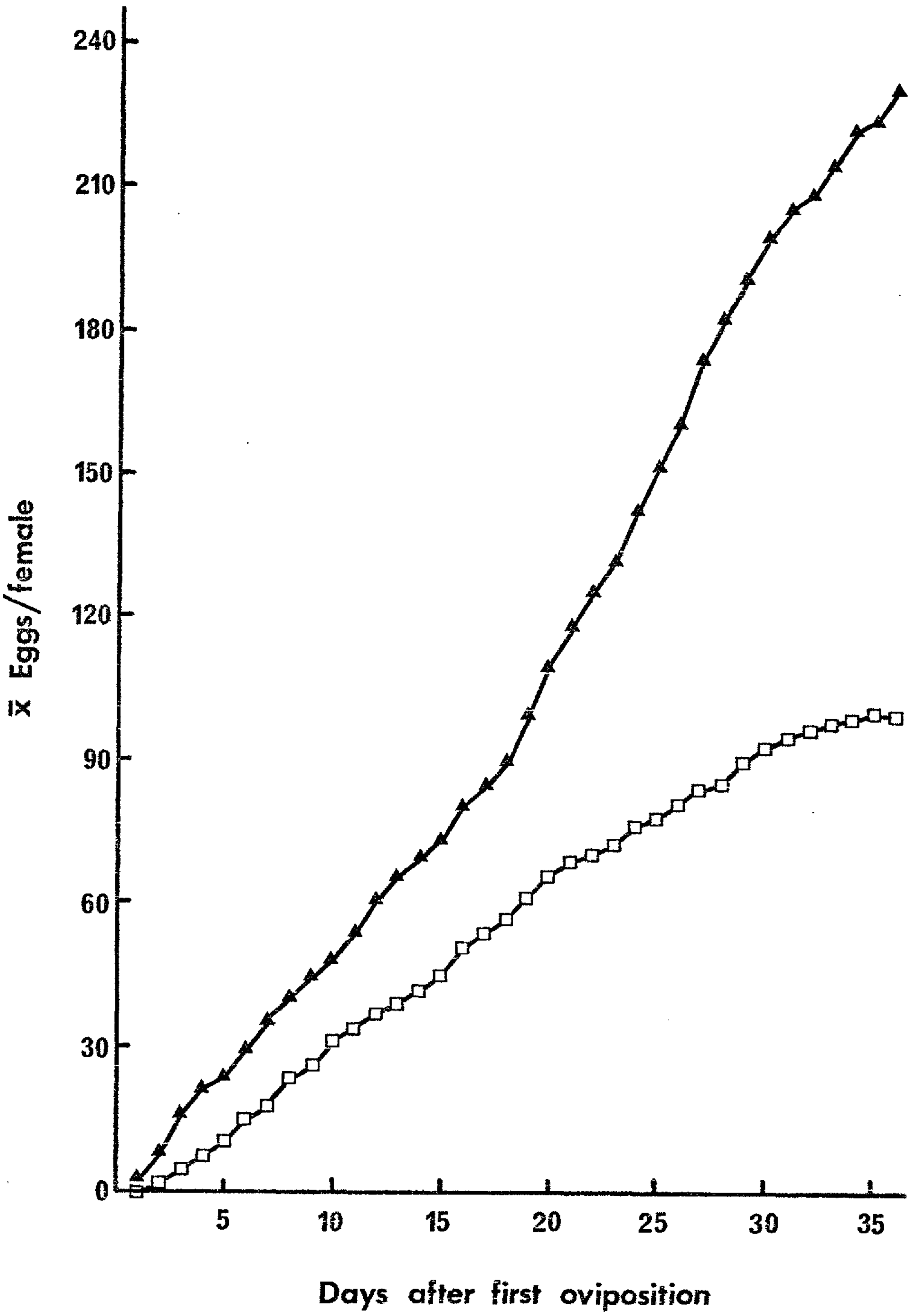
Table 69(b): Comparison of means by Duncan's new multiple range test

Value of p	2	3	4	5	6	7	8	9	10	11	12
Significant Studentized Range (SSR)	2.80	2.95	3.05	3.12	3.18	3.22	3.26	3.29	3.32	3.36	3.4
Least Significant Range (LSR)	12.21	12.86	13.30	13.60	13.86	14.04	14.21	14.34	14.48	14.65	14.82

6.2 7.4 8 12.7 16 18.5 22.8 23 46.2 68.7 81.4

Any two means not underscored by the same line are significantly different (p = .05).

Figure 39: Cumulative total number of eggs per diapause emerged female (▲——▲) and non-diapausing female (□——□) of *A. brassicae* at 25°C.


x̄ Eggs/female
240
210
180
150
120
90
60
30
0
5
10
15
20
25
30
35
Days after first oviposition

D. DISCUSSION

The cabbage whitefly, A. brassicae, shows a long-day type of response to photoperiod. Consequently, in summer when photoperiods are long, temperature optimum, and food abundant, the reproductive rate is at its height. Generation times are short and under summer conditions several generations are produced in a year (multivoltine). The number is dependent on the prevailing weather conditions.

Like most temperate multivoltine insects e.g. Oncopeltus fasciatus (Dingle, 1974), and mites e.g. Metatetranychus ulmi (Lees, 1950, 1953a), the cabbage whitefly, A. brassicae, is exposed to shorter photoperiod and lower temperature in autumn. The low autumn temperature may not necessarily fall below the threshold for development. Butler (1938) reported that the fall in autumn temperature was responsible for the cessation of breeding activity in the cabbage whitefly, A. brassicae. However, under laboratory conditions of LD16:8 and 10°C, oviposition continues uninterruptedly.

From the laboratory results of the influence of temperature and photoperiod on the incidence of reproductive diapause (Table 58 and Fig. 31), photoperiod, rather than temperature, is the main environmental factor that initiates diapause in the cabbage whitefly, A. brassicae. Photoperiod has been shown to be a major environmental factor in controlling the induction and maintenance of diapause in many insects. I do not, however, underestimate the importance of low temperature in inducing diapause. Hodek (1971) showed high incidence of diapause when females of the bug, Pyrrhocoris apterus, were exposed to low temperature.

Beck (1962a, b) showed that the incidence of diapause in the European corn borer, Ostrinia nubilalis, was very high when the cool phase of the thermoperiod occurred during the dark portion of the photoperiod (scotophase). Similar results have been reported by Goryshin (1964) in three lepidopterous species. Under the natural environment of the cabbage whitefly, A. brassicae, the low scotophase temperature of autumn and winter will reinforce the effect of short photoperiod in diapause induction.

Temperature may modify or abolish insects' reaction to photoperiod. In the cabbage whitefly, A. brassicae, a temperature of 20°C did not avert diapause but 25°C did. The prevention of photoperiodic induction of diapause by high temperature was first reported in Diataroxia oleracea by Way and Hopkins (1950). Similar observations have been reported in the fruit tree spider mite, M. ulmi, (Lees, 1950) and the root maggot, Euxesta notata, (McLeod, 1964). Beck (1968) suggested that temperature extremes lead to a bypassing of the photoperiodic response system or they may be the result of the critical photoperiod having been shifted to a point lying outside the range of photoperiods to which the insects were exposed.

Some characteristics of an insect population that are of great importance to its adaptation to seasonal changes have been outlined by Beck (1968). These include:

1. the critical photoperiod for diapause determination;
2. the growth stage at which diapause is determined;
3. the growth stage at which the response is manifested;
4. the effect of temperature on the critical photoperiod; and
5. the temperature characteristics of the insects growth.

The critical photoperiod (causing diapause in 50% of individuals) is of great ecological importance because it determines the calendar time of diapause initiation in nature. The critical photoperiod for the cabbage whitefly, A. brassicae, was found to be 15 hrs 45 minutes at 15°C with 60% diapause (Table 57 and Fig. 31).

Photoperiodic response curves at medium temperatures are usually asymmetrical and show a steep transition at one side of the optimum. Withrow (1959) pointed out that the steepness indicates the precision of the time-measuring effect of the photoperiodic induction process and determines its reliability as an indicator of the season. Fig. 31 therefore illustrates the sensitivity of the cabbage whitefly, A. brassicae, to a change as short as 15 minutes in the duration of light period. Lees (1955) remarked that some insects are sensitive to a change of 15 minutes in the duration of light period.

At suboptimal photoperiods the incidence of diapause fell gradually to the zero level. Such gradual fall off with increased photoperiod has been reported in Grapholitha (Dickson, 1949). Constant illumination did not induce any diapause in the cabbage whitefly, A. brassicae. Tauber and Tauber (1972) made a similar observation in Chrysopa nigricornis. De Wilde et al, (1959) reported a 50% diapause in the Colorado beetle, L. decemlineata, under constant illumination.

Though 100% diapause occurred in the cabbage whitefly, A. brassicae, at 20°C with LD14:10, it should not be assumed that the critical photoperiod at this temperature is the same as at 15°C. This is because temperature influences critical photoperiods. Extrapolation from Fig. 31 shows that the critical photoperiod at 20°C is 15 hrs 15 min. - a decrease of 30 mins. for 5°C rise in temperature. Lees (1963) showed that the critical photoperiod for ovipara production by the aphid Megoura viciae decreased approximately 15 minutes for every 5°C. In the Asiatic bollworm, Chloridae obsoleta, the critical photoperiod changes by 60 minutes for a

5°C change in the constant temperature (Goryshin, 1958). However, Saunders (1970) reported that the critical photoperiod in the flesh-fly, *Sarcophaga argyrostoma*, was about the same at both 15° and 20°C.

Although laboratory data are not directly applicable to field conditions, they indicate the limits of the factors under observation. The mean photoperiod in the last week of July 1975 was 15 hrs 44 mins. From the laboratory results of the critical photoperiod at 15°C (15 hrs 45 mins), it will be expected that a high percentage of eggs laid as from late July by non-diapausing females will give rise to diapausing adults. With a drop in temperature at this point in time, and consequent lengthening of the development time (52 days at 15°C), diapausing adults will be expected to emerge in the 3rd week of September. Since development rate proceeds faster under fluctuating temperatures (Ludwig, 1926; Shelford, 1927; Cloudsley-Thompson, 1953) diapausing adults may emerge earlier. El-Khidir (1963) reported that autumn generation of the cabbage whitefly, *A. brassicae*, emerges by mid September. Thus, there is a close agreement between the laboratory determined critical photoperiod and the approximate time of photoperiodic induction of diapause and also the appearance of diapausing females in nature.

The stages of development which monitor the photoperiodic cues vary from species to species. In the cabbage whitefly, *A. brassicae*, the stages include the eggs, instars I, II, and early instar III. Both instar IV and teneral adults are indifferent to photoperiod. In *Chrysopa nigricornis* the sensitive stages are instars I, II, and the free living instar III (Tauber and Tauber, 1972). In *Wyeomyia smithii* the early instars are the sensitive stages (Evans and Brust, 1972). In *O. fasciatus* maximum sensitivity occurs in the late instar V (Dingle, 1974). Sensitivity in the adult stage has been reported in *L. decemlineata* (de Wilde *et al*, 1959), Coccinella novemnotata (McMullen, 1967), and in Hippodamia tredecimpunctata (Storch and Vaundell, 1972). Sensitive stages to photoperiod are not always the responsive stages. In the cabbage whitefly, A. brassicae, the responsive stage is the adult. In Aleurochiton complanatus the responsive stage is the pupa (Muller, 1962).

A knowledge of the reproductive biology of the cabbage whitefly, A. brassicae, elucidates the significance of the photoperiodic induction by the early immature stages. The non-diapausing females are often reproductively mature on emergence. A shift of the sensitive stage to the adult stage may lead to a commencement of oviposition by a large proportion of the autumn generation, especially if the temperature is not below 10°C. Eggs thus laid may not reach maturity with the winter temperature falling below the threshold for development. Furthermore, the chances of the females surviving through winter will be reduced because of insufficient food reserves as a result of egg development. It seems logical that a maximum sensitivity in the adult stage will lead to extinction of the species with time. Thus, sensitivity to photoperiod by the early immature stages and its manifestation as gonotropic dissociation constitute a biological strategy to ensure the perpetuation of the insect.

In autumn and winter, immature stages of the cabbage whitefly, A. brassicae, are found in the field, provided the leaves of the host plant are able to stand the weather. Some of these immature stages, particularly instar IV, emerge as adults in spring when the ambient temperature is reasonably high. Such immature stages emerge as adults under suitable laboratory conditions. This is, therefore, a clear case of quiescence which is brought about by low temperature. The cabbage whitefly, A. brassicae, therefore combines a reproductive diapause (in the adult stage) with quiescence (in the immature stages) to overcome the stresses of the winter season.

Reproductive diapause was not induced in non-diapausing females of the cabbage whitefly, A. brassicae, fed field collected 'young' leaves of over-wintering Brussels Sprout. It was not prevented by feeding females, reared in diapause inducing conditions, on young summer foliage. Since the biochemical compositions of plants vary with seasons e.g. summer leaves of Viburnum tinus (the food plant of the viburnum whitefly) show higher concentrations of total amino acid than winter leaves, Southwood (personal communication), the quality of the food plant of the summer generations of the cabbage whitefly, A. brassicae, will be expected to differ from that on which the autumn generation feeds. However, the difference was not manifested in the form of reproductive diapause.

Reports on the influence of food on diapause seem to be conflicting. For example, Jermy and Saringer (1955) could not find any nutritional effect on the Colorado beetle, L. decemlineata, since feeding young beetles young potato leaves did not prevent diapause. But Grison (1956) reported that senescent leaves promoted diapause in the same insect. Larczenko (1957) showed that as the lipid: protein ratio increased, the incidence of diapause in L. decemlineata also increased. As the cabbage whitefly, A. brassicae, enters reproductive diapause as early as September, the role of food source in diapause induction is negligible.

Chilling was found to be a more effective factor in diapause termination than long photoperiod. Andrewartha (1952) and Lees (1955) have shown that the highest speed of diapause reactivation for temperate insects with winter diapause, usually occurs at temperatures below the level necessary for active life processes.

The time required by diapausing females field collected from September 1975 to February 1976 to complete their diapause development was longer in females collected before December and shorter in those collected as from January. Collyer (1967) made a similar observation in A. nemorum. The times to complete diapause development were longer in insects kept at 15°C with LD12:12 and shorter in those kept at the same temperature but with LD16:8 (Tables 64(a) and (b) and Fig. 38). At 20°C, a similar trend was followed though the durations were shorter in the latter temperature (Tables 63(a) and (b) and Fig. 38). The fact that the short photoperiod maintained a repressive effect on reproductive development seems to indicate that the diapausing females were still sensitive to photoperiod. Kamm (1973) has shown that in Chrysoteuchia topiaria short photoperiods also retard development during diapause. Tauber and Tauber (1976) reported the requirement of short-day for diapause termination in the univoltine Chrysopa downesi.

Females of the cabbage whitefly, A. brassicae, field collected in late February, 1976, oviposited within the first week when kept at temperatures of 10°C and above, whereas those collected in September, 1975, had mean durations of 5 weeks and 7 weeks at 20° and 15°C respectively. Butler (1938) reported that cabbage whitefly females brought into the laboratory at any time during autumn or winter, and placed under suitable conditions, always began to oviposit within the first week and usually within the first three days. If Butler's observations were correct, then the nature of the reproductive arrest should best be described as quiescence. However, detailed laboratory studies supported with field observations have clearly demonstrated that the dormancy in the cabbage whitefly is not a mere quiescence but diapause. It seems likely that Butler's observations were made on females that had experienced the cold winter temperature.

Opinions are divided as to what factors terminate diapause and synchronize it with spring development. The fact that cold temperature facilitates diapause development (physiogenesis) with ultimate resumption of morphogenesis in spring as temperature rises above the threshold for development, has led some workers (e.g. Andrewartha, 1952) to believing that temperature was the sole environmental factor that terminates diapause. Some authors (e.g. Beck, Cloutier and McLeod, 1963; Adkisson, 1964; McLeod, 1964) on the other hand, have proposed that in nature, the time of resumption of development is determined by the daylength and not temperature.

It has been demonstrated in Pieris brassicae that after the initiation of diapause, photoperiodic response is often sharply weakened, and in Barathra brassicae it is completely abolished. Photoperiodic reaction has also been reported to disappear completely after sufficient chilling. Since females of the cabbage whitefly, A. brassicae, field collected in February and reared at 10°, 15°, and 20°C respectively with LD16:8 and LD12:12 respectively for each temperature regime, commenced oviposition in the first week of collection whereas those kept at 5°C with LD16:8 maintained their diapause indefinitely, it is possible that the photoperiodic induction was so much weakened by the chilling effect that a rise in temperature above the threshold for development led to diapause termination. Thus, temperature seems to have an overriding influence in diapause termination. But since temperature and photoperiod are components of the environment in which the cabbage whitefly, A. brassicae, live, resumption of morphogenesis in spring could be as a result of the cumulative effects of both factors on the diapausing females.

Dingle (1974) pointed out that not much attention has been paid to the pattern of diapause emergence in insects. Diapause terminated females of the cabbage whitefly, A. brassicae, showed higher fecundity level than the non-diapausing ones. Soni (1976) obtained similar results with Erioischia brassicae. This observation is very significant because population density is usually very low in spring as a result of winter mortality.

The distribution of the cabbage whitefly, *A. brassicae*, in the United Kingdom is interesting. It is abundant in the southern counties, occurs sporadically in the midlands, but is almost unknown in the north and in Scotland.

Photoperiod is one of the most important isolating factors in intraspecific geographical distribution. Photoperiodic response of an insect species may differ according to the geographical latitude at which they occur. Such insects may differ in intensity of photoperiodic response, effect of temperature on response, and critical photoperiod. With increase in latitude, temperature decreases, causing a restriction in the number of generations.

In central Scotland (lat. 56.4 N), *Anthocoris nemorum* has only one generation in a year (Hill, 1957) whereas in southern England (lat. 51.24 N), two or more generations have been reported (Anderson, 1962; Collyer, 1967). It is possible that the distribution of the cabbage whitefly, *A. brassicae*, has been influenced by differences in latitude, temperature, and photoperiod. With the aid of photothermographs (Ferguson, 1957), the relative importance of these factors in the distribution pattern of the cabbage whitefly, *A. brassicae*, can be ascertained.

By entering diapause in winter, the cabbage whitefly, *A. brassicae*, ensures that its biology synchronizes with that of the host plant and also with the seasonal climatic cycle. The manifestation of diapause in the adult stage as gonotropic dissociation enhances its flight ability, thus enabling the insect to move from its deteriorating habitat to overwintering quarters.

SECTION IV: FLIGHT BEHAVIOUR OF THE CABBAGE WHITEFLY, *A. BRASSICAE*.

A. INTRODUCTION

Insect flight has attracted much attention for many years and has been studied both qualitatively and quantitatively.

El-Khidir (1963) remarks that the little available information on flight of aleyrodids is mainly qualitative. His quantitative study, with the aid of suction traps, provides information on the daily and seasonal flight rhythm of the cabbage whitefly, A. brassicae.

The citrus whitefly, A. citri, are said to cover a flight range of about 1¾ miles (Morrill and Back, 1911). The range of flight of insects, particularly pests, is of great practical importance, and has been assessed by various methods.

The method of marking and releasing of insects yields reliable results provided the range of flight is limited and the insect is readily trapped in large numbers. It is not very useful where there is a combination of long flight range and difficult terrain. A further defect of this method is that it is difficult to be sure that the known distance covered was the result of a single flight rather than a number of flights.

Another method which has given much information on flight range of insects is the observation of dispersion from known restricted breeding sites (e.g. Waloff and Bakker, 1963; Rose, 1973). Some information obtained in this way could be misleading because of possible distribution of insects by other artificial means. For example, Morrill and Back (1911) reported that during periods of migration in Florida, large numbers of the citrus whitefly, A. citri, alight upon automobiles, carriages, wagons, and railroad coaches.

Qualitative data on flight range of insects have been obtained by Blanton et al (1950); Wilson (1951); Hocking and Richards (1952), from observations on the rate of infiltration of insects into an area previously cleared of them by the application of insecticide. Field observations also provide information on flight range, especially with large conspicuous insects. The annual migrations of the monarch butterfly, Danaus plexippus, from Canada to the southern U.S.A. (Urquhart, 1960) and the occasional occurrence of african locusts in Britain are well known. Rainey (1976) has developed a method of relating insect movement and that of air masses. This synoptic approach has shown how insects may regularly move hundreds of miles.

Hocking (1948) quoted in Hocking (1953) suggested the possibility of estimating flight range from a consideration of the energy available to the animal and the rate at which this is used up in flight. On the basis of this, he made preliminary calculations of the flight range of a mosquito.

Flight ability of insects has been studied by measuring their speed of flight by direct timing in the open with a stopwatch. Similar timing technique has been used under various controlled conditions, such as flight towards a window in a room, or towards a light at the end of a tube (Bentley, 1914), observations in a wind tunnel (Kennedy, 1939); comparison with the speed of a train or other vehicle (Fernald, 1925; Twinn et al, 1948; Nielsen and Nielsen, 1950).

Flight speed of insects has also been measured by means of flight mills (Hocking, 1953; Henson, 1962). The technique of flying insects tethered to pins has been used by many workers (e.g. Cockbain, 1961a; Dingle, 1966, 1968a, b; Caldwell and Hegmann, 1969). Kennedy and Booth (1963a) remarked that tethered flight, whether in still air or in an appropriate relative wind, does not provide an adequate approximation to flight when some other aspects of it are under study. For example, Cockbain (1961b) noted that his fixed aphids continued 'flying' for considerably longer than free aphids were estimated to fly in the field. Rose (1972) remarked that the pin on which his leafhopper was held should be regarded as an inhibitory factor since 'non-fliers' on pins flew in collection tubes. Kennedy and Booth (1963a) stressed the point that when the purpose is to study the interaction between flight and alternative behaviour patterns, the use of the tethered insects may distort the results owing to abnormal sensory inputs both during the fixed flapping and when the insects are transferred from the suspension to some test situation.

The flight chamber invented by Kennedy and Booth enables the natural sequence of flight, settling, and acceptance or rejection of the host plant by an insect to be studied in detail without handling the insects. Free flight in a flight chamber was considered the most appropriate method in the study of flight behaviour of the cabbage whitefly, _A. brassicae_, and was, therefore, used.

Dingle (1974) pointed out that the introduction of experimental methods into the study of insect migration is a relatively recent phenomenon; earlier studies having been based mainly on field observations. Data from experimental approaches could now be combined with field data to provide an integrated view of the whole migration process (Johnson, 1969; Dingle, 1972).

The main aims of the investigation described in this section were to assess

i. the teneral periods at constant temperatures and distinguish between the developmental and behavioural components;

ii. the relationship between leaf age, temperature, and take-off with age; and

iii. the general flight behaviour of the cabbage whitefly, A. brassicae.

If the results of the experiment were considered side by side with El-Khidir's (1963) field data, a complete view of the insects' migratory process would be obtained.

The flight study was confined to females since only females are responsible for future population increase.

B. MATERIALS AND METHODS

1. Take-off chamber

A black-walled cylindrical chamber (50 cm high and 10 cm diameter) with a chimney at one end, was constructed (Fig. 40). The inner surfaces of both the cylinder and the chimney were smeared with a sticky substance to ensure that any insect that took off did not return to the leaf.

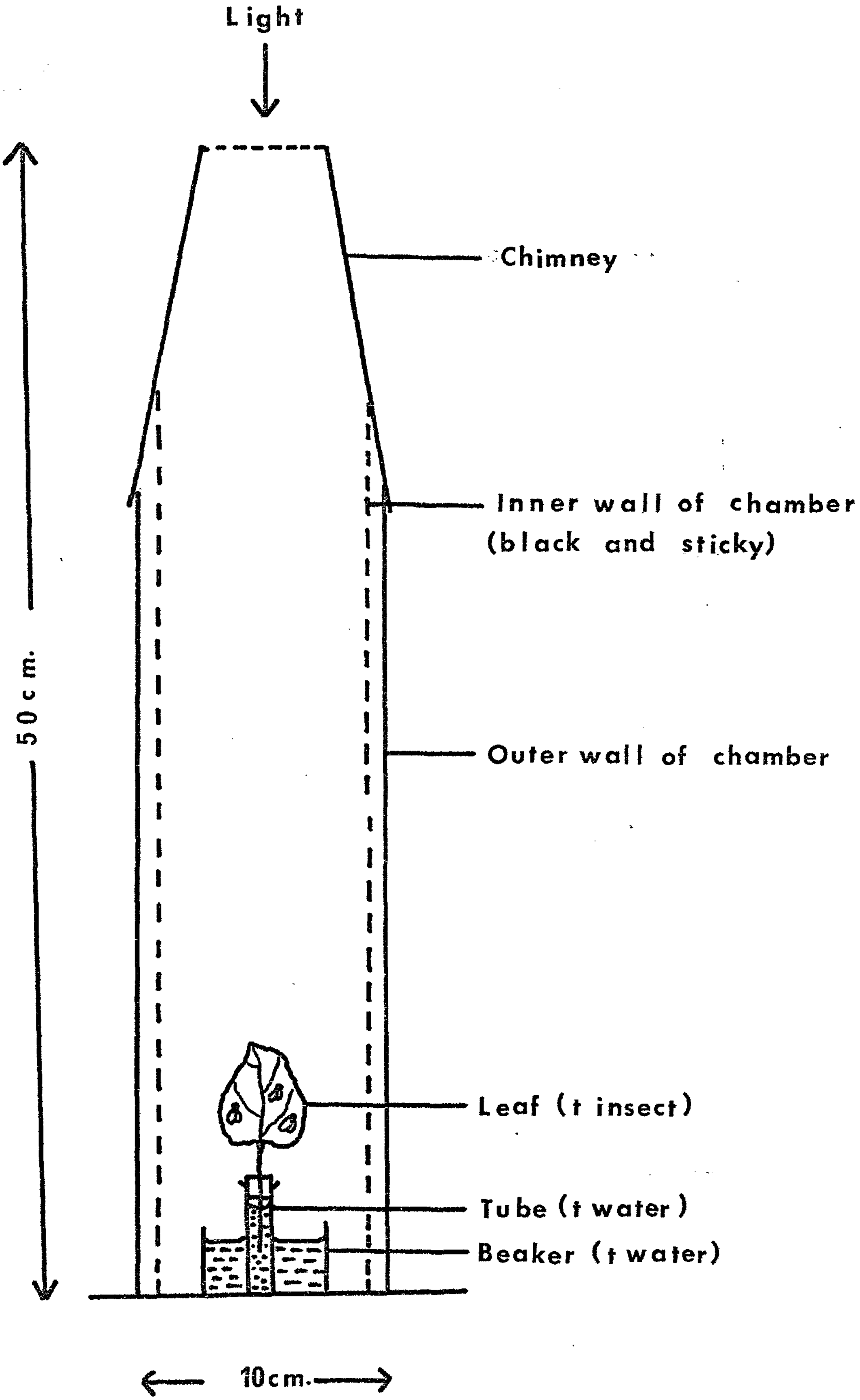
Leaves with experimental insects were detached from the potted plants and their petioles dipped in water in a corked tube. The top surface of the cork was also coated with the sticky substance to trap any insect that walked off the leaf. The tube was in turn placed in a vessel containing water - a further measure to prevent insects from reaching the wall by any means other than flying. An array of chambers thus constructed was placed under fluorescent tubes during experiment. Smaller chambers (8 cm high and 2.5 cm diameter) were used for teneral period experiments.

2. Flight chamber

The flight chamber used was a vertical wind tunnel described by Kennedy (1974), Kennedy and Ludlow (1974), and Laughlin (1974). It was similar in principle to that originally described by Kennedy and Booth (1963a) but now formed part of a closed-circuit airflow system. The flow of air through the working section was not confined to the central illuminated area as in the previous model, but extended beyond it on all sides.

The vertical airflow through the working section was produced by setting up a pressure differential between the upper and lower plenum chambers. The flap valves provided a very sensitive control of the airflow through the working section and were actuated via a counter balanced lever system by the operator while standing at the open front of the working section. From there, it was possible to watch the flying whitefly and hold

Figure 40: Take-off chamber.


Light
Chimney
Inner wall of chamber (black and sticky)
Outer wall of chamber
Leaf (+ insect)
Tube (+ water)
Beaker (+ water)
50 cm.
10 cm.

it at 5-15 cm below the roof screen by continually adjusting the rate of downward airflow to balance the insect's rate of climb toward the light.

One of the flap-valve spindles carried a cam actuating a potentiometer, the voltage across which was fed into a chart recorder to provide a continuous record of the airspeed and therefore of the insect's rate of climb. The cam had been shaped so that the voltage across the potentiometer varied approximately linearly with the air speed at the flying insect's level under the centre of the lit area of the roof screen.

When a flying cabbage whitefly began to sink, instead of climbing, the flap valves were used to reverse the direction of airflow from downward to upward, through the working section. A sinking flier could be kept airborne and its sinking speed recorded.

3. Determination of teneral period

Leaves infested with instar IV were field collected on 10-x-75 and kept at four constant temperatures (25°, 20°, 15°, and 10°C) until adults emerged.

Immediately on emergence, some females were placed on young leaves and others on senescent leaves which had been trimmed to fit the apparatus. Experiments were set up at the respective temperatures with the chambers arranged under a fluorescent tube. The insects were examined hourly from the time of emergence till they took off and landed on the sticky wall. Insects which took off during the interval were assumed to have done so at the midpoint between one inspection and the next. Thus, the time from emergence to take-off was taken as the teneral period.

4. Determination of flight development period

The experimental procedure was similar to that described above except that the insects used were not allowed to take-off voluntarily. Instead, on emergence they were transferred to young and senescent leaves respectively and their ability to fly was tested by dropping them from a known height (68 cm) above the floor of a light cabinet. Drop-tests were first made at $\frac{1}{2}$ hr after emergence and subsequently at hourly intervals. The behaviour of each insect was observed as it dropped off. For example, whether the wings were closed or opened, beat weakly or strongly; whether the insect flew horizontally or upwards to source of light. The time between emergence and flight was taken as the time required by the adults to become "flight-mature".

5. Take-off of 'winter' morphs with age

Female insects bred at 15°C with LD12:12 (diapause inducing condition) were used. Emergence often occurred between 7 a.m. and 11 a.m. This made it possible to work with females of the same age. Usually females that emerged within 30 minutes were regarded and treated as of the same age. Each group of 6 females was caged on young leaves of Brussels Sprout and kept at 15°C with LD12:12 until the required age for take-off experiment was attained. 24 days was the limit of the age tested.

To avoid any possible excitatory or depressive effect on the ability of the insects to take-off, carbon dioxide was not used to anaesthetize them. Instead, insects were transferred to a constant temperature room at 10°C for about 15 minutes during which the experiments were set up as shown in Fig. 40. Each chamber was carefully transferred to the appropriate temperature under investigation. The duration of the experiment was 5 hours after which the experiment was stopped and records of the number of insects that took off, walked off, or did not take-off were taken. The experiment was repeated at 20°C to test the effect of different temperatures on take-off with age.

6. Take-off of 'summer' morphs with age

Females of cabbage whitefly bred at 15°C with LD16:8 (diapause preventing condition) were used. Adults were collected and treated as described for 'winter' morphs except that they were kept at LD16:8 until the required age for take-off experiment was reached. But because of the commencement of oviposition, it became necessary to move the insects to new leaves so as to standardize conditions on the holding leaf. The limit of the age tested was 16 days. The experiment was repeated at 20°C for comparison with 15°C.

7. Effect of leaf age on take-off

The effect of young and senescent leaves on take-off was determined for 'summer' morphs at 20°C. The method used was similar to that described above.

8. Flight ability of winter and summer morphs

The winter morphs were field collected as late instar IV in November, 1975. These were kept at 15°C with LD12:12 until adults emerged. Only 2-day old females were used. To ascertain whether the females were diapausing or not, some were reared at LD12:12 and others at LD16:8 but under the same temperature. Test insects were usually warmed by keeping them at 20°C for about 1 hour.

'Summer' morphs were reared at 15°C with LD16:8 and the females were flight tested at 2-day old stage.

The flight ability of winter and summer morphs was assessed in terms of the number of take-offs each insect required to reach a cumulative total of 40 seconds of flight.

First take-offs were usually from leaf surfaces into the flight chamber. These were either voluntary (as in winter morphs) or induced by prodding with a camel-hair brush (as in summer morphs). Summer morphs were prodded after about 60 secs during which all winter morphs had taken off. Subsequent take-offs, spontaneous in winter morphs but induced in summer morphs, were either from the wall or floor of the chamber. Both the duration of flight and the number of take-offs were read off from the chart of the recorder.

The experiment was replicated twice, each consisting of 6 winter morphs and 7 summer morphs.

The results were analysed by the Mann-Whitney U test (Siegel, 1956).

Insects that had flown for some time suddenly dropped on the floor of the cabinet. These were thought to be exhausted but the fact that they were able to take-off again, though not flying persistently (less than 5 secs) necessitated the use of the term 'drop-out'. Insects that provided data for the duration of flights were flown to drop-out.

9. Effect of food deprivation on flight ability of summer morphs

The difference in the flight ability of food-supplied and food-deprived summer females was based on the number of stimulated flights required to achieve 40 seconds of continuous flight. The means were compared by the t-test.

10. Photokinetic response

The photokinetic response of the cabbage whitefly was measured as the rate of climb. The rates of climb were measured as averages over 60 sec which could be read to the nearest 0.5 cm/sec from the recorder charts with the aid of a graduated cursor (Kennedy, 1965).

11. Rebound principle

The mean rates of climb (cm/sec) in the last 60 sec before landing and the first 60 sec after re-take-off were measured. The difference between the two values was tested by Wilcoxon matched-pairs signed-ranks test (Siegel, 1956).

C. RESULTS

1. Effects of temperature and leaf age on teneral period

The length of teneral period of A. brassicae females on young and senescent leaves of Brussels Sprout at 25°, 20°, 15°, and 10°C is presented in Table 70.

Fig. 41 illustrates the relationship between temperature and the duration of teneral development as well as the speed of development.

Analysis of variance are shown in Tables 71 (a) - (d).

The variance ratio (F) for leaf age effect was highly significant ($p < .001$ at 25°, 15°, and 10°C respectively, and $p < .01$ at 20°C).

The teneral periods were longer on young leaves than on senescent. The differences were also highly significant ($p < .001$).

The slopes of the regression lines of rate of teneral development on temperature were 0.273 and 0.864 on young and senescent leaves respectively.

2. Flight development time

Insects tested for 'flight maturity' by 'forced-dropping' at $\frac{1}{2}$ hr. from emergence fell to the floor of the light cabinet without opening their wings. All those tested after $1\frac{1}{2}$ hrs feebly beat their wings and landed on the floor. When tested after $2\frac{1}{2}$ hrs, the insects flew horizontally to the wall of the cabinet while most of those tested after $3\frac{1}{2}$ hrs flew upwards to the source of light. Thus, the insects were flight mature after about $2\frac{1}{2}$ hrs when kept on senescent leaves at 20°C.

3. Effect of temperature and age of insect on take-off

(a) Winter morphs

Data on take-off with age of winter morphs at 20° and 15°C are

Table 70: Teneral period of *A. brassicae* females on young and old leaves at four constant temperatures.

Temperature °C	Young leaf No. of insects	x̄ teneral period (hrs)	Standard deviation (S.D)	Old leaf No. of insects	x̄ teneral period (hrs)	Standard deviation (S.D)
25	8	16.4	± 8.60	13	5.7	± 1.88
20	7	25.3	± 10.95	6	6.8	± 1.89
15	10	29.3	± 7.01	10	7.7	± 1.49
10	9	57.8	± 9.33	9	28.3	± 1.76

Figure 41: Temperature-time curve of teneral development in A. brassicae on (a) young leaves, and (b) senescent leaves of Brussels Sprout at constant temperatures.

Standard deviations are indicated by horizontal lines.

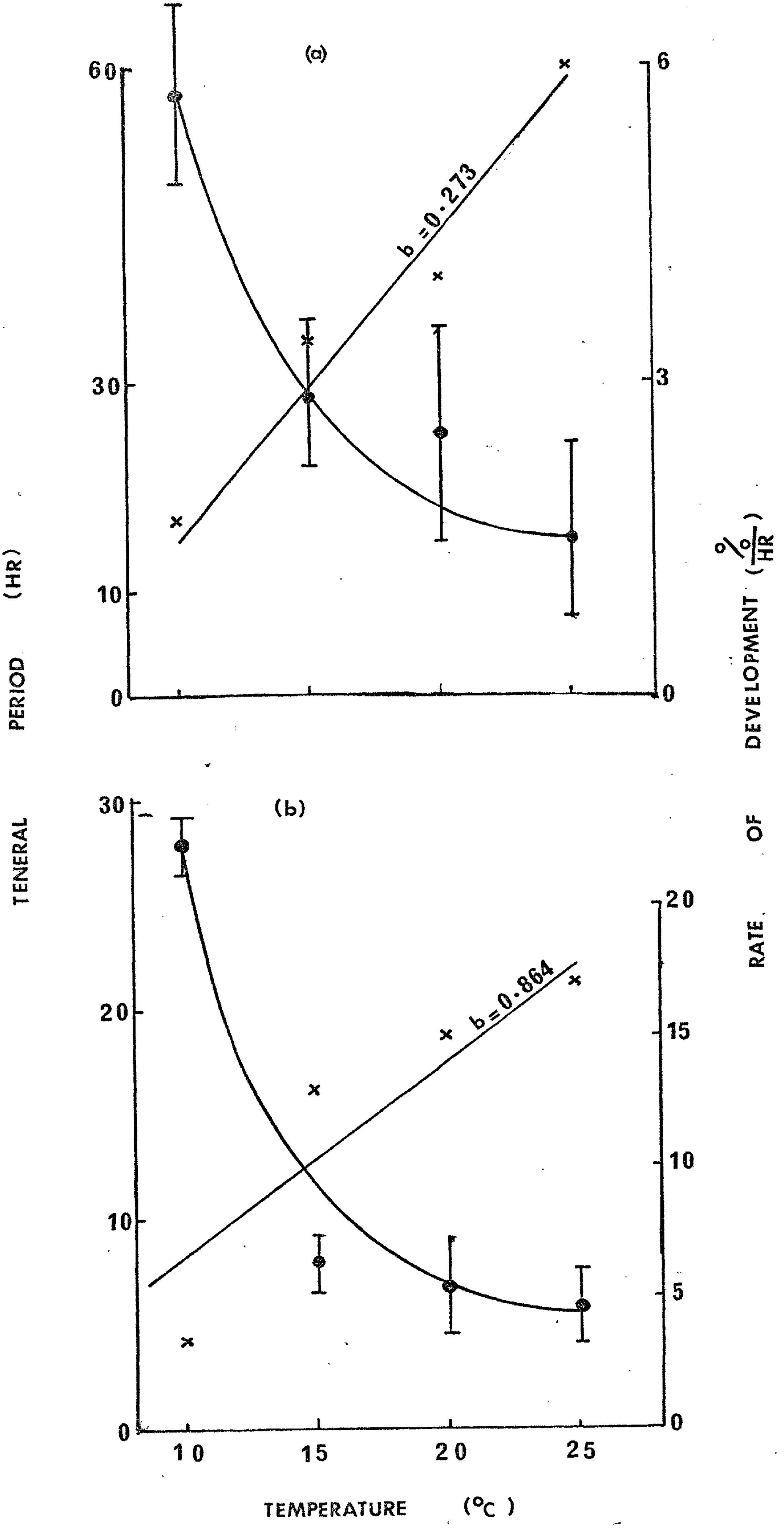

(a)
60
30
10
0
6
3
0
b = 0.273
(b)
30
20
10
0
20
15
10
5
0
b = 0.864
10
15
20
25
TEMPERATURE (°C)
TENERAL PERIOD (HR)
RATE OF DEVELOPMENT (%/HR)

Table 71(a): Analysis of variance for leaf age effect on teneral period at 25°C.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Treatment	1	557.06	557.06	19.1*
Residual	19	554.18	29.17	
Total	20	1111.24		

* Denotes significance at $p < .001$

Table 71(b): Analysis of variance for leaf age effect on teneral period at 20°C.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Treatment	1	1100.05	1100.05	16.26*
Residual	11	744.26	67.66	
Total	12	1844.31		

* Denotes significance at $p < .01$

Table 71(c): Analysis of variance for leaf age effect on teneral period at 15°C.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Treatment	1	2332.8	2332.8	90.84*
Residual	18	462.2	25.68	
Total	19	2795		

* Denotes significance at $p < .001$

Table 71(d): Analysis of variance for leaf age effect on teneral period at 10°C.

Source of variation SV	Degrees of freedom DF	Sums of squares SS	Mean Square MS	Variance Ratio F
Treatment	1	3901.38	3901.38	17.82*
Residual	16	3502.56	218.91	
Total	17	7403.94		

* Denotes significance at $p < .001$

summarized in Tables 72(a) and (b) respectively and illustrated graphically in Fig. 42.

There was no outstanding peak at any particular age. Percentage take-offs were consistently high (above 75%) at both temperatures in the first 24 days of adult life.

The values obtained at both temperatures were compared by the Sign Test and found not to differ significantly. Thus, the ability of the winter morphs to take-off was unaffected by the temperatures tested.

(b) <u>Summer morphs</u>

Tables 73(a) and (b) show the percentage take-off of the summer morphs with age at 20° and 15°C respectively. Both are illustrated in Fig. 42.

The percentage take-off reached a peak (45%) at both temperatures in the first couple of days of adult life. Thereafter, it decreased steadily with age, with the values at 20° consistently higher than those at 15°C.

4. Effect of leaf age on take-off of summer morphs

The results are shown in Tables 73(a) and 74 for young and senescent leaves respectively and also in Fig. 42.

Leaf age had a profound effect on take-off. 100% take-off was recorded on senescent leaves at the 2-day old stage. Though the percentage take-offs decreased after reaching the peak, it did not fall below 60% in the first 16 days of the test. The results on young leaves were the same as described above for temperature and age effects.

Table 72(a): Relationship between age and take-off in *A. brassicae* (winter morphs) at 20°C.

Age of Insect (days)	No. tested	% take-off
2	35	83
4	37	92
6	60	88
8	51	82
10	32	88
12	36	97
14	26	81
16	21	76
18	21	78
20	40	88
22	32	88
24	42	88

Table 72(b): Relationship between age and take-off in *A. brassicae* (winter morphs) at 15°C.

Age of Insect (days)	No. tested	% take-off
2	18	56
4	36	83
6	20	85
8	57	90
10	34	85
12	31	77
14	26	89
16	22	82
18	17	82
20	12	75
22	23	91
24	15	80

Table 73(a): Relationship between age and take-off in *A. brassicae* (summer morphs) at 20°C.

Age of Insect (days)	No. tested	% take-off
1	59	44
3	34	38
4	69	40
5	54	35
7	32	31
9	24	29
10	20	25
11	21	14
13	23	17
16	40	10

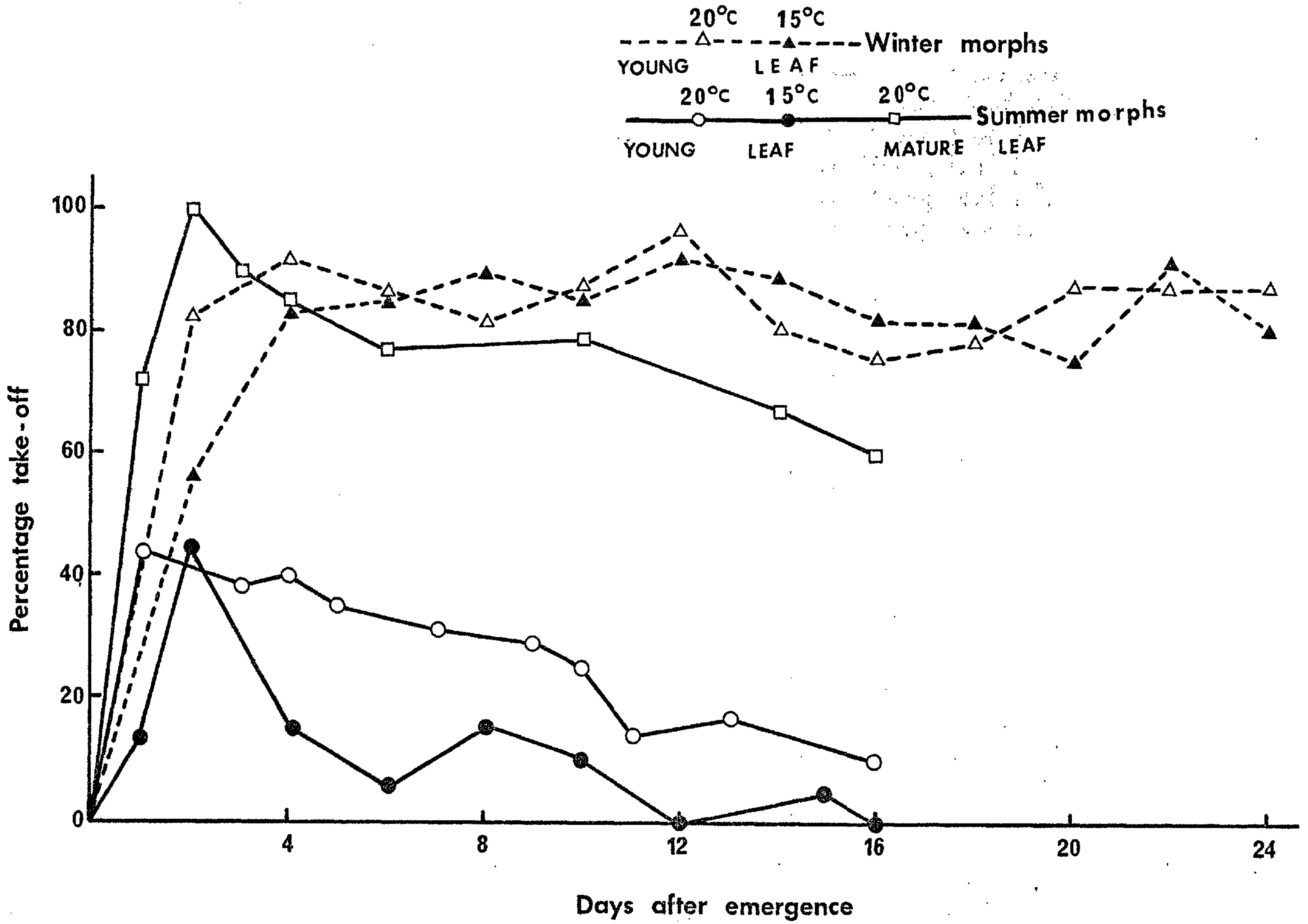
Table 73(b): Relationship between age and take-off in *A. brassicae* (summer morphs) at 15°C.

Age of Insect (days)	No. tested	% take-off
1	16	13
2	20	45
4	40	15
6	38	5
8	23	15
10	21	10
12	15	0
15	38	5
16	18	0

Table 74: Effect of leaf age on take-off with age of *A. brassicae* females (summer morphs) at 20°C.

Age of Insect (days)	No. tested	% take-off
1	36	72
2	35	100
3	38	90
4	27	85
6	31	77
10	24	79
14	21	67
16	30	60

Figure 42: Relationship between leaf age, temperature, and take-off with age in A. brassicae (winter and summer morphs).


20°c 15°c
Winter morphs
YOUNG LEAF
20°c 15°c 20°c
Summer morphs
YOUNG LEAF
MATURE LEAF
Percentage take-off
0
20
40
60
80
100
4
8
12
16
20
24
Days after emergence

5. Flight ability of summer and winter morphs

The number of flights made by the cabbage whitefly summer morphs (SM) and winter morphs (WM) to reach a cumulative total of 40 seconds of flight and the analysis of results by the Mann-Whitney U test are shown in Tables 75(a) and (b). The number of flights did not exceed one in the winter morphs. The range was 2 to 13 flights in the summer morphs.

The difference between the flight ability of the two morphs was highly significant (p = .001)

Replicate 1 Table 75(a): Number of flights

S.M. scores	6	8	13	2	5	3	9
W.M. scores	1	1	1	1	1	1	

Scores ranked in order of increasing size

1	1	1	1	1	1	2	3	5	6	8	9	13
W.M.	W.M.	W.M.	W.M.	W.M.	W.M.	S.M.	S.M.	S.M.	S.M.	S.M.	S.M.	S.M.

$n_1 = 6$, $n_2 = 7$, $U = 0$, $p = .001$

Replicate 2 Table 75(b): Number of flights

S.M. scores	13	4	7	2	3	12	9
W.M. scores	1	1	1	1	1	1	

Scores ranked in order of increasing size

1	1	1	1	1	1	2	3	4	7	9	12	13
W.M.	W.M.	W.M.	W.M.	W.M.	W.M.	S.M.	S.M.	S.M.	S.M.	S.M.	S.M.	S.M.

$n_1 = 6$, $n_2 = 7$, $U = 0$, $p = .001$

n_1 = the number of W.M. (the smaller of the two groups).

n_2 = the number of S.M. (the larger of the two groups).

U = the number of times that a score in the group with n_2 cases precedes a score in the group with n_1 cases in the ranking.

6. Effect of food deprivation on flight ability of summer morphs

Results of the number of stimulated flights to achieve 40 seconds of continuous flight by food supplied and food deprived females are shown in Table 76. The mean number of flights was compared by the t-test.

The mean number of flights were 3.82 and 2.00 for food supplied and food deprived insects respectively. The difference between the means was significant ($p < .02$). Thus, food deprivation enhanced the readiness of summer morphs to fly.

7. Behaviour of winter morphs in free flight

(a) Rate of climb

Fig. 43 illustrates a typical behaviour of the cabbage whitefly during flight. Results of the mean rates of climb in the 1st, 2nd, 3rd, 7th, 8th, 9th, 13th, 14th, and 15th minutes during flight are presented in Table 77 and illustrated in Fig. 44. A frequency distribution of the mean rates of climb is shown in Fig. 45.

Fig. 46 represents a frequency distribution of durations of first flights.

The mean duration of first flights and the mean rates of climb for winter and summer morphs are compared in Table 78.

The winter morphs took off spontaneously and flew in the central illuminated area of the chamber. The rates of climb fluctuated in the

Table 76: Comparison of flight ability of fed and starved female *A. brassicae* (summer morphs).

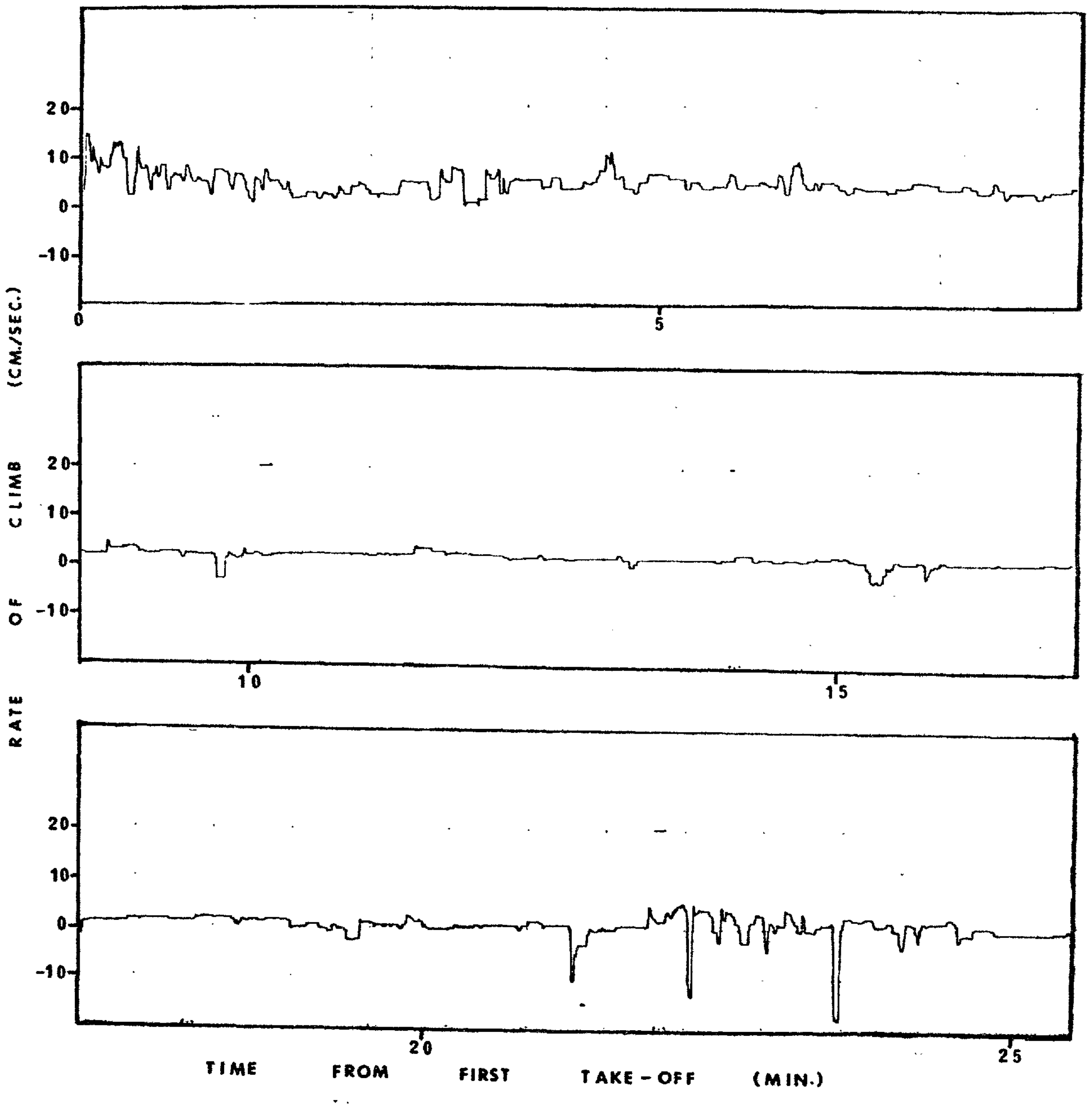
	No. stimulated flights to achieve 40 secs of continuous flight (Food supplied)	No. stimulated flights to achieve 40 secs of continuous flight (Food deprived)
1	4	1
2	4	1
3	6	1
4	5	1
5	7	1
6	1	2
7	1	7
8	4	1
9	1	1
10	5	3
11	4	3
	$\bar{x} = 3.82$	$\bar{x} = 2.00$
	$s^2 = 4.16$	$s^2 = 3.40$

Applying the formula $d = \dfrac{\bar{x}_1 - \bar{x}_2}{\sqrt{\dfrac{s_1^2}{n_1} + \dfrac{s_2^2}{n_2}}}$

$= 2.6491$

With 20 degrees of freedom, the difference between the number of flights to achieve 40 secs of continuous flight in fed and food deprived summer *A. brassicae* females is significant ($p < .02$).

Figure 43: Excerpts from the record of one uninterrupted first flight of 25 min. showing the three phases of behaviour of *A. brassicae* (winter morph) during flight.


20
10
0
-10
0
5
20
10
0
-10
10
15
20
10
0
-10
20
25
RATE OF CLIMB (CM./SEC.)
TIME FROM FIRST TAKE-OFF (MIN.)

first minute of flight. The fluctuation was profound in some insects. This first phase was followed by a second phase of steady flight. The duration of this second phase varied from one individual to another. In one individual that had the longest first flight, it lasted for over 60 mins. The third phase of behaviour showed fluctuating rates of climb similar to those recorded at the initial stages of flight but were lower in magnitude. The third phase was often followed by landing. The three phases are shown in Fig. 43.

The highest mean rate of climb occurred in the first minute of flight. The highest value recorded in the experiment was 20 cm/sec and the lowest was -4 cm/sec (Table 77). The rates of climb declined progressively with time (Table 77 and Fig. 44). From a typical flight record of one insect, a cumulative height of 42 m was reached in 15 minutes (Fig. 44).

(b) Duration and number of flights to drop-out

The mean number of flights of more than one minute per individual was 3.9 (range 1 to 10). The mean total duration of all flights more than 1 minute per individual was 29.5 min (range 2.5 to 133.67). The mean duration of first flights was 14.42 min (range 0.57 to 133.67). First flights accounted for an average of 55% (range 2-100).

In the frequency distribution of durations of first flights (Fig. 46), 67% of the insects had flight durations of between 1-9 minutes. The rest had durations of 10 minutes and above.

Insects that flew longer in first bouts showed shorter duration in subsequent bouts while those that flew for a very short time in the first bout flew longer in the second.

Table 77: Mean rates of climb of *A. brassicae* females (winter morphs).

	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)
	1st min.	2nd min.	3rd min.		7th min.	8th min.	9th min.		13th min.	14th min.	15th min.	
1	20	16	14	16.7	10	10	8	9.3	6	6	6	6.0
2	18	16	12	15.3	9	10	10	9.6	8	8	6	7.3
3	17	12	8	12.3	4	4	3	3.7	2	2	1	1.7
4	14	8	7	9.7	3	4	3	3.3	3	3	3	3.0
5	10	7	8	8.3	5	4	3	4.0	2	2	2	2.0
6	12	6	6	8.0	5	3	3	3.7	1.5	1	2	1.5
7	12	6	6	8.0	.5	- .5	- 2	- .7	0	0	0	0
8	10	6	6.5	7.5	4	4	4	4.0	3	3	3	3.0
9	10	5	5.5	6.8	7	7	7	7.0	5	5	4	4.7
10	9	4	4	5.7	6	7	4	5.7	3	4	2	4.3
11	12	2	3	5.7	4	4	4	4.0	3	3	3	3.0
12	9	4	4	5.7	3	3	3	3.0	2	2	2	2.0
13	8	5	4	5.7	3	3	2.5	2.8	1	1	1	1.0
14	6	6	5	5.7	3	3	3	3.0	2	2	2	2.0
15	6	4	4	4.7	4	6	4	4.7	5	4	3	4.0
16	6	4	3	4.3	3.8	3	3	3.3	2	1.5	1.5	1.7

Table 77: Continued

	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)	$\bar{x}$ rate of climb (cm/sec)			Total $\bar{x}$ rate of climb (cm/sec)
	1st min.	2nd min.	3rd min.		7th min.	8th min.	9th min.		13th min.	14th min.	15th min.	
17	5	3	4.5	4.2	5	4	5	4.7	3	3	3	3.0
18	8	2	1.5	3.8	2.5	2	2	2.2	1.5	1	1	1.2
19	6	3	2	3.7	4	3	4	3.7	3	3	3	3.0
20	5	3	3	3.7	2	2	2	2.0	1	1	0	0.7
21	5	2	2.5	3.2	1	.5	1	0.8	0	1.8	0	0.6
22	4	3	2	3.0	2	1	2	1.7	1	1	1	1.0
23	4	3	2	3.0	1.5	2	2	1.8	1	2	1	1.3
24	2	3	3	2.7	1	.5	0	0.5	0	0	0	0
25	3	1	1	1.7	3	3	4	3.3	2	1	.5	1.2
26	4	1	0	1.7	1	0	- 1	0	- 1	- 1	- 1	- 1
27	1	1	1	1.0	1	.5	.5	0.7	0	0	0	0
28	0	1	0	0.3	2	2	1.5	1.8	2	1	1	1.3
29	- 2	1	1	0	- 2	- 2	- 2	- 2	- 3	- 4	- 4	- 3.7
30	- 4	0	- 2	- 2.0	- 4	- 4	- 6	- 4.7	- 1	- 1	- 1	- 1.0
MEAN	7.33	4.6	4.05		3.14	2.97	2.58		1.93	1.88	1.53	
S.E.	± 1.03	± 0.73	± 0.63		± 0.51	± 0.55	± 0.55		0.40	± 0.41	± 0.37	

Figure 44: Relationship between rates of climb and time in flight of *A. brassicae* (winter morphs), and the cumulative height (meters) reached by one insect in 15 min. Standard errors are indicated by horizontal lines.

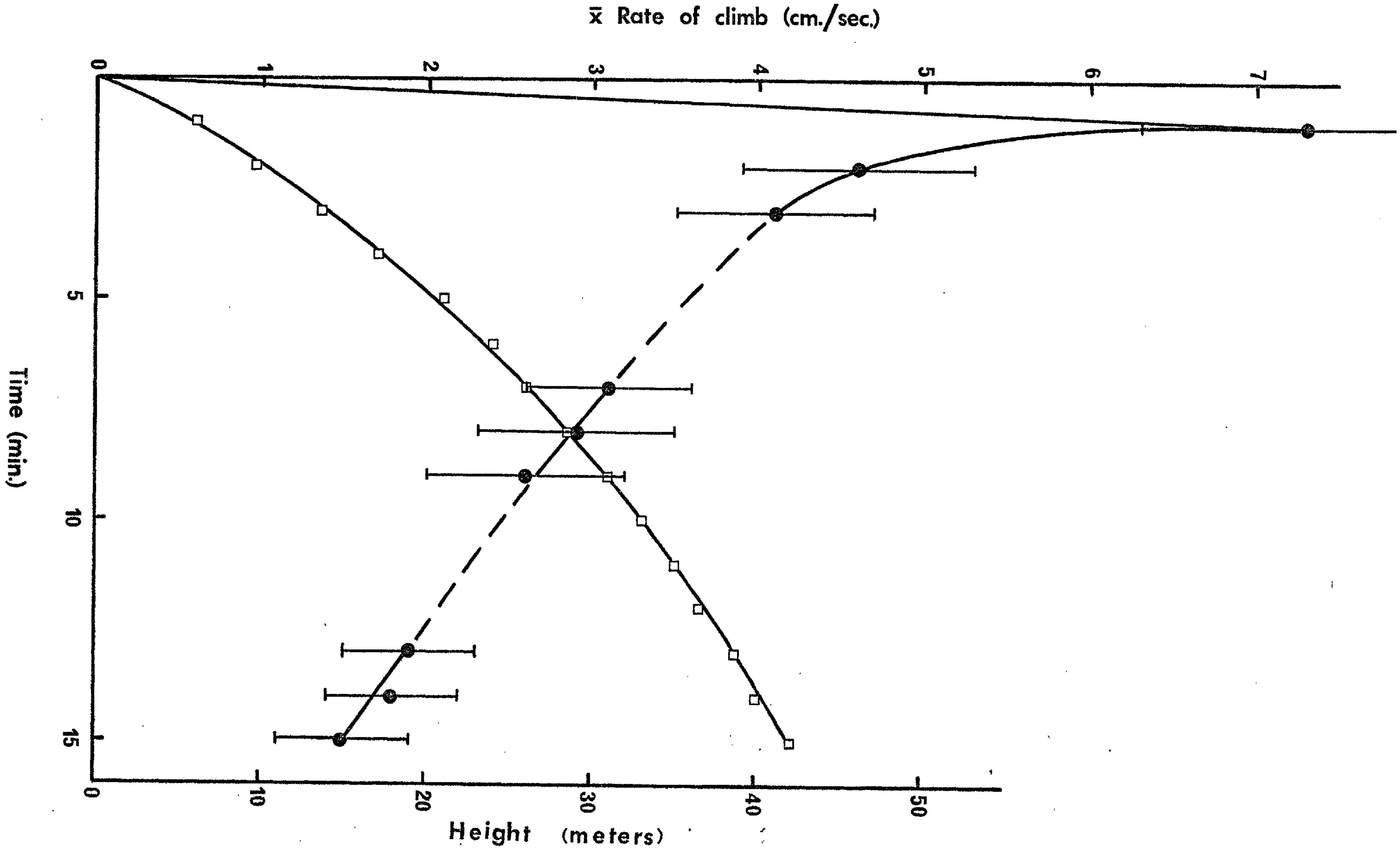

x̄ Rate of climb (cm./sec.)
0
1
2
3
4
5
6
7
Time (min.)
5
10
15
Height (meters)
0
10
20
30
40
50

Figure 45: Frequency distribution of mean rates of climb (cm/sec) over (a) 1st minute of continuous flight; (b) 1st to 3rd minute; (c) 7th to 9th minute; and (d) 13th to 15th minute for winter morphs.

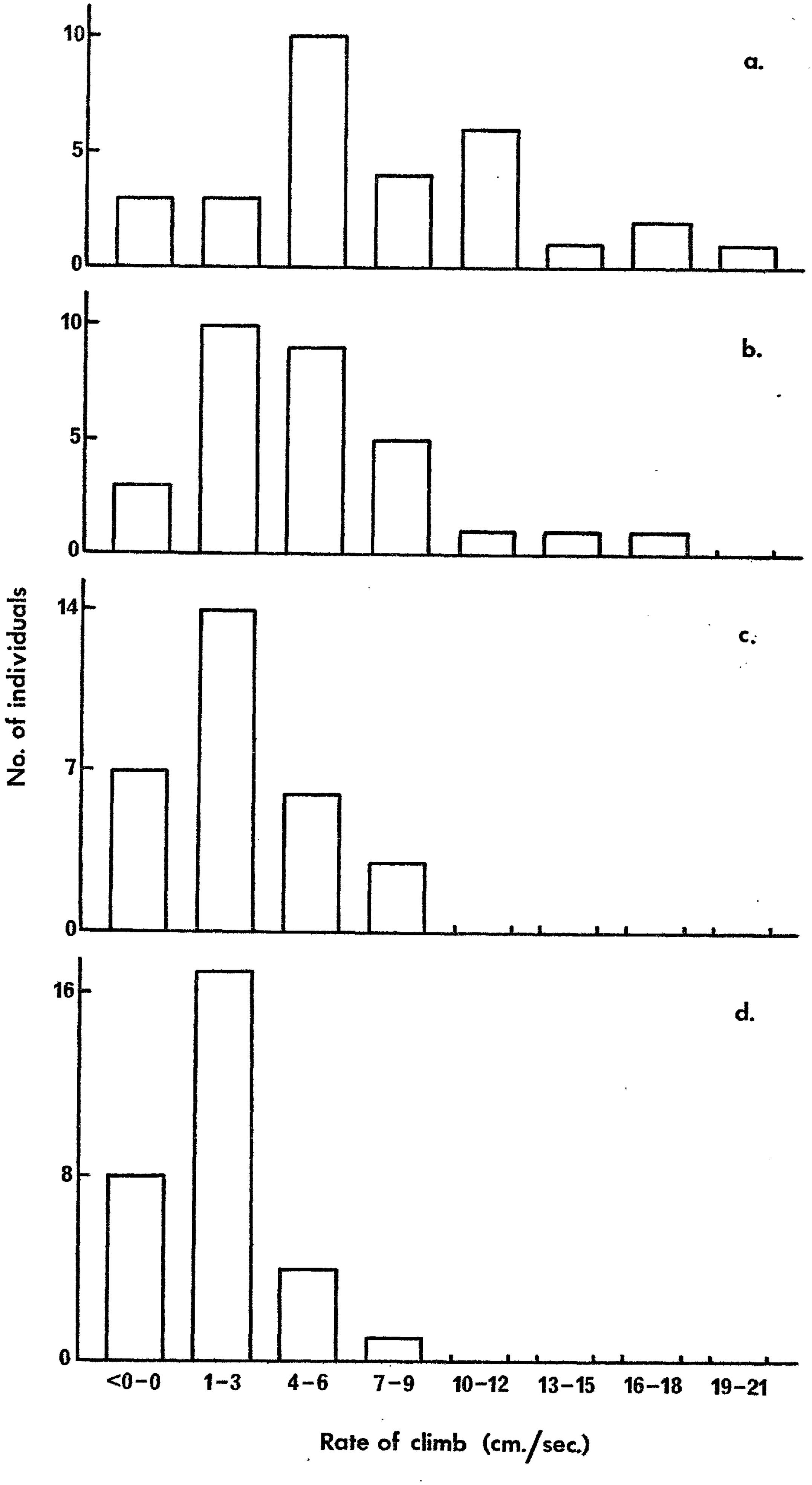

a.
b.
c.
d.
10
5
0
10
5
0
14
7
0
16
8
0
No. of individuals
<0–0
1–3
4–6
7–9
10–12
13–15
16–18
19–21
Rate of climb (cm./sec.)

Figure 46: Frequency distribution of durations of uninterrupted first flights.

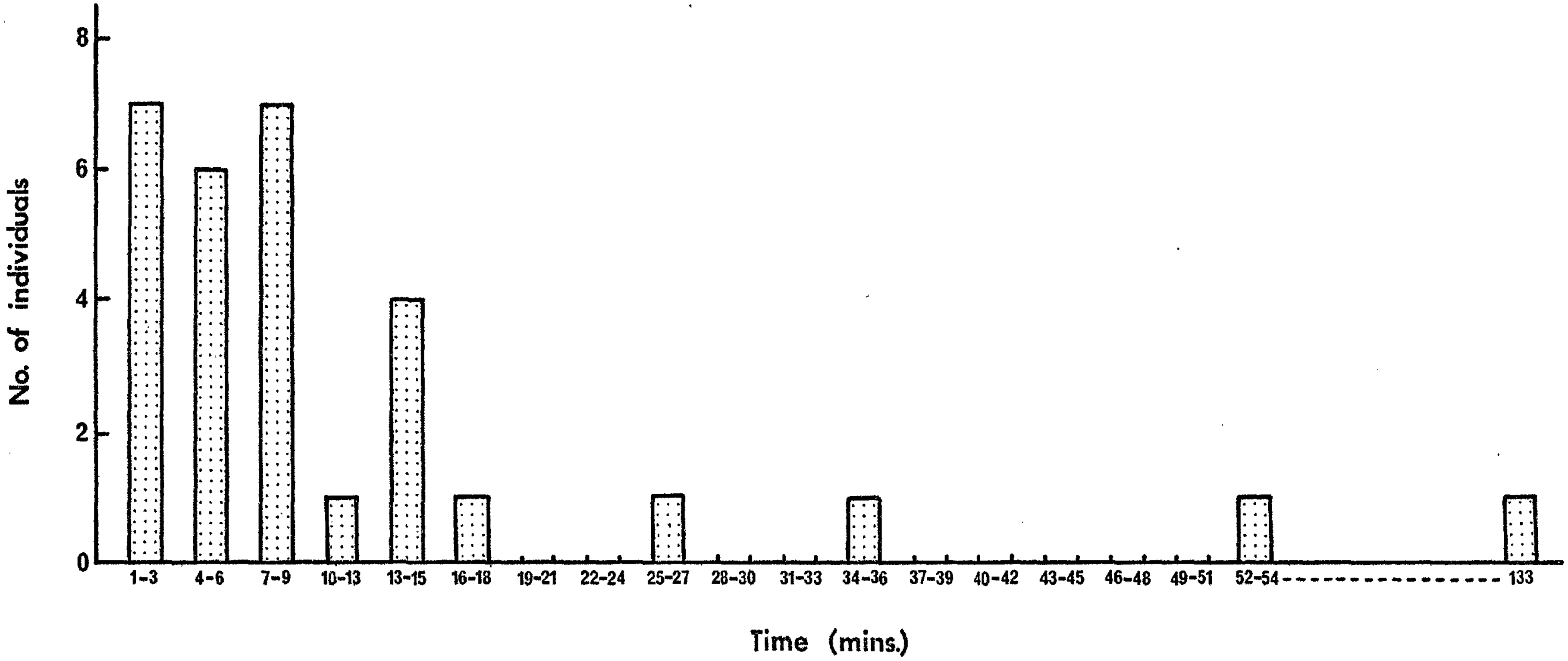

No. of individuals
0
2
4
6
8
1-3
4-6
7-9
10-13
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
37-39
40-42
43-45
46-48
49-51
52-54
133
Time (mins.)

Table 78: Comparison of the mean duration of first flights and mean rates of climb of winter and summer morphs of *A. brassicae*.

	Winter morph	Summer morph
$\bar{x}$ duration of first flights range	14.42 min. 0.57 to 133.67	0.31 min. 0.03 to 1.13
$\bar{x}$ rate of climb (cm/sec) in the first 5 secs of first flights range	12.57 5 to 21	- 8.92 - 20 to 7

Table 79: Comparison between mean rate of climb immediately before landing on wall and immediately after retake-off.

	$\bar{x}$ rate of climb (cm/sec) (1 min. before landing) (x)	$\bar{x}$ rate of climb (cm/sec) (1 min. after retake-off) (y)	Difference (y - x)	Rank of difference	Rank with less frequency
1	1	2	1	+ 3	
2	2	3	1	+ 3	
3	0	4	4	+ 11.5	
4	5	7	2	+ 6.5	
5	5	6	1	+ 3	
6	3	6	3	+ 9	
7	5	8	3	+ 9	
8	0	1	1	+ 3	
9	3	6	3	+ 9	
10	4	8	4	+ 11.5	
11	1	0	- 1	- 3	3
12	2	4	2	+ 6.5	
13	3	11	8	+ 13	
					$T = \bar{3}$

The mean rate of climb before landing was significantly lower than the mean rate of climb on retake-off ($p = .005$ for one-tailed test).

Unlike the winter morphs, the summer morphs did not take off spontaneously. Even when induced to take off, they consistently avoided the brightly illuminated centre of the chamber and flew either to the black wall of the chamber or out of the chamber. The mean duration of first flights was 0.31 min (range 0.03 to 1.13) (Table 78).

Instead of climbing, the insects began to sink from the time of take-off but were kept airborne. The mean rate of climb in the first 5 seconds of first flight was - 8.92 (range - 20 to 7) (Table 78).

(c) Rebound

Results of the mean rates of climb in the last 60 seconds before landing and the first 60 seconds of retake-off are shown in Table 79. The mean rate of climb after retake-off was significantly higher ($p = .005$) than that before landing by Wilcoxon matched-pairs signed- ranks test.

D. DISCUSSION

The interval between eclosion of the alate imago and flight when flight is not extrinsically activated or inhibited was termed the teneral period by Taylor (1957) with reference to *Aphis fabae*. El-Khidir (1963) applied the term 'teneral period' to the same stage in the cabbage whitefly, *A. brassicae*.

The mean teneral periods of the cabbage whitefly, *A. brassicae*, on senescent leaves of Brussels Sprout were found to be 5.7, 6.8, 7.7, and 28.3 hours at 25°, 20°, 15°, and 10°C respectively. El-Khidir (1963) obtained the following values under field conditions: 5.0, 6.7, 8.0, and 22.0 hours at 25.7°, 19.6°, 15.5°, and 11.5°C respectively. These two sets of results are closely comparable.

If teneral stage involves only developmental processes limited by temperature, then teneral development times should be fairly constant at a given constant temperature for a given species. However, this is not the case with *A. brassicae* since the difference between the teneral periods on senescent and young leaves under the same constant temperature, was very highly significant ($p < .001$), being shorter on the senescent leaf. Woodford (1969) obtained a significant difference between the teneral periods of *M. persicae* on bean leaves and paper leaves.

The fact that the teneral period was shorter on senescent leaves than on young leaves is very interesting because in nature, adult cabbage whitefly, *A. brassicae*, emerge on senescent or mature leaves. Thus the length of time spent on leaves before trivial flight (in summer morphs) and migratory flight (in winter morphs) will be short, other factors being favourable.

With the highly significant difference between the teneral periods on senescent and young leaves at each of the constant temperatures, the 'forced-dropping' method was used to ascertain the length of time it took newly emerged cabbage whiteflies to be capable of flying, in other words, the time required by the insects to reach 'flight-maturity'. The results of the experiment showed that the insects were flight-mature after about 2½ hours. If teneral period were defined as the time between adult emergence and flight-maturity (in the sense explained above), then the teneral period for the cabbage whitefly, A. brassicae, at 20°C would be 2½ hours - about 4 hours less than when the definition of teneral period refers to unforced take-off by the insect. The question, therefore, arises as to what factor or factors are responsible for the inhibition of flight after flight-maturity has been attained.

Taylor (1957) remarked that climatic factors such as wind speed or humidity may delay the departure of the flight-mature aphids, thereby increasing the teneral time. Kennedy (1958) reported that when A. fabae makes contact with some solid non-host surface, the host inhibits flight and excites the host response of probing the surface with the rostrum. A plausible explanation for the delayed take-off in A. brassicae after reaching flight-maturity is that the insect responds to the arresting sensory input from the surfaces.

Blest (1960b) is of the opinion that movements that end in take-off are held in abeyance until external stimuli are strong enough or a series of subliminal stimuli adds up to a strength needed to overcome the inhibitory influences in the central nervous system. The strengths of stimuli needed to induce take-off vary with the stage of balance between internal inhibition and excitations, and this varies with age, sexual state, and other internal factors (Johnson, 1969). Take-off by a flight-mature insect also depends on the temperature being suitable for efficient muscular activity.

The summer morphs of the cabbage whitefly, A. brassicae, showed an age-dependent capacity to take-off. A peak of 45% was reached on the second day after adult emergence. Since the mean pre-oviposition periods of the cabbage whitefly, A. brassicae, are 1.4 days at 20° and 3.2 days at 15°C, the maximum take-off occurred, therefore, during the pre-reproductive stage.

The effect of temperature (20° and 15°C) on take-off with age was not evident until peaks had been reached; thereafter take-off was consistently higher at 20° than at 15°C.

Leaf age had a remarkable effect on take-off. When senescent leaves on which immature stages developed to adults were used, a peak of 100% was reached on the second day of adult life (Fig. 42). The shape of the curve was similar to that obtained on young leaves. In nature therefore, emergence of adults on senescent leaves enables many of the insects to fly to young leaves of the same plant or of a neighbouring one.

The winter morphs showed a very high percentage take-off (above 75%) irrespective of age (Fig. 42). In other words, take-off was not age-dependent. This is obviously related to their reproductive immaturity.

There was no significant difference between the percentage take-offs with age at 20° and 15°C by the Sign Test. This result fits with what happens under natural conditions since the winter morphs emerge early in the autumn (mid September) when the temperature may be fluctuating between 20° and 15°C.

Take-off by the summer morphs was not spontaneous during the free flight experiment. They also showed a negative response to light, often fluttering away from the brightly illuminated centre of the flight chamber to the black walls, or to the floor, or even out of the chamber into the dark room. The winter morphs on the other hand took off voluntarily and flew toward the light source.

Kennedy (1961) pointed out that the bright predominantly short wavelength light from the sky induces a sharp rise in locomotor excitability resulting in flight. Insects responding positively to the light stimulus move out of the vegetal cover into the free-circulating air. From the light reactions of the summer and winter morphs of the cabbage whitefly, A. brassicae, the latter are more likely to fly out of the under-surfaces of leaves while the light avoidance reaction of the summer morphs will tend to confine them to the under-surfaces of leaves except, however, when they fly from the lower older leaves to the top younger ones. Pienkowski (1976) remarked that a negative phototaxis and positive thigmotaxis tend to direct an insect into hiding places.

The migratory flight of insects is measurable under laboratory conditions in terms of the climbing flight directed phototactically toward the source of light in a flight chamber (Kennedy and Ludlow, 1974). A comparison of the mean durations of flight and mean rates of climb in the summer and winter morphs will further reveal their migratory or non-migratory ability.

The mean durations of flight were 0.3 minute (range 0.03 to 1.13) for summer morphs and 14.4 minutes (range 0.5 to 133.6) for winter morphs. The mean rates of climb were - 8.92 cm/sec (range - 20 to 7) and 12.57 cm/sec (range 5 to 21) in the first 5 seconds of first flights of summer and winter morphs respectively. The highest rates of climb were reached in the first minute of first flights and ranged from - 4 to 20 cm/sec in the winter morphs.

Winter morphs which flew for long durations in the first flights flew for shorter times in the subsequent flight bouts whereas those that flew for a very short time in the first flight flew longer in the second bout.

Flying insects which landed either on the wall or floor of the flight chamber and took off again showed a higher rate of climb immediately on retake-off than just before landing. The landing on walls or floor of the cabinet could be regarded as landing on a non-host plant during flight in the field. The ecological significance of the higher rate of climb after retake-off - 'rebound' (Kennedy and Ludlow, 1974) is that it enhances the chances of the insect to reach a suitable host plant.

Williams (1958) defined migration as "a continued movement in a more or less definite direction in which both movement and direction are under the control of the animal concerned'. Kennedy (1961) considered a more complete characterization of a migratory behaviour to be "persistent, straightened-out movement that is accompanied by and dependent upon the maintenance of an internal inhibition of those 'vegetative' reflexes that will, eventually, arrest it". The straightened-out movement which may have no directionally adaptive significance is a result of sensorimotor function, and the 'vegetative' reflexes are those associated with growth e.g. feeding and reproduction.

With reference to Kennedy's definition of migratory behaviour, the summer morphs of the cabbage whitefly, A. brassicae, are obviously non-migratory because they are incapable of flying for a long time and also have a very low rate of climb. Furthermore, reproductive activity is not arrested.

The long flights of the winter morphs represent the persistent movement while the flight pattern in which the first phase consists of a widely fluctuating rate of climb and a second steadier phase - the 'cruising' phase (Kennedy and Booth, 1963a) will represent the straightened out aspect of the definition. Dingle (1964) remarked that the cruising phase in nature, would probably be straightened out. Gonadal development is also arrested. Thus the winter morphs qualify as migrants.

Taylor (1958, 1974) used the term 'boundary layer' to delimit the layer of air near the earth's surface 'in which air movement is less than flight speed or within which the insects' sensory mechanisms and behaviour permit active orientation to the ground'. Within the boundary layer, the insect may arrive at or attempt to reach a point towards which it heads. Since most of the summer morphs of the cabbage whitefly, A. brassicae, fly from the lower older leaves to the upper ones for the purpose of feeding and oviposition - 'trivial' or 'appetitive' flight (Southwood, 1962; Johnson, 1969; Dingle, 1972), they may possibly be operating within their boundary layer. El-Khidir (1963) remarked that his suction trap catches of the summer morphs did not reflect the total population on the crop. From the flight behaviour of the summer morphs, his catches could be as a result of 'vagrancy' (Southwood, 1962): an involuntary consequence of non-migratory behaviour - possibly flitting. My supposition is supported by the fact that some drift may occur within an insect's boundary layer (Johnson, 1969).

El-Khidir (1963) commented that his suction trap catches of summer morphs consisted, possibly, of individuals that had just completed their teneral development. From my laboratory results on take-off with age, his supposition was correct since maximum take-off was both age-dependent and pre-reproductive. However, occurrence of already ovipositing females in the catches cannot be completely ruled out.

Summer morphs deprived of food showed a higher flight ability than fed ones. However, food deprivation did not result in sustained flight. Hocking (1953) remarked that 'hungry' insects could not make sustained flights, and mere lack of food would not account for a prolonged flight of many migrants.

From the positive phototaxis and the high rate of climb shown by the winter morphs, they are presumably, capable of penetrating the boundary layer, as does A. fabae (Kennedy, 1961; Kennedy and Booth, 1963a, b), where migratory travelling occurs on the wind (Johnson, 1969; Kennedy and Fosbrooke, 1972).

The cumulative height reached by one winter morph under laboratory conditions was 42 meters in 15 minutes. Species of whitefly have been caught at various heights in the air. The cotton whitefly, B. gossypiperda, were caught at a height of about 12 m (Trehan, 1944). Glick (1939) trapped whiteflies at heights of about 61 m and 305 m; Glick and Noble (1961) captured whiteflies at about 61 m, 152 m, and 305 m by means of traps attached to aeroplanes. Those caught at 61 m and 152 m included Trialeurodes abutilonea.

Thus from the flight behaviour of the winter morphs of the cabbage whitefly, A. brassicae, widespread displacement on the wind is apparent.

Dingle (1974) commented that the most conspicuous alternation of migrant and non-migrant pathways occurs in those insects with alary polymorphism. He added that those environmental inputs which signal that conditions are favourable for reproduction often result in apterous or brachypterous morphs. Since summer conditions favour reproduction and winter induces its arrest in the cabbage whitely, A. brassicae, wing polymorphism should be expected. Indeed El-Khidir (1963) confirmed a significant difference in the lengths of forewings of summer and winter morphs of *A. brassicae*, those of the summer morphs being shorter.

Henson (1962) reported that in the scolytid beetle *Conophthorus coniperda*, degeneration of the flight muscles occurs at the time of gonadal activity making it impossible for the reproductive females to fly. Edwards (1969a, b) found that in some species of *Dysdercus* e.g. *D. fasciatus*, the flight muscles of the females histolyse shortly after adult emergence thus rendering them flightless. Dingle and Arora (1973) reported flight muscle histolysis in *D. fasciatus* induced by feeding. It is possible that the inability of the summer morphs to fly persistently is as a result of weak flight apparatus. Another possible explanation is that the summer morphs could be individuals with heritable non-migratory characteristics. These speculations need experimental confirmation.

The fact that egg development begins after migration in many female insects led Johnson (1969) to describe the relationship between the two biological processes as 'oogenesis-flight syndrome'. If the flight apparatus becomes fully mature while the ovaries remain immature, the insect may become a migrant. The phenomenon of oogenesis-flight syndrome is applicable to the winter morphs of the cabbage whitefly, *A. brassicae*.

The cabbage whitefly, *A. brassicae*, undertakes a 'return' migratory flight. From field records this occurs in April and May (El-Khidir, 1963) when the ambient temperature is sufficiently high to warm the flight muscles. I, however, hesitate to describe the flight as post-diapause migration until the state of the ovary of the females has been ascertained. But from the results of diapause induction and termination discussed in Section III of this thesis, the reproductive development of the females should have reached an advanced stage by April and May. Thus the flight could be described as post-diapause, but with some reservation. It would be interesting to compare the flight behaviour of these females with those of the autumn migrants and summer non-migrants.

GENERAL DISCUSSION

The cabbage whitefly feeds and breeds on crucifers. Most cultivated cruciferous vegetables are short lived because they are harvested not long after planting. Most of these plants had this type of habitat in the wild. The habitat of the whitefly is, therefore, unstable.

For the cabbage whitefly, A. brassicae, to survive under such unpredictable conditions, certain conditions have to be fulfilled. These include:

1. short pre-oviposition period,
2. short development time,
3. maximum fecundity rate to be reached early in adult life, and
4. high intrinsic rate of natural increase.

The pre-oviposition period of the cabbage whitefly is short (3.2 days at 15° and 0.8 day at 25°C). Since development is usually faster under fluctuating temperature conditions, the pre-oviposition periods may be shorter in nature.

The development time which lengthens with low temperature and shortens with high is approximately 19 days at 25°, 25 days at 20°, and 52 days at 15°C. Under field conditions the speed of development will also be expected to be faster.

The maximum fecundity rate (m_x) is usually reached in the first two weeks of adult life. The highest recorded value was 37 when the insects were reared on young leaves of Mustard at 25°C.

As a consequence of the short pre-oviposition period, short development time, and early attainment of maximum fecundity rate, the intrinsic rate of increase is high. The highest value obtained under laboratory conditions was 1.445. Thus the cabbage whitefly, *A. brassicae*, is fully adapted for maximum exploitation of its ephemeral habitat.

Environmental factors such as food and long photoperiod which stimulate and sustain breeding activity reduce the flight ability of the summer generations. In summer, therefore, when breeding activity is at its height, females of the cabbage whitefly, *A. brassicae*, do not show any appreciable readiness to take-off spontaneously except, however, in the first two days of emergence during which they fly from lower older leaves on which they emerged to top younger ones. Thus flights are restricted to short bouts - trivial - for the purposes of feeding and breeding.

The number of generations produced each year depends largely on the sum of effective temperatures. A year of very warm spring and hot summer is more likely to favour the production of many generations than one of cold spring and cool summer. This is most likely to be the cause of the difference in the number of generations of the cabbage whitefly reported by some authors. The conflicting reports could be reconciled if the temperatures of the seasons when the observations were made are given. Whatever the number of generations may be, it has to be completed between May/June and August/September. This point will be explained later.

Temperature has often been quoted as being the environmental factor responsible for cessation of breeding activity of the cabbage whitefly, *A. brassicae*, in winter. On the contrary, photoperiod is the main factor that triggers a physiological response of reproductive arrest - diapause.

The cabbage whitefly, *A. brassicae*, has a narrow critical photoperiod (LD $15\frac{3}{4} : 8\frac{1}{4}$ at 15°C). The mean temperature in July/August is generally in the neighbourhood of 15°C and the photoperiod at this time of year is about the critical stated above. July/August therefore, seems to be the time of year beyond which no further generations of non-diapausing females can be produced. Thus the number of non-diapausing generations is produced between May/June and August/September.

When a second or third generation of the summer morphs emerges in July/August, adults who in their early immature stages experienced photoperiods longer than the critical, will be non-diapausing. Those whose early instars experienced the critical photoperiod will consist of both non-diapausing and diapausing individuals. On the other hand, females that developed from immature stages that experienced photoperiods significantly shorter than the critical will be mostly diapausing. At this time of year therefore, field populations of the cabbage whitefly, A. brassicae, will consist of both non-diapusing, weakly diapausing and strongly diapausing females.

Eggs laid by the last generation of the non-diapausing females will encounter low autumn/winter temperatures. This does not automatically imply that development will be arrested. The temperature thresholds of development is highest in the embryonic stage and declines with age, reaching its lowest value in the second instar but rises abruptly in the fourth instar. Development, therefore, continues in all stages in autumn/winter but becomes temporarily arrested only when the temperature falls below their respective thresholds. All adults resulting from these eggs constitute the last generation in a given year and are the diapausing winter morphs.

The photoperiodic cue which is monitored by the early immature stages is manifested in the adult as gonotropic dissociation. With breeding activity suppressed, flight ability is enhanced. Thus the cabbage whitefly, A. brassicae, illustrates the phenomenon analagous to "alternation of generations": a breeding, non-migrating generation alternates with non-breeding, migrating generation.

Deteriorating habitat has often been quoted as the stimulus that initiates migratory flights in some insects. This does not, however, seem to be the case in the cabbage whitefly, A. brassicae, which begins flying even when the habitat is reasonably suitable. It is, perhaps, more appropriate to regard the migratory flight as an integral part of the biology of the insect.

Diapausing females field collected in September and reared under laboratory conditions of high (20°) and intermediate (15°) temperatures, long photoperiod (LD 16:8), and young plants raised in the laboratory under summer conditions, spent longer time before diapause was broken than those females field collected in February. Thus neither high temperature nor long photoperiod nor high food quality was strong enough to effect an immediate termination of diapause. Since chilling facilitated diapause termination under laboratory conditions, it is reasonable to conclude that the low winter temperatures facilitate diapause development (physiogenesis) which accounts for an earlier termination of diapause among females field collected in February.

As the temperature rises in spring above the threshold for development, morphogenesis begins. However, the effect of the gradually increasing photoperiod cannot be completely ignored. It is, perhaps, better to consider the resumption of morphogenesis as a result of cumulative effects of both temperature and photoperiod.

Diapause termination is easily monitored if egg laying is taken as the criterion. Though diapause termination early in the spring may fall short of the actual oviposition, the fact that the ovaries have resumed development could be taken as indicating that diapause has been terminated. If this assumption is accepted, then flight of the cabbage whitefly females from their overwintering quarters to colonize the new plants in spring could be termed post-diapause migration.

The oviposition rate of the post diapause winter morphs is quite high. The total fecundity is also high though this does not contribute effectively to the value of the intrinsic rate of increase (r_m). From the high oviposition rate, it is tempting to assume that the intrinsic rate of increase will be high. This is, however, not the case because of the extraordinarily prolonged pre-oviposition period due to the intervention of reproductive diapause. While the diapause lowers the expected value of the intrinsic rate of increase, it on the other hand ensures the survival of the insect through winter and synchronizes its life cycle with the weather and the life cycle of the host plants.

Because of mortality in winter due to cold and possibly predation, the population density of the colonizers is quite low. With the spring flush, cool temperature, and the absence of population pressure, females of the first generation will be large in size. Since fecundity of the cabbage whitefly, _A. brassicae_, is proportional to her weight on emergence, many eggs will be laid. With a short pre-oviposition period and a maximum fecundity rate attained early in the reproductive life, the intrinsic rate of increase is high. Consequently, the finite rate of increase is also high. Thus the rate of population growth is fast in summer and a number of generations is produced until further increase is halted when the critical photoperiod is passed. Then the whole cycle is repeated.

SUMMARY

The effects of leaf age, variety, and species of Cruciferae on population parameters of the cabbage whitefly, A. brassicae, were assessed under laboratory conditions. The photoperiodic response of the insect as well as the flight behaviour of the two seasonal morphs were determined.

Whilst leaf age had no effect upon adult survival, it influenced fecundity which was higher on young leaves than on mature leaves.

The varieties of cabbage did not differ significantly in their effects on both longevity and fecundity, but the different species did have distinct effects.

Life-tables were constructed based on weekly fecundity and survival rates.

The insects lived longer at 15° than at 20° or 25°C.

In general, more eggs were laid at 15° than at 20° or 25°C.

Maximum fecundity rate occurred early in the reproductive life at 20° and 25°C respectively. At 15°C its occurrence was erratic.

The speed of development of the immature stages was highest in the second instar, followed by the third instar, the first instar, and the fourth instar. It was lowest in the embryonic stage.

The threshold of development of the immature stages decreased with age, being highest in the embryonic stage and lowest in the second instar but rose abruptly in the fourth instar to a level approximately equal to that of the embryonic stage.

High larval density prolonged the mean duration of development to

adult stage.

Both longevity and fecundity decreased with increased number of virgin females.

Virgin females caged singly laid more eggs than mated females caged as bisexual pairs. When the fecundity of virgin females caged in unisexual pairs was compared with that of mated females, there was no significant difference.

Photoperiod rather than temperature initiated reproductive diapause in the cabbage whitefly.

The critical photoperiod was ~~Length~~ Light:Dark (LD) $15\frac{3}{4}:8\frac{1}{4}$ at 15°C.

The sensitive stages of development to photoperiod were the embryonic stage and the first, second, and early third instars.

Continuous light (LD 24:0) and a temperature of 25°C respectively averted diapause.

Chilling under laboratory conditions facilitated diapause termination.

'Winter' leaves did not induce diapause in females reared under diapause preventing conditions nor did 'Summer' leaves prevent diapause in females reared under diapause inducing conditions.

Overwintering females field collected in September 1975 and kept under laboratory conditions of high (20°) and medium (15°) temperatures, long photoperiod (LD 16:8) and high food quality ('Summer' plants) spent longer time before first eggs were laid than females field collected in January/ February 1976.

The time between adult emergence and flight differed significantly on different surfaces kept at the same temperature (20°). It was shorter on senescent leaves than on young leaves.

Among the non-diapausing summer morphs, the capacity to take off was both age-dependent and pre-reproductive. It was enhanced by senescent leaves.

For the diapausing winter morphs, take-off was independent of age. The percentage take-off with age was consistently higher in the winter morphs than in the summer morphs.

Summer morphs, in general, did not take off spontaneously. They were negatively phototactic and consequently had very low rates of climb. Food deprivation improved their flight ability but did not induce sustained flight.

Winter morphs on the other hand took off voluntarily and were positively phototactic. As a consequence of their positive response to light, they had higher rates of climb than the summer morphs.

The summer morphs represent the actively breeding, non-migrating generation that alternates with the winter morphs which are the reproductively diapausing, migrating generation.

ACKNOWLEDGEMENTS

It is my great pleasure to thank Professor T. R. E. Southwood, my supervisor, for his encouragement and constructive criticism of the manuscript and also for granting facilities for this work.

I would especially like to thank Mrs. P. M. Reader, my adviser, for her stentorious encouragement and useful discussions in the course of this work.

My thanks are also due to Professor A. D. Lees F.R.S., for his critical comments on the photoperiodic aspect of this work and to Professor J. S. Kennedy F.R.S., for the use of his flight chamber and for very helpful suggestions and discussions on the flight behaviour of my experimental insect.

I am grateful to Mr. A. R. Ludlow for technical assistance, Mrs. E. A. Barnard for drawing the graphs, and Miss C. Collins for typing the manuscript.

I am indepted to my mum and all my brothers, sisters, and friends whose fervent prayers strengthened me.

To my niece, Mary Nwankiti, sister in-law, Cela Iheagwam, and brother, Jerry Iheagwam I owe much gratitude for their help in constructing some of the leaf cages.

Finally, I gratefully acknowledge the 2-year financial support from the University of Nigeria, Nsukka, which enabled me to undertake this work.

REFERENCES

ADKISSON, P. L. (1964). Action of photoperiod in controlling insect diapause. Amer. Natur. 98: 357-374.

ALLEE, W. C. (1931). Animal aggregations. The University of Chicago Press, Chicago.

ANDERSON, N. H. (1962). Bionomics of six species of *Anthocoris* (Heteroptera: Anthocoridae) in England. Trans. R. ent. Soc. Lond. 114: 67-95.

ANDREWARTHA, H. G. (1952). Diapause in relation to the ecology of insects. Biol. Rev. Cambridge Phil. Soc. 27: 50-107.

ANDREWARTHA, H. G. and BIRCH, L. C. (1954). The Distribution and Abundance of Animals. The University of Chicago Press, Chicago, Illinois.

ARNAUD, G. (1918). Les Asterinees. Ann. Ec. Agric. Montpellier. 52-66.

AVIDOV, Z. (1956). Bionomics of the tobacco whitefly (*Bemisia tabaci* Gennad.) in Israel. Ktavim (Eng. edn.) 7: 25-41.

BAKER, R. R. (1968). A possible method of evolution of the migratory habit in butterflies. Phil. Trans. R. Soc. B, 253: 309-341.

BARLOW, C. A. (1962). The influence of temperature on the growth of experimental populations of *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) (Aphididae). Can. J. Zool. 40: 145-156.

BARNES, H. F. (1952). Studies of fluctuations of insect populations. xii: Further evidence of prolonged larval life in the wheat blossom midges. Ann. appl. Biol. 39: 370-374.

BECK, B. D. A. and CHANT, S. R. (1958). A preliminary investigation on the effect of mosaic virus on Manihot utilissima Pohl. in Nigeria. Trop. Agric. Trin. 35: 59-64.

BECK, S. D. (1962a). Photoperiodic induction of diapause in an insect. Biol. Bull. 122: 1-12.

BECK, S. D. (1962b). Temperature effects on insects: Relation to periodism. Proc. N. Central Branch, Entomol. Soc. Am. 17: 18-19.

BECK, S. D. (1968). Insect photoperiodism. New York: Academic Press.

BECK, S. D.; CLOUTIER, E. J., and McLEOD, D. G. R. (1963). Photoperiod and insect development. Proc. 23rd Biol. Colloq. Oregon State Univ. pp. 43-64.

BENTLEY, C. A. (1914). Notes on experiments to determine the reactions of mosquitoes to artificial light. Indian J. med. Res. Suppl. 5: 9-11.

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). Bull. ent. Res. 64: 413-420.

BIRCH, L. C. (1948). The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15-26.

BLANTON, F. S., TRAVIS, B. V., SMITH, N. and HUSMAN, C. N. (1950). Control of adult mosquitoes in Alaska with aerial sprays. J. econ. Ent. 43: 347-350.

BLEST, A. D. (1960b). The resting position of Cerodirphia speciosa (Cramer) (Lepidoptera: Saturniidae): the ritualization of a conflict posture. Zoologica, N.Y. 45: 81-90.

BODENHEIMER, F. S. (1951). Arrested development and arrested activity in insect life. Trans. IXth Int. Congr. Ent. 1: 22-40.

BOHM, H. (1960). Der Ein fluss der Wirtsptlanze auf das Vermehrungs potential des weissem Barenspinners (Hyphantria cunea D.). Int. Congr. Ent. XI (Wien.) 2: 6-10.

BONNER, J. T. (1965). Size and cycle: an essay on the structure of biology. Princeton University Press, Princeton, N.J.

BOYD, C. E. (1968). Fresh-water plants: A potential source of protein. Econ. Bot. 22: 359-368.

BOYD, C. E. (1970a). Amino acid, protein and caloric content of vascular aquatic macrophytes. Ecology 51: 902-906.

BROWN, H. D. (1972). The suitability of some crops to infestation by the wheat aphid Schizaphis graminum (Homoptera: Aphididae). Ent. exp. & appl. 15: 128-138.

BUTLER, C. G. (1938). On the ecology of Aleurodes brassicae Walk. (Hemiptera). Trans. R. ent. Soc. Lond. 87: 291-311.

CALDWELL, J. and PRENTICE, I. W. (1942). A mosaic disease of Broccoli. Ann. appl. Biol. 29: 366-373.

CALDWELL, R. L. and HEGMANN, J. P. (1969). Heritability of flight duration in the milkweed bug Lygaeus kalmii. Nature, Lond. 223: 91-92.

CAMPBELL, A., FRAZER, B. D., GILBERT, N., GUTIERREZ, A. P. and MACKAUER, M. (1974). Temperature requirements of some aphids and their parasites. J. appl. Ecol. 11: 431-438.

CAMPBELL, A. and MACKAUER, M. (1975). Thermal constants for development of the Pea Aphid (Homoptera: Aphididae) and some of its parasites. Can. Ent. 107: 419-423.

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

CLEMENTS, A. N. (1963). The physiology of mosquito. Pergamon Press, London and New York.

CLOUDSLEY-THOMPSON, J. L. (1953). The significance of fluctuating temperatures on the physiology and ecology of insects. The Entomologist 86: 183-189.

COCHRAN, W. G. and COX, M. X. (1957). Experimental Designs. John Wiley & Sons, Inc. New York, London, Sydney.

COCKBAIN, A. J. (1961a). Fuel utilization and duration of tethered flight in *Aphis fabae* Scop. J. exp. Biol. 38: 163-174.

COCKBAIN, A. J. (1961b). Viability and fecundity of alate alienicolae of *Aphis fabae* Scop. after flights to exhaustion. J. exp. Biol. 38: 181-187.

COLE, L. C. (1954). The population consequences of life history phernomena. Q. Rev. Biol. 29: 103-137.

COLLYER, E. (1967). On the ecology of *Anthocoris nemorum* (L.) (Hemiptera: Heteroptera). *Proc. R. ent. Soc. Lond* (A) *42*: 107-118.

CROMBIE, A. C. (1942). The effect of crowding upon the oviposition of grain-infesting insects. *J. exp. Biol*. *19*: 311-340.

DAHMS, R. G., SNELLING, R. O. and FENTON, F. A. (1936). Effect of several varieties of sorghum and other host plants on biology of the chinch bug. *J. econ. Ent*. *29*: 1147-1153.

DANILEVSKY, A. S. (1948). Photoperiodic reactions of insects in conditions of artificial illumination (in Russian). *Dokl. Akad. Nauk. S.S.S.R*. (N.S), *60*: 481-484.

DANILEVSKY, A. S. (1949). The dependence of geographical distribution of insects on the ecological peculiarities of their life cycles. *Ent. Obozr*. *30*: 194-201.

DANILEVSKY, A. S. (1951). On the conditions favouring a several year diapause in Lepidoptera. *Ent. Obozr*. *31*: 386-392.

DANILEVSKY, A. S. (1956). Photoperiodicity as a regulator of the seasonal cycles of insects. *Acad. Sci. U.R.S.S., Vol. Mem., H. A. Cholodkovsky*, 32-55.

DANILEVSKY, A. S. (1965). Photoperiodism and seasonal development of insects. Oliver and Boyd, London.

DANILEVSKY, A. S., GORYSHIN, N. I. and TYSCCHENKO, V. P. (1970). Biological rhythms in terrestrial arthropods. *A. Rev. Ent*. *15*: 201-244.

DAVEY, K. G. (1965). Copulation and egg-production in *Rhodnius prolixus*: The role of the spermathecae. *J. exp. Biol*. *42*: 373-378.

DAVIDSON, J. (1925). Factors affecting the infestation of Vicia faba with Aphis rumicis. Ann. appl. Biol. 12: 472-507.

DAVIDSON, J. (1944). On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13: 26-38.

DEAN, G. J. (1974). Effects of temperature on the cereal aphids Metopolophium dirhodum (Wlk.), Rhopalosiphum padi (L.) and Macrosiphum avenue (F.) Hemiptera: Aphididae. Bull. ent. Res. 63: 401-409.

DeLOACH, C. J. (1974). Rate of increase of populations of Cabbage, Green Peach, and Turnip Aphids at constant temperatures. Ann. Entomol. Soc. Am. 67: 332-340.

DESPHANDE, V. G. (1933). On the anatomy of some British Aleurodidae. Trans. R. ent. Soc. Lond. 81: 117-132.

DETHIER, V. G. (1947). Chemical insect attractants and repellents. Blakiston Co., Philadelphia.

DICKSON, R. C. (1949). Factors governing the induction of diapause in the oriental fruit moth. Ann. Entomol. Soc. Am. 42: 511-537.

DINGLE, H. (1965). The relation between age and flight activity in the milkweed bug, Oncopeltus. J. exp. Biol. 42: 269-283.

DINGLE, H. (1966). Some factors affecting flight activity in individual milkweed bugs (Oncopeltus). J. exp. Biol. 44: 335-345.

DINGLE, H. (1968a). Life history and population consequences of density, photoperiod, and temperature in a migrant insect, the milkweed bug Oncopeltus. Amer. Natur. 102: 149-163.

DINGLE, H. (1968b). The influence of environment and heredity on flight activity in the milkweed bug Oncopeltus. J. exp. Biol. 48: 175-184.

DINGLE, H. (1972). Migration strategies of insects. Science (N.Y.) 175: 1327-1335.

DINGLE, H. (1974). Diapause in a migrant insect, the milkweed bug Oncopeltus fasciatus (Dallas) (Hemiptera: Lygaeidae). Oecologia (Berl.) 17: 1-10.

DINGLE, H. (1974). The experimental analysis of migration and life-history strategies in insects. Experimental Analysis of Insect Behaviour (ed. L. B. Brown). Springer-Verlag Berlin, Heidelberg, New York.

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

DUCLAUX, M. E. (1869). De l'influence de froid de l'hiver sur le développement de l'embryon du ver à soie, et sur l'éclosion de la graine. C. R. Acad. Sci., Paris 69: 1021.

EDWARDS, F. J. (1969a). Development and histolysis of the indirect flight muscles in Dysdercus intermedicus. J. Insect Physiol. 15: 1591-1599.

EDWARDS, F. J. (1969b). Environmental control of flight muscle histolysis in the bug Dysdercus intermedicus. J. Insect Physiol. 15: 2013-2020.

EL-KHIDIR, E. (1963). Ecological studies on Aleyrodes brassicae with special reference to dispersal. Ph.D. Thesis, London University.

VAN EMDEN, H. F. (1969b). The differing reactions of Brevicoryne and Myzus to leaf age, turgidity and soluble nitrogen in brassicas. Ann. appl. Biol. 63: 324-326.

VAN EMDEN, H. F. and BASHFORD, M. A. (1969). A comparison of the reproduction of Brevicoryne brassicae and Myzus persicae in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. Ent. exp. appl. 12: 351-364.

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. Ent. exp. & appl. 14: 349-360.

ENTWISTLE, P. F. and LONGWORTH, J. F. (1963). The relationship between cacao viruses and their feeding vectors: the feeding behaviour of three mealybug (Homoptera: Pseudococcidae) species. Ann. appl. Biol. 52: 387-391.

EVANS, A. C. (1938). Physiological relationship between insects and their host plants. 1. The effect of the chemical composition of the plant on reproduction and production of winged forms in Brevicoryne brassicae (Aphididae). Ann. appl. Biol. 25: 558-572.

EVANS, K. W. and BRUST, R. A. (1972). Induction and termination of diapause in Wyeomyia smithii (Diptera: Culicidae) and larval survival studies at low and subzero temperatures. Can. Ent. 104: 1937-1950.

FEENY, P. P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565-581.

FERGUSON, J. H. A. (1957). Photothermographs a tool for climate studies in relation to the ecology of vegetable varieties. *Euphytica* *6*: 97-105.

FERNALD, H. T. (1925). Rapidity of flight of a dragonfly. *J. econ. Ent.* *18*: 638.

FRAENKEL, G. (1953). The nutritional value of green plants for insects. *Trans. IXth Intern. Congr. Entom. Amsterdam* *2*: 90-100.

FRAZER, B. D. (1972). Life tables and intrinsic rates of increase of apterous black bean aphids and pea aphids, on broad bean. Homoptera: Aphididae. *Can. Ent.* *104*: 1717-1722.

FUJITA, H. (1954). An interpretation of the changes in type of the population density effect upon the oviposition rate. *Ecology* *35*: 253-257.

GLICK, P. A. (1939). The distribution of insects, spiders and mites in the air. *Tech. Bull. U.S. Dept. Agric.* *673*: 150 pp.

GLICK, P. A. and NOBLE, L. W. (1961). Airborne movement of the Pink Bollworm and other arthropods. *Tech. Bull. U.S. Dept. Agric.* *1255*: 20 pp.

GORYSHIN, N. I. (1958). An ecological analysis of the seasonal cycle of the cotton bollworm (*Chloridea obsoleta* F.) in the northern areas of its range. *Sci. Mem. Lenin. State Univ.*, *240*: 3-20.

GORYSHIN, N. I. (1964). The influence of diurnal light and temperature rhythms on diapause in Lepidoptera. *Entomol. Rev.* *43*: 43-46.

GRISON, P. (1947). Développement sans diapause des chenilles de Euproctis phaeorrhaea L. (Lep. Liparides). C. R. Acad. Sci. Paris 225: 1089-1090.

GRISON, P. (1956). Effects de la qualite de l'alimentation sur divers caracteres physiologiques de deux lepidopteres. C. R. Acad. Sci. Paris. 242: 414-416.

GUPPY, J. C. and MUKERJI, M. K. (1974). Effects of temperature on developmental rate of the immature stages of the alfalfa weevil Hypera postica (Coleoptera: Curculionidae). Can. Ent. 106: 93-100

GUPTA, P. D. and THORSTEINSON, A. J. (1960). Food plant relations of the diamond-black moth, Plutella maculipennis Curt. 11. Sensory regulation of oviposition of the adult female. Ent. exp. & appl. 3: 305-314.

HARGREAVES, E. (1914). The life history and habits of the greenhouse whitefly (Aleurodes vaporariorum Westd.). Ann. appl. Biol. 1: 303-334.

HARWARD, R. F. and TAKATA, N. (1965). Effect of photoperiod and temperature on fatty acid composition of the mosquito Culex tarsalis. J. Insect Physiol. 11: 711-716.

HAUPT, H. (1935). Aleurodina, in Die Tierwelt Mitteleuropas. Hemiptera 4: 253-260 Leipzig.

HENDERSON, C. F. and HOLLOWAY, J. K. (1942). Influence of leaf age and feeding injury on the citrus red mite. J. econ. Ent. 35: 683-686.

HENNEBERRY, T. J. (1962). The effect of host plant nitrogen supply and age of leaf tissue on the fecundity of the two-spotted mite. J. econ. Ent. 55: 799-800.

HENNEGUY, L. F. (1904). Les insects: morphologie, reproduction, embryogénie. Paris: Masson et Cie p. 56.

HENSON, W. R. (1962). Laboratory studies on the adult behaviour of Conophthorus coniperda Coleoptera: Scolytidae). III. Flight. Ann. Entomol. Soc. Am. 55: 524-530.

HILL, A. R. (1957). The biology of Anthocoris nemorum (L.) in Scotland (Hemiptera: Anthocoridae). Trans. R. ent. Soc. Lond. 109: 379-394.

HOCKING, B. (1948). Some aspects of the biting fly problem in Canadian Sub-Arctic Regions. M.Sc. Thesis, Univ. Alberta.

HOCKING, B. (1953). The intrinsic range and speed of flight of insects. Trans. R. ent. Soc. Lond. 104: 223-345.

HOCKING, B. and RICHARDS, W. R. (1952). Biology and control of Labrador black flies. Bull. ent. Res. 43: 237-257.

HODEK, I. (1971). Induction of adult diapause in Pyrrhocoris apterus L. by short cold exposure. Oecologia (Berl.) 6: 109-117.

HODJAT, S. H. (1968). The effects of crowding on the survival, rate of development, size, colour and fecundity of Dysdercus fasciatus Sign. (Hem., Pyrrhocoridae) in the laboratory. Bull. ent. Res. 58: 487-504.

HODSON, A. C. and AL RAWY, M. A. (1956). Temperature in relation to developmental thresholds of insects. Proc. 10th int. Congr. Ent. Montreal 2: 61-65.

HOWE, R. W. (1953a). Studies on beetles of the family Ptinidae. VIII. The intrinsic rate of increase of some ptinid beetles. Ann. appl. Biol. 40: 121-133.

HOWE, R. W. (1953b). The rapid determination of the intrinsic rate of increase of an insect population. Ann. appl. Biol. 40: 134-151.

HOWE, R. W. (1967). Temperature effects on embryonic development of insects. A. Rev. Ent. 12: 15-42.

HUSAIN, M. A. and TREHAN, K. N. (1933). Observations on the life history and control of the whitefly of cotton Bemisia gossypiperda M. & L. Indian J. agric. Sc. 3: 701-753.

HUSSAIN, M. A. and TREHAN, K. N. (1942). The nature and extent of damage caused by Bemisia gossypiperda M. & L. the whitefly of cotton in the Punjab. Indian J. agric. Sci. 12: 793-821.

HUSSEY, N. W. (1965). Possibilities for integrated control of some glasshouse pests. Ann. appl. Biol. 56: 347-350.

HUSSEY, N. W. and GURNEY, B. (1959). Some host plant factors affecting fecundity of whiteflies. Annual Report Glasshouse Crops Research Inst. (Littlehampton, U.K.)

IHEAGWAM, E. U. (1974). The effect of variety, leaf age and leaf toughness of some cruciferous plants on the fecundity of the cabbage whitefly Aleyrodes brassicae Wlk. (Hemiptera: Homoptera). M.Sc. Thesis, London University.

JERMY, T. and SARINGER, G. (1955). Die Rolle der Photoperiode in der Auslösung der Diapause des Kartoffelkäfers (*Leptinotarsa decemlineata* Say) und des Amerikanischen weissen Bärenspinners (*Hyphantria cunea* Drury). *Acta Agron. Acad. Sci. Hung.* *5*: 419-440.

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

JOHNSON, G. G. (1940). Development, hatching and mortality of the eggs of *Cimex lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature. *Parasitology* *32*: 127-173.

KAMM, J. A. (1973). Role of environment during diapause on the phenology of *Chrysoteuchia topiaria* (Lepidoptera: Pyralidae). *Ent. exp. & appl.* *16*: 407-413.

KENNEDY, J. S. (1939). The visual responses of flying mosquitoes. *Proc. zool. Soc. Lond.* *109*: 221-242.

KENNEDY, J. S. (1953). Host plant selection in Aphididae. *Trans 9th Int. Congr. Ent., Amsterdam*, 1951, *2*: 106-113.

KENNEDY, J. S. (1958). The experimental analysis of aphid behaviour and its bearing on current theories of instinct. *Proc. 10th int. Congr. Ent. Montreal* (1956) *2*: 397-404.

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

KENNEDY, J. S. (1965). Co-ordination of successive activities in an aphid. Reciprocal effects of settling on flight. *J. exp. Biol.* *43*: 489-509.

KENNEDY, J. S. (1974). Changes of responsiveness in the pattern of behavioural sequences. Pp. 1-6 in Experimental analysis of insect behaviour (ed. L. B. Browne). Heidelberg: Springer-Verlag.

KENNEDY, J. S. and BOOTH, C. O. (1950). Methods for mass rearing and investigating the host relations of Aphis fabae Scop. Ann. appl. Biol. 37: 451-470.

KENNEDY, J. S. and BOOTH, C. O. (1951). Host alternation in Aphis fabae. 1. Feeding preferences and fecundity in relation to the age and kind of leaves. Ann. appl. Biol. 38: 25-64.

KENNEDY, J. S. and BOOTH, C. O. (1963a). Free flight of aphids in the laboratory. J. exp. Biol. 40: 67-85.

KENNEDY, J. S. and BOOTH, C. O. (1963b). Co-ordination of successive activities in an aphid. The effect of flight on the settling responses. J. exp. Biol. 40: 351-369.

KENNEDY, J. S. and FOSBROOKE, I. H. M. (1972). The plant in the life of an aphid. Insect/Plant Relationships. Symp. R. ent. Soc. Lond. No. 6: 129-140.

KENNEDY, J. S. and LUDLOW, A. R. (1974). Co-ordination of two kinds of flight activity in an aphid. J. exp. Biol. 61: 173-196.

KIRCHNER, H. A. (1939). Versuche über die Fruchtbarkeit von Dixippus Carausius morosus bei abgestufter Wohndichte und Raumgrosse. Z. Ang. Ent. 25: 151-160.

KOGURE, M. (1933). The influence of light and temperature on certain characters of the silkworm Bombyx mori. J. Dept. Agr. Kyushu Imp. Univ. 4: 1-93.

KOROBITZIN, V. G. (1967). To the cognition of Aleroids (Homoptera, Aleyrodidae) of the Crimea (in Russian). Trudygos. nikit. bot. Sada 39: 305-365.

LAMB, K. P. (1961). Some effects of fluctuating temperatures on metabolism, development, and rate of population growth in the cabbage aphid, Brevicoryne brassicae. Ecology 42: 740-745.

LARCZENKO, K. (1957). Feeding and diapause of the Colorado potato beetle. Roczniki Nauk Rolniczych 74: 287-314.

LAUGHLIN, R. (1974). A modified Kennedy flight chamber. J. Aust. ent. Soc. 13: 151-153.

LEES, A. D. (1950). Diapause and photoperiodism in the fruit tree red spider mite (Metatetranychus ulmi Koch). Nature, Lond. 166: 874.

LEES, A. D. (1953a). Environmental factors controlling the evocation and termination of diapause in the fruit tree spider mite Metatetranychus ulmi Koch (Acarina: Tetranychidae). Ann. appl. Biol. 40: 449-486.

LEES, A. D. (1953b). The significance of the light and dark phases in the photoperiodic control of diapause in Metatetranychus ulmi Koch. Ann. appl. Biol. 40: 487-497.

LEES, A. D. (1954). Photoperiodism in Arthropods. Proc. 1st Intern. Photobiol. Congr., Amsterdam 36-45.

LEES, A. D. (1955). "The Physiology of Diapause in Arthropods". Cambridge Univ. Press, London and New York.

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

LEES, A. D. (1963). The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid Megoura viciae Buckton. III. Further properties of the maternal switching mechanism in apterous aphids. J. Insect Physiol. 9: 153-164.

LUDWIG, D. (1926). Effects of temperature on the rate of development of the 'Jap' beetle Popilia japonica. Anat. Rec. 39: 121.

MacARTHUR, R. H. (1960). On the relative abundance of species. Amer. Natur. 94: 25-36.

MACKERRAS, M. J. (1933). Observations on the life histories, natural requirements and fecundity of blow-flies. Bull. ent. Res. 24: 353-362.

MANSINGH, A. (1971). Physiological classification of dormancies in insects. Can. Ent. 103: 983-1009.

MARCOVITCH, S. (1924). The migration of the Aphidae and the appearance of the sexual forms as affected by the relative length of daily light exposure. J. Agr. Res. 27: 513-522.

MATHUR, R. N. (1941). Certain observations on the nitrogen nutrition of the sugar cane plant in relation to susceptibility to attack of whitefly. Proc. Xth Conv. Sug. Tech. Assoc. India p. 45-53.

McLEOD, D. G. R. (1964). Diapause in Euxesta notata (Weidemann). Proc. Entomol. Soc. Ontario 94: 61-62.

McMULLEN, R. D. (1967). The effects of photoperiod, temperature and food supply on rate of development and diapause in Coccinella novemnotata. Can. Ent. 99: 578-586.

MELLANBY, H. (1937). Experimental work on reproduction in the tsetse fly, Glossina palpalis. Parasitology 29: 131-141.

MESSENGER, P. S. (1964a). Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host - parasite system. Ecology 45: 119-131.

MESSENGER, P. S. (1964b). The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid Therioaphis maculata. J. econ. Ent. 57: 71-76.

MILLER, R. S. (1964). Larval competition in Drosophila melanogaster and D. simulans. Ecology 45: 132-148.

MILNE, W. M. (1971). Factors affecting aphid populations on broad beans. Ph.D Thesis, London University.

MORAN, V. C. and BUCHAN, P. R. (1975). Oviposition by the citrus psylla Trioza erytreae (Homoptera: Psyllidae), in relation to leaf hardness. Ent. exp. & appl. 18: 96-104.

MORRILL, A. W. (1903). Notes on some *Aleyrodes* from Massachusetts, with descriptions of new species. *Mass. agric. Exp. Sta. Bull.* *1*.

MORRILL, A. W. and BACK, E. A. (1911). Whiteflies injurious to citrus in Florida. *Bull. Bur. Ent. U.S. Dept. Agric.* *92*: 109 pp.

MOUND, L. A. (1965c). The effect of whitefly (*Bemisia tabaci*) on cotton in the Sudan Gezira. *Emp. Cott. Grow. Rev.* *42*: 290-294.

MÜLLER, H. J. (1957). Über die Diapause von *Stenocranus minutus* Fabr. Homoptera: Auchenorrhyncha. *Beitr. Entomol.* *7*: 203-205.

MÜLLER, H. J. (1962). Über den Saisondimorphen entwicklungszyklus die Aufhebung der Diapause bei *Aleurochiton complanatus* (Baerensprung).

MÜLLER, H. J. (1965). Problems der Insekten diapause verh. Dt. Zoo. Ges. in Jena. *Zool. Anz.* *29*: 192-222.

NIELSEN, E. T. and NIELSEN, A. T. (1950). Contributions towards the knowledge of the migration of butterflies. *Amer. Mus. Novit.* *1471*: 29 pp.

NORRIS, M. J. (1950). Reproduction in the African migratory locust (*Locusta migratoria migratorioides* R. & F.) in relation to density and phase. *Anti-Locust Bull.* No. 6: 48 pp.

NORRIS, M. J. (1952). Reproduction in the desert locust (*Schistocerca gregaria* Torsk.) in relation to density and phase. *Anti-Locust Bull.* No. 13: 49 pp.

ODHIAMBO, T. R. (1968). The effects of mating on egg production in the cotton stainer, *Dysdercus fasciatus* Sign. *Ent. exp. & appl.* *11*: 379-388.

PAINTER, R. H. (1936). The food of insects and its relation to resistance of plants to insect attack. Amer. Natur. 70: 547-566.

PEAIRS, L. M. (1947). Insect pests of farm, garden, and orchard. 4th Ed. New York & London p. 20 and 443-445.

PIENKOWSKI, R. L. (1976). Behaviour of the adult alfalfa weevil in diapause. Ann. Entomol. Soc. Am. 69: 155-157.

PEARL, R. and PARKER, S. L. (1922). On the influence of density of population upon the rate of reproduction in Drosophila. Proc. Nat. Acad. Sci. (U.S.A.) 8: 212-219.

POLLARD, D. G. (1971). The use of polyporus for the investigation of stylet behaviour in the Hemiptera. Ent. exp. & appl. 14: 283-296.

PRADHAN, S. and BHATIA, S. K. (1956). The effect of temperature and humidity on the development of sugar cane stem borer Chilio infuscatellus (Snell). Proc. 43rd Indian Sci. Congr. 111: 399.

RAINEY, R. C. (1976). The flying insect and its environment: Insect flight (edited by R. C. Rainey). Symp. R. ent. Soc. Lond. 7: 75-112.

RICHARDS, O. W. (1927). Sexual selection and allied problems in the insects. Biol. Rev. 2: 298-364.

RICHARDS, O. W. (1940). The biology of the small white butterfly Pieris rapae with special reference to the factors controlling its abundance. J. Anim. Ecol. 9: 243-88.

ROSE, D. J. W. (1972). Dispersal and quality in populations of Cicadulina species (Cicadellidae). J. Anim. Ecol. 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. *Bull. ent. Res.* *62*: 497-505.

ROUBAUD, E. (1930). Suspension évolutive et hibernation larvaire obligatoire provoquées par la chalent chez le moustique commun *Culex pipiens* L. *C. R. Acad. Sci. Paris* *190*: 326-327.

SAUNDERS, D. S. (1971). The temperature-compensated photoperiodic clock 'programming' development and pupal diapause in the flesh-fly, *Sarcophaga argyrostoma*. *J. Insect Physiol.* *17*: 801-812.

SHELFORD, V. E. (1927). An experimental investigation of the relation of the codling moth to weather and climate. *Bull. Illinois Nat. Hist. Survey* *16*: 307-440.

SHELFORD, V. E. (1929). Laboratory and field ecology. The responses of animals as indicators for correct working methods. Baltimore: Williams & Wilkins. P. 56.

SIDDIQUI, W. H., BARLOW, C. A. and RANDOLPH, P. A. (1973). Effects of some constant and alternating temperatures on population growth of the pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae). *Can. Ent.* *105*: 145-156.

SIEGEL, S. (1956). Nonparametric statistics for the behavioural sciences. McGraw-Hill Kogakusha, Ltd.,

SLOBODKIN, L. B. (1962). Growth and Regulation of Animal Populations. Holt, Rinehart and Winston, New York.

SONI, S. K. (1976). Effect of temperature and photoperiod on diapause induction in Erioischia brassicae (Bch.) (Diptera, Anthomyiidae) under controlled conditions. Bull. ent. Res. 66: 125-131.

SOUTHWOOD, T. R. E. (1962). Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37: 171-214.

SOUTHWOOD, T. R. E. (1968). The abundance of animals. Inaugural Lect. Imp. Coll. Sci. Technol. 8: 1-16.

SOUTHWOOD, T. R. E. (1968). Ecological methods. Chapman and Hall. London.

SOUTHWOOD, T. R. E. (1971). The role and measurement of migration in the population system of an insect pest. Trop. Sci. 13: 275-278.

SOUTHWOOD, T. R. E. (1972). Insect/plant relationships - an evolutionary perspective (ed. H. F. van Emden). Symp. R. ent. Soc. Lond. 6: 3-30.

SOUTHWOOD, T. R. E., MAY, R. M., HASSELL, M. P. and CONWAY, G. R. (1974). Ecological strategies and population parameters. Amer. Natur. 108: 791-804.

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. J. Anim. Ecol. 45: 313-325.

STANILAND, L. N. (1924). The immunity of apple stocks from attacks of woolly aphids (Eriosoma lanigerum, Hausmann). 11. The causes of the relative resistance of the stocks. Bull. ent. Res. 15: 157-170.

STEEL, R. G. D. and TORRIE, J. H. (1960). Principles and procedures of statistics. McGraw-Hill London.

STORCH, R. H. and VAUNDELL, W. L. (1972). The effect of photoperiod on diapause induction and inhibition in *Hippodamia tredecimpunctata* (Coleoptera: Coccinellidae). *Can. Ent.* *104*: 285-288.

STRAATMAN, R. (1962). Notes on certain lepidoptera ovipositing on plants which are toxic to their larvae. *J. Lepid. Soc.* *16*: 99-103.

TANTON, M. T. (1962). The effect of leaf 'toughness' on the feeding of larvae of the Mustard beetle, *Phaedon cochleariae* Fab. *Ent. exp. & appl.*, *5*: 74-78.

TARR, S. A. J. (1951). Leaf curl disease of cotton. *Commonw. Mycol. Inst. London* 55 pp.

TAUBER, O. E., DRAKE, C. J. and DECKER, G. C. (1945). Effects of different food plants on egg production and adult survival of the grasshopper, *Melanoplus bivittatus* (Say). *Iowa St. Coll. J. Sci.* *19*: 343-359.

TAUBER, M. J. and TAUBER, C. A. (1972). Larval diapause in *Chrysopa nigricornis*: Sensitive stages, critical photoperiod, and termination (Neuroptera: Chrysopidae). *Ent. exp. & appl.* *15*: 105-111.

TAUBER, M. J. and TAUBER, C. A. (1976). Environmental control of univoltinism and its evolution in an insect species. *Can. J. Zool.* *54*: 260-265.

TAYLOR, L. R. (1957). Temperature relations of teneral development and behaviour in Aphis fabae Scop. J. exp. Biol. 34: 189-208.

TAYLOR, L. R. (1958). Aphid dispersal and diurnal periodicity. Proc. Linn. Soc. Lond. 169: 67-73.

TAYLOR, L. R. (1974). Insect migration, flight periodicity and the boundary layer. J. Anim. Ecol. 43: 225-238.

THOMSEN, M. (1927). Parthenogenesis in Coccids and Aleurodids, and review. Z. Zellforsch. mikr. Anat. 5: 1-116.

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

TREHAN, K. N. (1940). Studies on the British whiteflies (Homoptera). Trans. R. ent. Soc. Lond. 90: 575-616.

TREHAN, K. N. (1944). Further notes on the bionomics of Bemisia gossypiperda M. & L., the whitefly of cotton in the Punjab. Indian J. agric. Sci. 14: 53-63.

TROUVELOT, B., LACOTTE, DUSSY, and THENARD (1933). Les qualites elementaires des plantes nourricieres du Leptinotarsa decemlineata et leur influence sur le comportement de l'insecte. C. R. Acad. Sci. Paris 197: 355.

TROUVELOT, B. and GRISON, P. (1935). Variations de fecundite du L. decemlineata Say avec le solanum tuberiferes consumes par l'insecte. C. R. Acad. Sci. Paris 201: 1053-1055.

TWINN, C. R., HOCKING, B., McDUFFIE, W. C. and CROSS, H. F. (1948). A preliminary account of the biting flies at Churchill, Manitoba. Canad. J. Res (D) 26: 334-357.

URQUHART, F. A. (1960). The Monarch Butterfly. 361 pp. (University of Toronto Press).

UTIDA, S. (1941a). Studies on experimental population of the azuki bean weevil *Callosobruchus chinensis* (L.). 1. The effect of population density on the progeny populations. *Mem. Coll. Agric.* Kyoto Imp. Univ. 48: 1-30.

VALENTINE, E. W. (1952). Some observations on the biology of *Dysdercus fasciatus* Sign. (Hemiptera: Pyrrhocoridae). Dip. Thesis, London, Imp. Coll.

VANDERPLANK, F. L. (1947). Experiments in the hybridisation of tsetse-flies (*Glossina*, Diptera) and the possibility of a new method of control. *Trans. R. ent. Soc. Lond.* 98: 1-18.

WALKER, F. (1852). List of the specimens of Homopterous insects in the collections of the British Museum. Part 4: 1091-1093.

WALOFF, N. and BAKKER, K. (1963). The flight activity of Miridae (Heteroptera) living on broom, *Sarothamnus scoparius* (L.). *J. Anim. Ecol.* 32: 461-480.

WATSON, T. F. (1964). Influence of host plant condition on population increase of *Tetranychus telarius* (Linnaeus) (Acarina: Tetranychidae). *Hilgardia* 35 (11): 272-322.

WATT, K. E. F. (1960). The effect of population density on fecundity in insects. *Can. Ent.* 92: 674-695.

WAY, M. J. and HOPKINS, B. A. (1950). The influence of photoperiod and temperature on the induction of diapause in *Diataraxia oleracea* L. (Lepidoptera). *J. exp. Biol.* 27: 365-376.

WENSLER, R. J. (1962). Mode of host selection by an aphid. Nature, London 195: 830-831.

WHEELER, M. W. (1893). A contribution to insect embryology. J. Morph. 8: 1.

WIGGLESWORTH, V. B. (1965). The Principles of Insect Physiology. London: Methuen & Co.

deWILDE, J. (1962a). Photoperiodism in insects and mites. A. Rev. Ent. 7: 1-26.

deWILDE, J. (1962b). Analysis of the diapause syndrome in the Colorado potato beetle (*Leptinotarsa decemlineata* Say): Behaviour and reproduction. Acta Physiol. Pharmacol. Neerl. 11: 525.

deWILDE, J., DUINTJER, C. S. and MOOK, L. (1959). Physiology of diapause in the adult Colorado beetle. 1. The photoperiod as a controlling factor. J. Insect Physiol. 3: 75-85.

WILLIAMS, C. B. (1917). Some problems of sex ratios and parthenogenesis. J. Genet. 6: 255-267.

WILLIAMS, C. B. (1935). A mass flight of the cabbage whitefly (*Aleurodes brassicae*). The Entomologist 68: 218-219.

WILLIAMS, C. B. (1958). Insect migration. Collins, London.

WILLIAMS, C. M. (1946). Physiology of insect diapause: The role of the brain in the reproduction and termination of pupal dormancy in the giant silkworm, *Platysamia cecropia*. Biol. Bull. 90: 234-243.

WILSON, C. S. (1951). Control of Alaskan biting insects. Publ. Hlth. Rep. Wash. 66: 917-922.

WITHROW, R. B. (1959). A kinetic analysis of photoperiodism. Symp. photoperiodism and related phenomena in plants and animals. 439-474. Am. Assoc. Adv. Sci., Washington, D.C.

WOODFORD, J. A. T. (1969). Behaviour and developmental components of the teneral stage in *Myzus persicae*. Ent. exp. & appl. 12: 337-350.