

Population Models for the Cabbage Aphid,
Brevicoryne brassicae (L.)

by

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ABSTRACT

This study aimed to provide a better understanding of the population dynamics of Brevicoryne brassicae (L.) within the summer season. Its primary parasitoid, Diaeretiella rapae (McIntosh) was also considered. Special emphasis has been placed on the construction of stage specific population models involving density dependence, in an attempt to describe the fluctuations of B. brassicae through the summer and the role played by D. rapae in regulating the aphid populations.

The stage distributions of B. brassicae have been investigated in the field and laboratory, using Brussels sprouts as the aphid's host plant. Several methods have been compared and used to evaluate the stability of the stage distribution of B. brassicae population under various conditions. Evidence suggests that the stage distributions were affected by population density. In the laboratory, the importance of density dependence in regulating B. brassicae populations has been assessed and attempts have been made to quantify these processes. Three important demographic parameters; fecundity rates, developmental rates, and survivorship are determined as being age-specific and density-dependent functions. Equations describing these processes are used as basic functions for a population model of B. brassicae. In these experiments, it was found that several types of survivorship curves considered by previous work (Pearl & Miner, 1935; Deevey, 1947; Slobodkin, 1962) can be generated by the aphid, merely by changing the initial population density.

In the laboratory, the functional responses of D. rapae to various instars of B. brassicae were investigated. It was found that D. rapae prefers to attack the older (i.e. the fourth instar and adult aphids)

rather than the younger stages of B. brassicae. The result and other biological information were incorporated into the simulation model of the aphid population.

Finally, the effects of including the parasitoid in the aphid population model have been investigated.

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Chapter One

General Introduction

Theoretical ecology has developed over the past half century to provide a framework for the study of species interactions. Relatively simple mathematical models describing, for example, competition and predation now exist, and have identified some underlying general principles.

When we turn, however, to the analysis of data collected from a natural population, adequate techniques and models are still largely lacking. It is only if the populations have discrete generations that the procedure is relatively straightforward (Leslie, 1945, 1948). For populations breeding continuously and with overlapping generations, there remain major problems in the estimation of crucial demographic parameters such as fecundity rates, developmental rates and survivorship. Although theoretical treatments of this subject date back to the beginnings of population ecology, there have been relatively few advances until the last decade, during which important contributions have been made in various fields (e.g. Charlesworth, 1980). For example a considerable amount of work has been done by demographers and wildlife management and fishery workers, focussing on the biological performance and the optimal hunting and harvesting age-structured populations, respectively. When considering agricultural pests, some species, such as aphids in Britain, have overlapping generations which considerably affects the ways that age-structured population models should be developed. The cabbage aphid, Brevicoryne brassicae (L.), has, therefore, been chosen as an experimental insect for this study because it has markedly overlapping generations and is convenient to study, both in the field, and under controlled conditions in the laboratory.

The cabbage aphid is host-specific to most members of the genus Brassica. It is autoecious on brassicas and produces sexual forms in late autumn in Britain. In warm places, (i.e. tropical and subtropical areas), the winter is passed anholocyclically. In this country, the eggs laid on brassica stems in late autumn hatch between the end of February and the end of April, and the alatae are produced from the end of May to July. These migrate to newly planted brassica crops, such as cabbage, cauliflower, Brussels sprouts, kale, rape, radish, swedes and mustard. B. brassicae reproduces parthenogenetically through spring, summer and autumn.

Outbreaks of B. brassicae were recorded as a major cause of brassica loss as early as 1929 in Britain (Barnes, 1931) and the yield loss of Brussels sprout crops due to the aphid has been estimated at about £1 million per year in England and Wales (Strickland, 1957). In the field, dense colonies may develop on the leaves, or on the flower of seed crops, causing considerable damage, particularly in warm dry weather.

A large amount of research on the reproduction of B. brassicae has already been carried out. In the Netherlands, there are six to eleven generations per year in the field (Hafez, 1961). In the laboratory, B. brassicae takes about ten days to grow from a newly born nymph to an adult on potted Brussels sprouts at 20°C and 16-hour photoperiod (Akinlosotu, 1973). In a different experiment, DeLoach (1974) placed B. brassicae on cabbage plants grown at various temperatures. The aphid reproduced after 33.2, 19.2, 12.3, 10.4 and 11.1 days at 10°C, 15°C, 20°C, 25°C and 30°C, respectively. DeLoach calculated that the time taken for a population to double in size at 10°C, 15°C, 20°C and 25°C was 16.5, 7.88, 5.17 and 7.07 days, respectively. This rapid

reproductive rate is the important factor in building up a highly dense colony and results in two particular characteristics - overlapping generations and complex age-distributions.

Considerable research has been done on various other aspects of the biology (Petherbridge and Mellor, 1936; Strickland, 1954; George, 1957; Hafez, 1960, 1961; Thompson, 1963; van Emden, 1963, 1965, 1966, 1969; Smith, 1969; van Emden and Bashford, 1969, 1971; Daiber, 1971; Wearing, 1972; DeLoach, 1974) and population dynamics (Hafez, 1961; Hughes, 1962, 1963; van Emden, 1965; Hughes and Gilbert, 1968; Dunn and Kempton, 1971; Chua, 1977; Raworth et al., 1984) of the cabbage aphid, but only a few attempts have been made to incorporate this information into mathematical models (Hughes, 1963; Hughes and Gilbert, 1968; Raworth et al., 1984). The reason for this is that detailed census figures are very difficult to obtain and interpret. Hafez (1961) lists the obstacles to an analytical approach to his data, as follows: (1) The generations overlap; (2) Most of the factors involved interact; (3) It has been impossible to obtain systematic observations on reproduction and migration as affected by the complex conditions prevailing in the field.

Way and Banks (1968) have used experimental exclusion techniques to test the effects of different factors on total population trends of Aphis fabae Scop. on spindle, Euonymus europaeus L., and Milne (1971) used a similar method for aphids on broad beans. Although the technique is extremely useful, it is likely to be of limited value for investigations of the complicated interactions caused by age structure. Based on the study of Williams (1961), Hughes (1962, 1963) developed a method for the study of B. brassicae (L.) that is still widely used. Mortality

was estimated as the difference between the potential rate of increase and the observed rate, and then partitioned among various causes according to indications of their magnitude from field samples. The potential rate of increase was obtained from the relative abundances of the first three instars, and the observed rate of increase estimated graphically from a series of total population counts ending at the sampling date. The validity of the analysis was confined to occasions when the instar-distribution was thought to be stable and the aphid population size increased geometrically (Carter, Aikman and Dixon, 1978). On the basis of this work, Hughes and Gilbert (1968) developed the first population simulation model for B. brassicae (L.), and the model was further developed with emphasis on a host-parasitoid relationship by Gilbert and Hughes (1971). In these models, it was assumed that the effects of density dependence on reproductive rate, polymorphism, emigration rate, and predation could make these rates decline exponentially as the population reaches a threshold density of 20,000 aphids per plant. It was also assumed that the stage distribution of the aphid population was stable and that parasitoids and predators search randomly for aphids. These artificial assumptions, however, were not based on experiments and were not validated by a further analysis (Carter, Aikman and Dixon, 1978).

A clear understanding of the implications of age-structure for such parameters as fecundity, development and survival rates is therefore necessary for a proper interpretation of experimental findings. Similarly, insect ecologists often wish to make predictions about the effects of density dependence on age-structured populations. For these reasons, the present study seems timely. The aim in this study, therefore, is to explore the ways in which these crucial demographic parameters can vary

with age, and to incorporate their effects in population models to show their potential influence on population dynamics. Dense colonies of B. brassicae are likely to be formed under natural conditions because of their strong tendency to aggregate (Hayamizu, 1982). Thus the ways in which age-specific density-dependent processes play in population growth are a central part of this study.

The first topic to be investigated is the population growth of B. brassicae in the field, in field cages and in the laboratory. To simplify complex age-structured affects on population dynamics, most mathematical models of aphid populations have assumed stable age distributions. Several methods of evaluating the stability of stage distributions are compared in Chapter Two and applied to B. brassicae populations grown under various conditions. The effect of intraspecific competition measured as a density dependent demographic processes, is discussed in Chapter Three, and the important demographic parameters of fecundity rates, developmental rates and survivorship as age-specific density-dependent functions are considered in Chapter Four. Inter-stage-class processes and the resulting effects on competition are also considered in this chapter. The equations developed from this set of data are then used as basic functions for an age-specific and density-dependent population model for B. brassicae. Chapter Five considers the incorporation of these functions into a differential equation model for an age-structured population. Such a model simulates the population fluctuations of B. brassicae and aids in the understanding of the cause of such fluctuations.

Finally, in Chapter Six the inclusion of parasitism in the aphid population model is briefly considered. Some experiments on the host stage preference and functional responses of Diaeretiella rapae (McIntosh)

to various stages of the aphid provide information on which the model is based. A simulation model of the aphid population with the parasitoid is then developed and used to study the possible within season impact that the parasitoid can have on the aphid population growth.

Chapter Two

**Stage Distribution of Cabbage Aphid
Population during the Summer**

2.1 Introduction

One of the most beneficial results of incorporating specific hypotheses into mathematical models is that it forces some simplification, thus helping to make a problem more tractable and understandable. This, however, may sometimes lead to outcomes which are, to a lesser or greater degree, unrealistic. To avoid analytical difficulties, a number of mathematical theories of population growth have assumed pure exponential increase when the population lives in a non-limiting environment (e.g. models of simple population growth (Stearns, 1976), population genetics (Crow and Kimura, 1970; Kimura and Ohta, 1971), competition (MacArthur, 1972; May, 1974a) and predation and parasitism (Murdoch and Oaten, 1975; Hassell, 1978)). In these cases both continuous breeding populations with overlapping generations and populations breeding at discrete intervals and starting growth with an arbitrary age distribution, will assume a stable age distribution (SAD) sometime in the future as long as the ideal conditions of constant age-specific death and birth rates without immigration or emigration are maintained (Lotka, 1922). On reaching its stable age distribution, the population will grow in a purely exponential manner (i.e. increasing in geometric progression (Sharpe & Lotka, 1911; Lotka, 1922)), and, if displaced from this stable form will spontaneously revert to its SAD.

In general, insects and mites are age-grouped by stages which are of unequal length. As the age (in units of time) of a given stage will vary with environmental conditions and between individuals (Southwood, 1978, p. 388), the age of an individual should not be equated with stage. The stage of development of an insect should rather be considered as a function of time, environment, and other factors. On this basis,

under similar environmental conditions, a stable stage distribution (SSD) can be analogous to a SAD.

The attainment, or at least an assumption, of a SAD/SSD is a necessary condition if the intrinsic rate of increase (r_m) is to be calculated prior to the construction of a population model. Such a situation is rarely found in natural insect populations, a series of experiments were undertaken in the field, in field cages and in the laboratory, in order to investigate fully the stage distribution of B. brassicae populations. The next section describes experiments designed to illustrate the fluctuation of stage distribution under these three different conditions, and several methods previously used to investigate SAD or SSD are then reviewed. In the subsequent section the result of experiments are presented, and the relationships between population density and stage distribution are discussed. Finally, in the last section, the most important factor influencing B. brassicae populations is considered and further extension of the study is proposed.

2.2 Stage Structure of Brevicoryne brassicae Populations

2.2.1 Materials and Methods

Studies on both field and laboratory populations of B. brassicae were carried out at Silwood Park from 1981 to 1983.

(1) Culturing procedure

Stock cultures of B. brassicae were kept in insect cages, 41 x 41 x 47 cm, covered with Acrylic sheet except for one side of Terylene net. To maintain the stock colony, one hundred apterae from the old stock colony were transferred every two weeks to young uninfested Brussels sprouts plants in a clean cage. The old stock colonies were discarded after one month, thus reducing the danger of infestation by parasitoids.

Standard cohort cultures were started from the stock cultures. Parthenogenetic virginoparous apterae of B. brassicae were placed on a Brussels sprouts plant (Brassica oleracea L. var. bullata gemmifer) in an insect cage. The infested plant was then kept for 24 hours in a constant temperature room at a temperature of $25 \pm 1^{\circ}\text{C}$ with a 16-hour photoperiod and a relative humidity of 60–70%, after which the adult aphids were placed on another plant. The original plant, now infested by neonates, was kept in a separate cage. This procedure was repeated daily to maintain the standard cohorts for the experiments, the adult B. brassicae being replaced with fresh ones every 6–7 days. The culturing procedure is shown schematically in Fig. 2.1.

(2) Experiment I – The stage structure and distributions of laboratory populations of B. brassicae.

The plants used in this experiment were grown to the 5–7 leaf stage in 10-cm diameter pots in the same controlled conditions as the cultures.

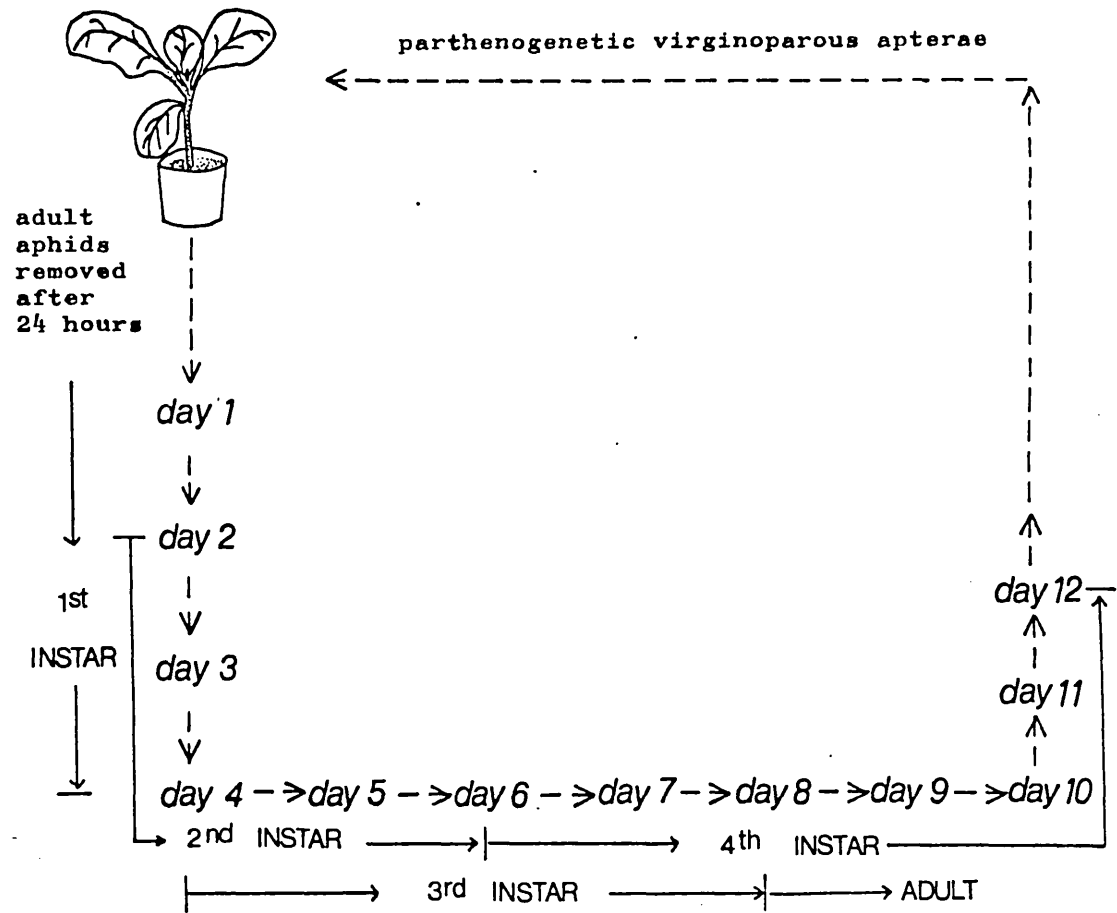
Before commencing the experiment, which was replicated 10 times, all insects were removed from the experimental plants. A cohort of apterous progeny of virginoparous B. brassicae was established by caging 10 reproducing apterous virginoparous adults from the standard 9-day old cohort on a leaf of each plant, using a leaf cage (dia. 2 cm height 1 cm). After 24 hours the leaf cages were removed, the adults killed and their progeny reduced to ten per plant. The plants were then placed in cylindrical polythene insect cages (dia. 23.5 cm, height 40 cm), covered by Terylene net. The aphid populations enclosed in this way on individual host plants, were considered to be closed populations, free from migration, parasitism, predation and climatic factors. During the experimental period of 40 days details of changes

Figure 2.1

Schematic diagram of the cultures of standard cohorts of B. brassicae used in the experiments. Conditions were as follows: temperature, $25 \pm 1^{\circ}\text{C}$; R.H., 60-70%; 16h photoperiod.

Brevicoryne brassicae cultures

partheno-
genetic
virgino-
parous
apterae



in the populations were recorded by counting the number of each aphid instar present.

(3) Experiment II - The stage structure and distributions of populations of B. brassicae maintained in field cages during the summer of 1983.

The general procedure was as in Experiment I but in this case the plants were grown to the standard stage of development in pots kept outdoors in cages measuring 52 x 52 x 80 cm, covered with Terylene net. The initial colonies of 10 first instar nymphs of B. brassicae were established on the potted plants in the C.T. room on 8th July, 1983. The potted plants were then placed in a field at Silwood Park and covered by field cages. A daily census was made for 39 days, from the 8th July, 1983 to the 15th August, 1983, when the plants began to wilt. There were again 10 replicates.

(4) The stage structure and distributions of field populations of B. brassicae during the summers of 1981 and 1982.

At Silwood Park in 1981 and 1982, Brussels sprouts were transplanted in the field in early June about 1 m apart in an area covering 40 x 30 m of Silwood Bottom. This provided 1,200 Brussels sprouts plants which were allowed to develop to the 10-leaf stage. The field population censuses of B. brassicae were carried out from July to October, 1981, and from July to September, 1982. The plants were initially chosen at random, and then examined two to three times a week as the colonies developed until the end of the experiments. The stage structure of the population of B. brassicae on each plant examined was recorded as well as the number of mummies, adult parasitoids (Diaeretiella rapae), and Syrphid larvae.

In 1981, 50 plants were initially censused. This was later reduced to 20 plants for the census of 1982 because of the high population densities and the limited time available. Because of the damage from other pests (eg., cabbage root flies, pigeons, rabbits), some experimental plants were destroyed and censussing hence not completed. As a result only 15 sets of population data have been analyzed for each year.

The aphid population census included examination of all the leaves on the plant, rather than the widely used "three leaf method" of Church and Strickland (1954) (e.g., Strickland, 1954, 1957; Hafez, 1961; Akinlosotu, 1973; and others). Church and Strickland considered a whole plant census by visual counting both laborious and unaccurate, but a later study by Chua (1975) has shown that the "all-leaf method" provides a far more accurate estimate of population density. Furthermore, Church and Strickland's "three leaf method" is destructive and can be easily biased by the uneven distribution of cabbage aphids found on Brussels sprouts plants. In the present study it was found that the aphid distribution was heaviest on the crown leaves in June and early July, approximately equal on both crown and middle leaves during July and August, and thereafter significantly increasing on the lower leaves. Towards the end of September most of the aphid population was found on the underside of these lower leaves. Because of this change in the aphid's distribution, the population census was carried out using the all-leaf method of visual counting.

The most widely used model for single species population growth is the logistic equation of Verhulst (1838) and Pearl & Reed (1920), namely:

$$N_t = K \cdot (1 + b \cdot e^{-\gamma \cdot t})^{-1} \quad (2.1)$$

where N_t denotes the population size at time t , K is the environmental carrying capacity, γ is the population instantaneous or intrinsic growth rate, and b is a constant related to the point of infection of the sigmoid population growth curve at time t' ($= \ln b/\gamma$). When the population size ($N_{t'}$) is always half of the carrying capacity (i.e. $N_{t'} = K/2$). Equation 2.1 has been used in analysis of experiments I and II as described in Section 3 below.

2.2.2 Methods of Analysis of Age or Stage Distributions

Census data are usually collected at fixed time intervals, which give a profile of the population's age structure. Several methods have been used to study age or stage distributions and their effects on population changes. Although a variety of such methods have appeared in the demographic literature (e.g. Sharpe and Lotka, 1911; Lotka, 1922, 1925; Lopez, 1961; Keyfitz, 1968, 1977; Pollard, 1973; Hoppensteadt, 1982), only in a few cases (e.g. Hughes 1962, 1963; Detinova, 1968; McMurtry and van de Vrie 1973; Carter, Aikman and Dixon, 1978; Dover et al., 1979; Takafujii, 1980; Carey, 1982a, 1982b) have they been applied to insect populations. The following review focusses on some widely used methods in ecological entomology, examining both empirical and theoretical approaches.

(1) Empirical Methods

The age distribution of insect populations of medical importance have been extensively reviewed by Detinova (1968). Using the criteria of rate of emergence, individual life spans and mortality in each physiological age, Detinova concluded that the age distributions of insect populations under natural conditions in temperate area are never

constant. In hot climates or tropical areas, however, where the environment is more generally favourable for the development and reproduction of certain species, the size and the age distribution of a population tend to remain more-or-less the same, this being determined by the continuous presence of fertile females in the population, by an equal seasonal duration for pre-imaginal development, and by a constant seasonal duration of gonotrophic cycles.

Detinova's method of analysis is an empirical one in which the total number of adult female age classes and their distribution in the population are estimated by dissection and expressed as percentages. By comparing these results visually, Detinova suggested that the conclusions reached were of doubtful values being influenced by the accuracy by which females are aged, the sample size, data on population size, and by the duration of the investigations. The lack of statistical comparisons of the results also increases the difficulties encountered from such methods.

McMurtry and van de Vrie (1973) showed that the stage distribution of European red mite (Panonychus ulmi (Koch)) populations in single leaf ecosystems initiated with a single female averaged approximately 68% eggs, 25% immatures, and 7% adults over a 33-day period. Another set of data for the same species, obtained from mite counts taken from apple orchard samples, gave 60% eggs, 30% immatures (14% larvae, 8% protonymphs and 8% deutonymphs), and 10% adults (2% preovipositing adult females and 8% ovipositing adult females). Dover et al. (1979) have applied this data to parameterize a stage-structured population model describing the biological control of P. ulmi by a phytoseiid mite. They assumed that the stage distribution data are constants in

the population model during the seasons. In study of the fluctuation of stage distributions of Tetranychus desertorum on golden-rod in Japan Takafujii (1980) found between 70-80% eggs, 10-25% immatures, and 2-10% adults. However, later in the season the percentage in each stage, except that of the adults, departed from these original ranges. Similar results were obtained by Carey (1982a) who reported that the average percentage of eggs, immatures, and adults of tetranychid mite complex on cotton in California was 66, 26 and 8%, respectively. He also found that these percentages changed as the season progressed. Finally, working with B. brassicae populations, DeLoach (1974) was able to compute the percentage of the population in each stage when the experimental population initiated from one aphid had reached a SSD. Unfortunately, he does not make it clear how he estimated these values.

All these stage distributions of mite and insect populations have been obtained from sampled populations and expressed in percentages. Unfortunately, most of the empirical methods discussed here used to calculate the average percentage of each stage compute arithmetic means without any statistical comparison of the results, and then fail to prove if the populations have actually reached a stable stage distribution.

(2) Theoretical Methods

Using Leslie matrices (Leslie, 1945), Carey (1982a) determined the percentage of each stage in the SSD of three species of mite populations, (Tetranychus urticae Koch, I. pacificus McGregor, and I. turkestanii (Ugarov and Nikolski)) on cotton plants, and examined the path of convergence to the SSD beginning with an arbitrary population size and age structure. He found that in relatively large, growing populations

there should always be a substantially greater proportion of egg and immature stages than adults. Within five to six weeks the age distribution will quickly approach the stable level, but the convergent process is oscillatory.

A particular requirement of the Leslie matrix is that the time intervals are exactly equal, yet insects or mites are generally age-grouped by stages in which individuals have variable development rates. Carey (1982a) avoided this problem by assuming that the mites developed uniformly. The analysis also rests on the assumption that the elements of the transition matrix, (i.e., fecundity of each age class and the age-specific survival probabilities), are constant over time and independent of population density. In these respects the analysis is much divorced from the biological reality of natural populations (e.g. Southwood, 1978; Begon and Mortimer, 1981).

Hughes (1962, 1963) suggested a method of determining whether a field population of B. brassicae had reached a SSD by testing whether the frequencies of the first three stages fitted a fixed geometric progression. He was able to show that this was the case for Australian populations of B. brassicae on kale where a SSD occurs frequently in the form of a geometric progression of the number in successive nymphal instars. Based on this approach, several population parameters, such as the overall mortality and the reproductive rate, have been estimated. A population simulation model was then developed to describe the population dynamics of B. brassicae (Hughes and Gilbert, 1968). It has recently been shown, however, that the method is insufficiently sensitive for adequately identifying stable stage distributions in this species (Carter, Aikman and Dixon, 1978). Carter et al. found that a stable stage distribution (a constant potential rate of increase

accurate to two decimal places and an χ^2 value of zero) did not occur in their simulation until 35 generations had elapsed.

If a set of samples are drawn from populations each with a geometric relation between the numbers in the first three stages, then the sum of the individual chi-square's should be acceptable as a valid test. However, they found that the census data reported by Hughes (1962, 1963) does not support this assumption of a SSD. A significant sum may be attributable to more than one alternative hypothesis, for example, to heterogeneous samples. Thus, as a set, the data have failed to support the assumption of a fixed geometric relation between stages. This suggests that the aphid populations censused by Hughes (1962, 1963) have not achieved a stable instar distribution although the majority of the individual sample values for chi-square have not been shown to differ significantly from this assumption. Although a primary aim common of these methods of analysis is to compute the SAD or SSD, another important objective that is often neglected, is to determine whether or not the population has indeed reached a SAD or SSD. The present work will approach the problem in the logical manner of first determining whether the population has reached a SSD and then, empirically, to determine the percentage of the population in each stage.

2.3 Results and Discussion

For two reasons, considerable importance is placed on the growth patterns and stage distributions of B. brassicae populations in laboratory, field cages, and field conditions. Firstly, since population growth processes are highly influenced by the environment, a comparison of the growth patterns of aphid populations under different conditions is meaningful to understand the influence of different growth environments (i.e. laboratory, field cage, and field) on crucial demographic

rates. Secondly, as the stage distributions of the aphid populations could be sensitive to changes in environmental conditions, a comparison of stage distributions under different environmental conditions is needed to determine if such data from the laboratory can be used as a standard.

2.3.1 Population Growth of B. brassicae

The population trends of B. brassicae from Expt. I and II are shown in Fig. 2.2. There were three plants in Expt. I which died before the 20th day and are thus omitted from the figure. Since, these population trends show a highly sigmoid pattern, the Verhulst-Pearl logistic model can be reasonably fitted to the data.

During the initial 25 days of both experiments, the population growth of B. brassicae showed similar patterns of increase, the average population density in Expt. II being slightly less than that of Expt. I. However, from the 25th day to the end of the experiments, the average population density of Expt. II is greater than that in Expt. I. After day 23, the slope of the population growth curve of Expt. I decreases, the average population density fluctuating between 600 and 800 aphids per plant. This reduction in the slope of the curve does not occur until 4 days later in Expt. II, on day 27, and fluctuates between 1,000 and 1,200 aphids per plants. During this period the parameters on the Verhulst-Pearl's logistic model (Table 2.1) give acceptable descriptions from the environmental carrying capacity, K , and the part of inflection of the curve on the time axis, t' ($= \ln b/r$), for both experiments.

Prior to day 25, the plants in both experiments were healthy. However, after this period those of Expt. I weakened, their leaves turned

Figure 2.2

Population trends of B. brassicae in (a) Expt. I (C.I. room) and in (b) Expt. II (field cage) and the curves described by the Verhulst-Pearl logistic model fitted to the total population size against time.

(a) $K = 712$, $b = 279$, $r = 0.2525$;

(b) $K = 1138$, $b = 2816$, $r = 0.30005$.

AVERAGE POPULATION SIZE PER PLANT

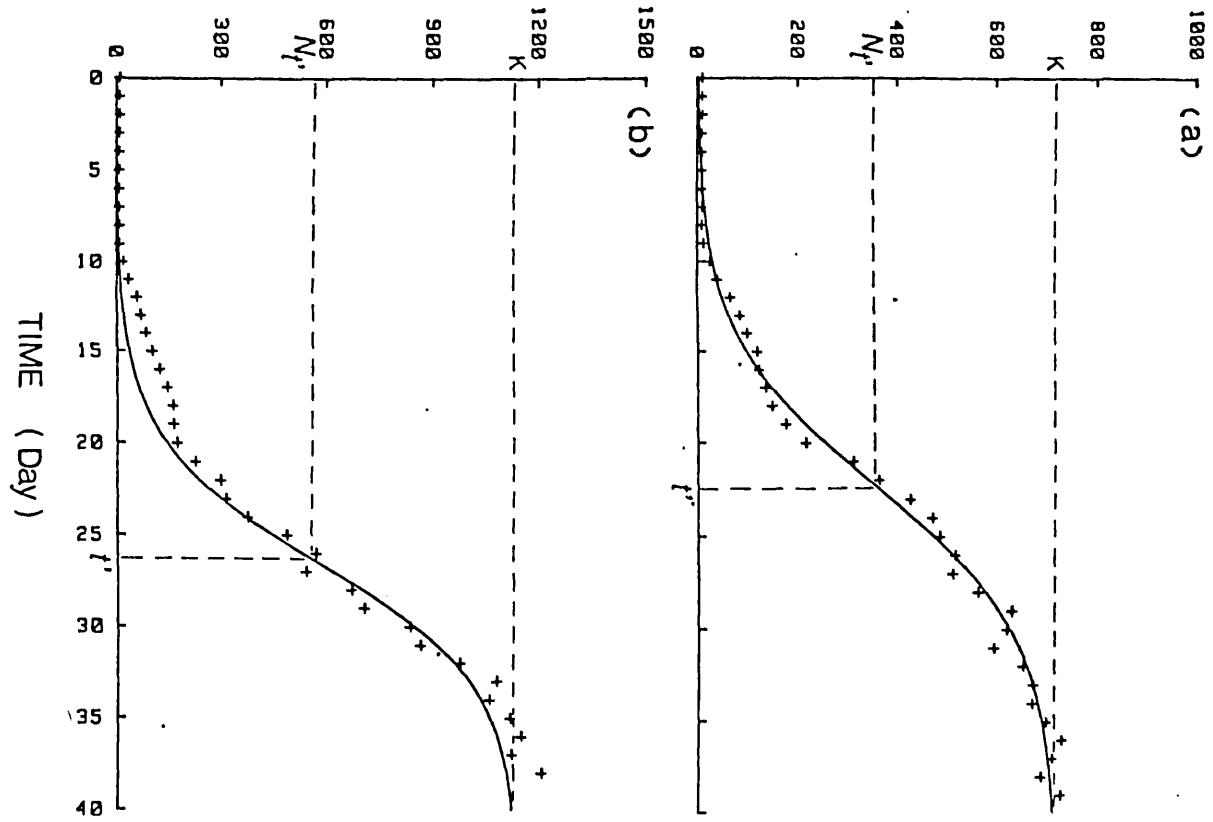


Table 2.1

Estimated parameters ($\pm$ 95% confidence limits) obtained by fitting the Verhulst-Pearl logistic model (see Eq. 2.1) to the population growth curves in Fig. 2.2 using a non-linear least squares procedure.

Expt.	The Environmental	The population			
	Carrying Capacity, K	growth rate, r	b	$t'_{(1)}$	$N_{t'}^{(2)}$
I	712 $\pm$ 21	0.2525 $\pm$ 0.0225	279 $\pm$ 127	22.3	356
II	1138 $\pm$ 80	0.30005 $\pm$ 0.00001	2816 $\pm$ 427	26.5	569

(1) $t' = \ln b/r$

(2) $N_{t'} = K/2$

pale green with the commencement of senescence. Plants of both experiments began wilting on day 35.

The number of aphids per plant (combined totals) through the seasons of 1981 and 1982 are presented in Fig. 2.3 and 2.4, respectively. In July 1981 the populations ranged from 0 to less than 150 aphids per plant. The populations then remained at less than 150 aphids per plant, with relatively small variation between populations, until mid-August after which the inter-population variation increased rapidly, some reaching almost 1,100 aphids per plants, while others remained lower than 100 aphids per plant. The 1982 situation differed considerably. The population size was lower than in the previous year and the inter-population variation was relatively smaller, being at its highest from July 1982 to mid-August. From then until mid-September, the variation remained very low, most populations being less than 50 aphids per plant.

Although temperatures declined towards the end of August (Fig. 2.5) reducing physiological rates and hence the intrinsic rate of increase of B. brassicae, this did not result in a population decline in September. Raworth et al. (1984) cites predators, such as Aphidoletes aphidimyza (Rond.) (Diptera:Cecidomyiidae) and syrphid larvae, as the major factor suppressing aphid population growth during summer. They found that the early appearance of Diaeretiella rapae had little influence on the aphid population, but when the predator populations declined with temperatures, the aphid population increased rapidly. The correlation between aphid and natural enemies is suggestive but requires further work.

Figure 2.3

Total population size of cabbage aphids found on whole Brussels sprout plants examined from 16 July to 15 October, 1981, Silwood Park, Berkshire, England.

1981

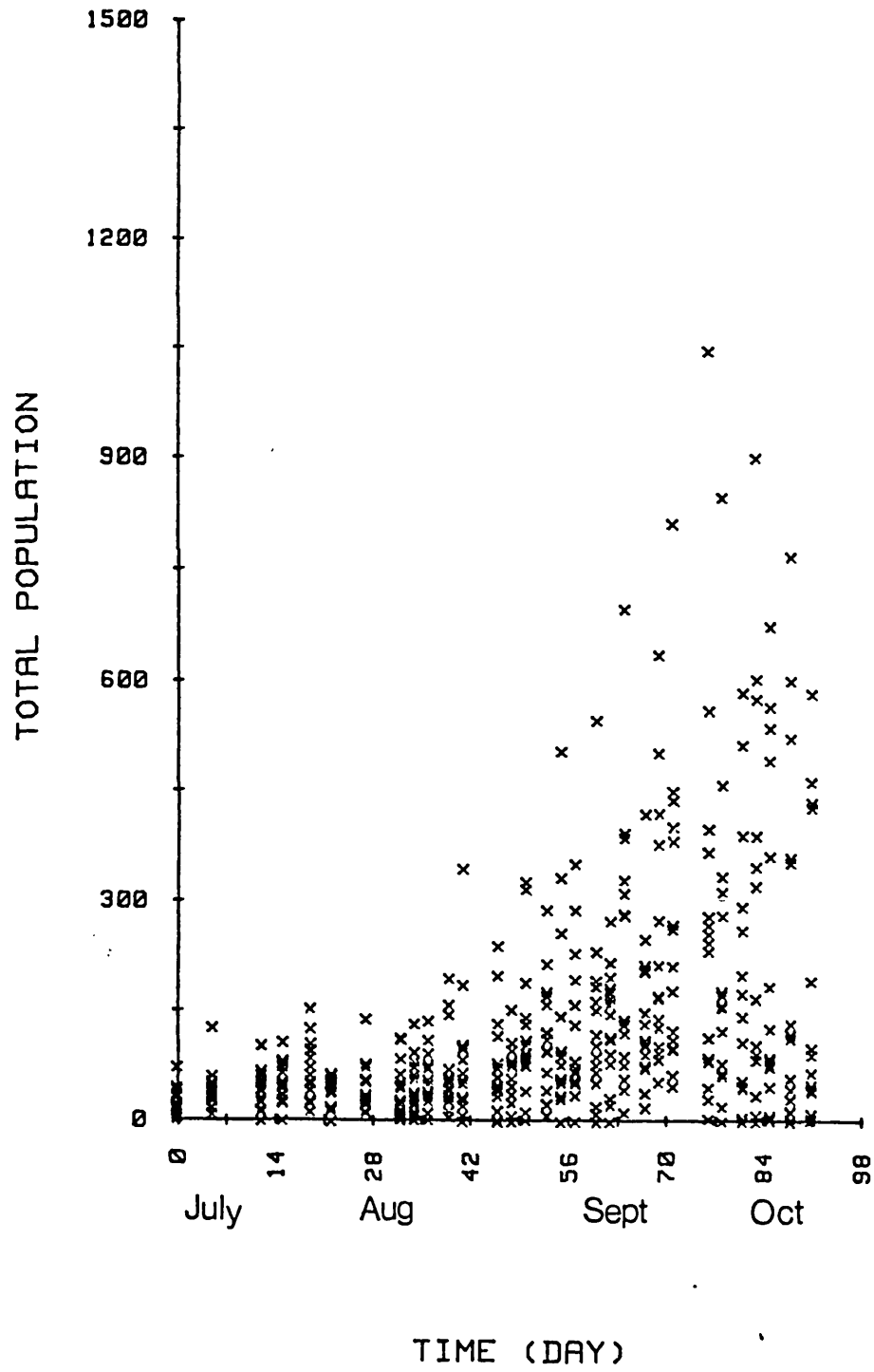


Figure 2.4

Total population size of cabbage aphids found on whole Brussels sprout plants examined from 21 July to 22 September, 1982, Silwood Park, Berkshire, England.

1982

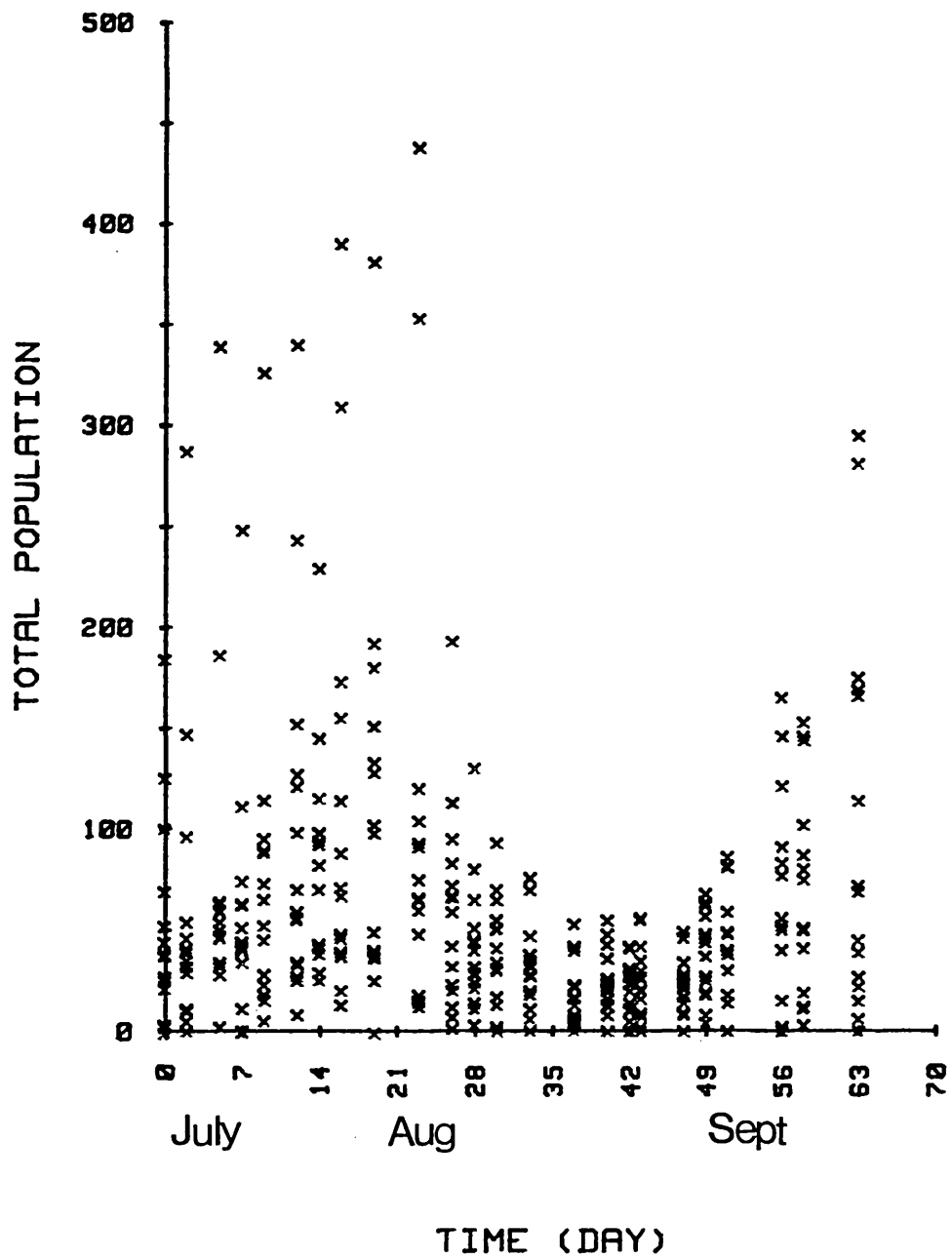
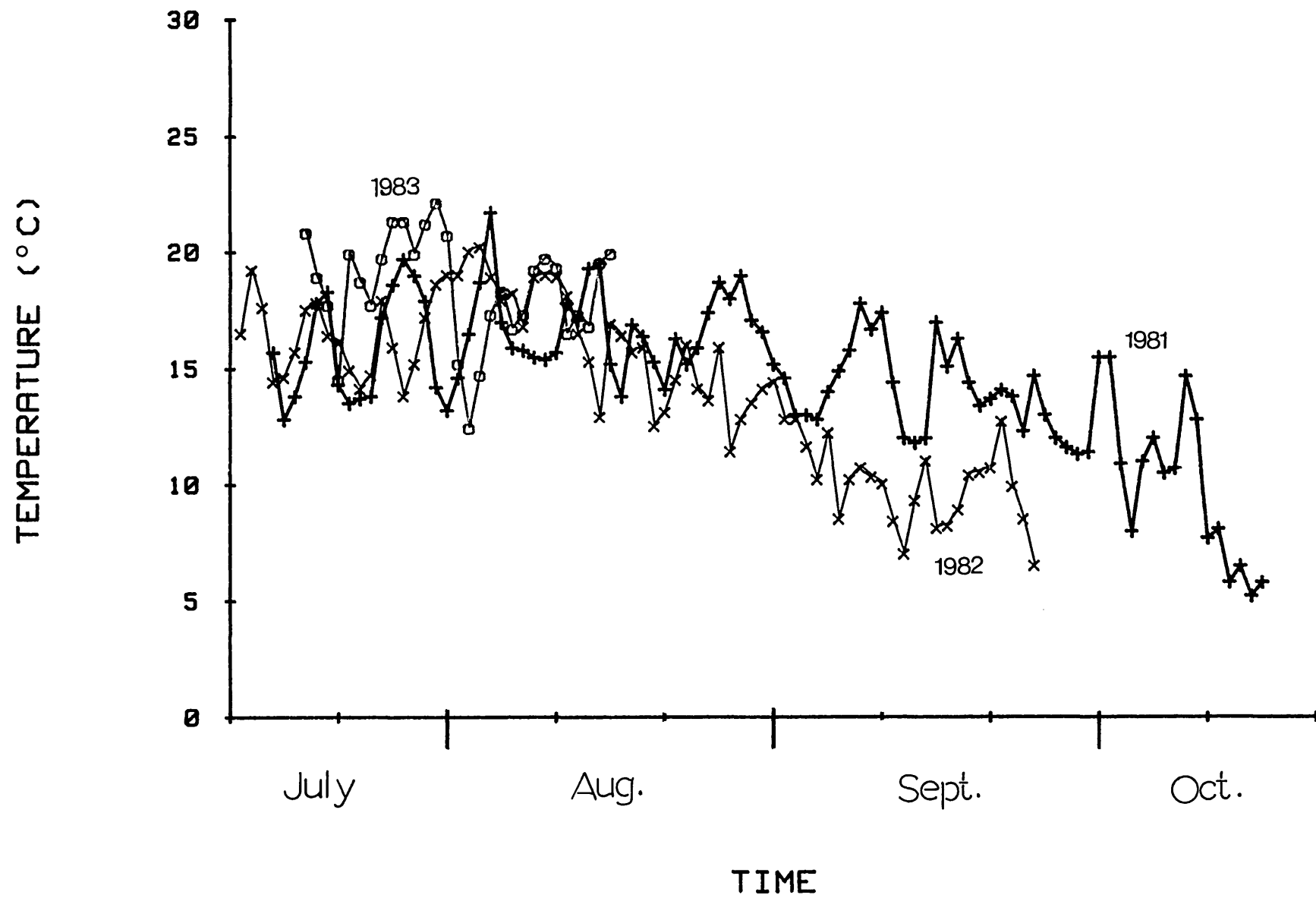


Figure 2.5

Daily average temperatures in Silwood Park, Berkshire, during the experimental periods in 1981 (black, +), 1982 (red, x) and 1983 (green, o).



2.3.2 Stage distributions in B. brassicae populations

The average stage distributions of B. brassicae populations on Brussels sprouts plants in Experiment I and II are shown in Fig. 2.6 and 2.7, respectively. By comparing these figures some interesting points emerge. Although the temperature in the two experiments were different, the patterns of fluctuation of the stages is similar. This implies that the stage distributions in the aphid populations are largely independent of temperature. That is, at different temperatures the mean chronological age of the aphid populations could be varied, but the mean physiological age (developmental stage or instar) remains approximately the same. The average temperature of Expt. II, carried out in field cages, was $18.5 \pm 2.3^{\circ}\text{C}$. During day time the maximum temperature reached 30.5°C , at night the minimum temperature 8°C .

The method of Hughes (1962) comparing the frequencies of the observed first three instar nymphs with the calculated distribution assuming that the frequencies should be in geometric progression can be used to test whether the populations in Expt. I and II are approaching or already achieved a SSD. A χ^2 test was applied to test the significance of the observed stage-distributions of the aphid populations, and figures 2.8A shows the values for 35 stage-distributions (instar 1 - 3) in Expt. I, 25 of which gave values of χ^2 low enough ($p > 0.05$) for the hypothesis of geometric progression of frequencies to be assumed valid. Figure 2.8B shows the 19 of the 32 stage-distributions from Expt. II that were assumed valid ($p > 0.05$).

Carter, Aikman, and Dixon (1978) have argued that if a set of samples are drawn from populations each with a geometric relation between the numbers in the first three instars, then the accumulated χ^2 value, summed

Figure 2.6

The stage distributions over time of B. brassicae populations on Brussels sprouts under C.T. conditions. (a) first instar, (b) second instar, (c) third instar, (d) fourth instar, (e) adult, and (f) average population growth curve during the experiment.

The symbols "x", "v" and "o" represent the data points obtained during the experimental period from the first ten days, the final seven days, and the days between, respectively.

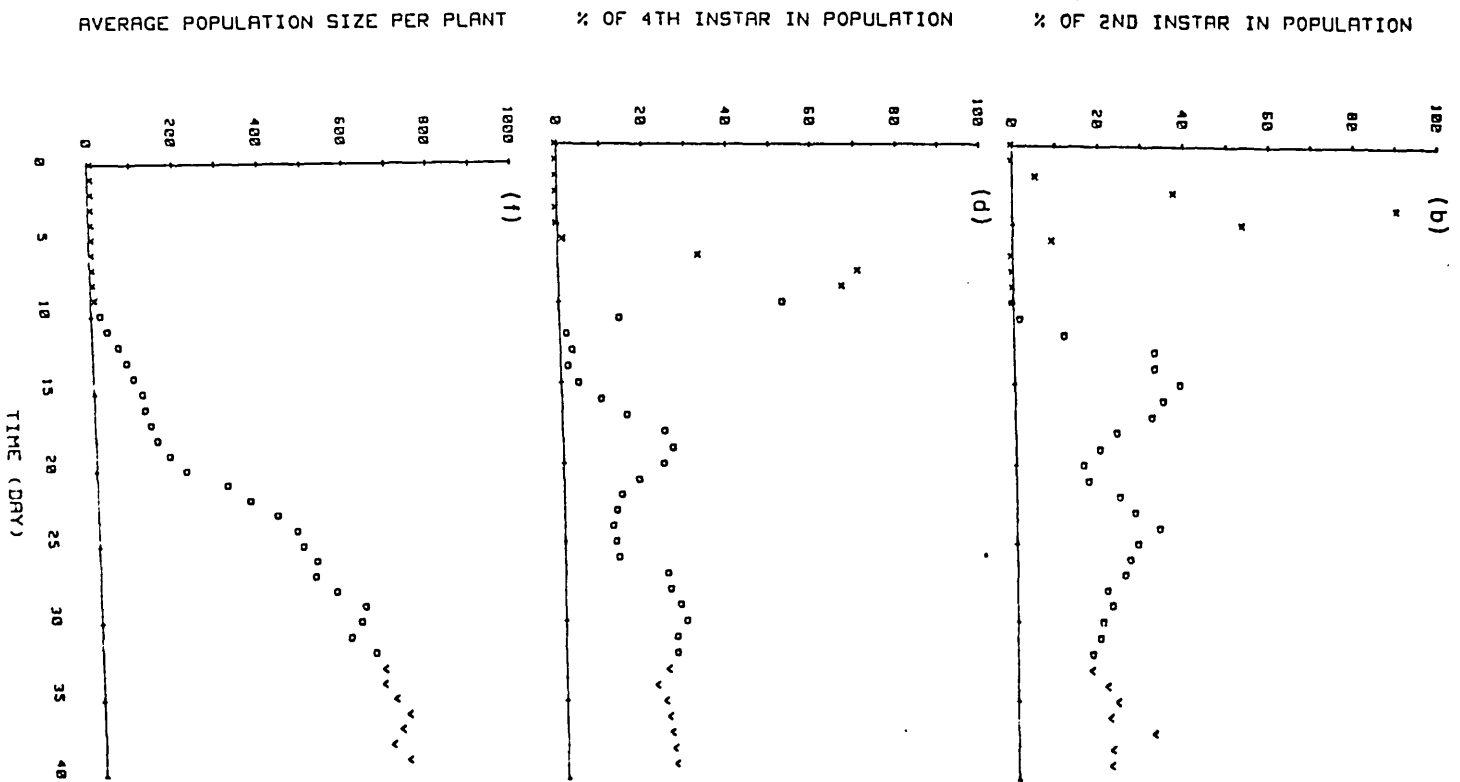
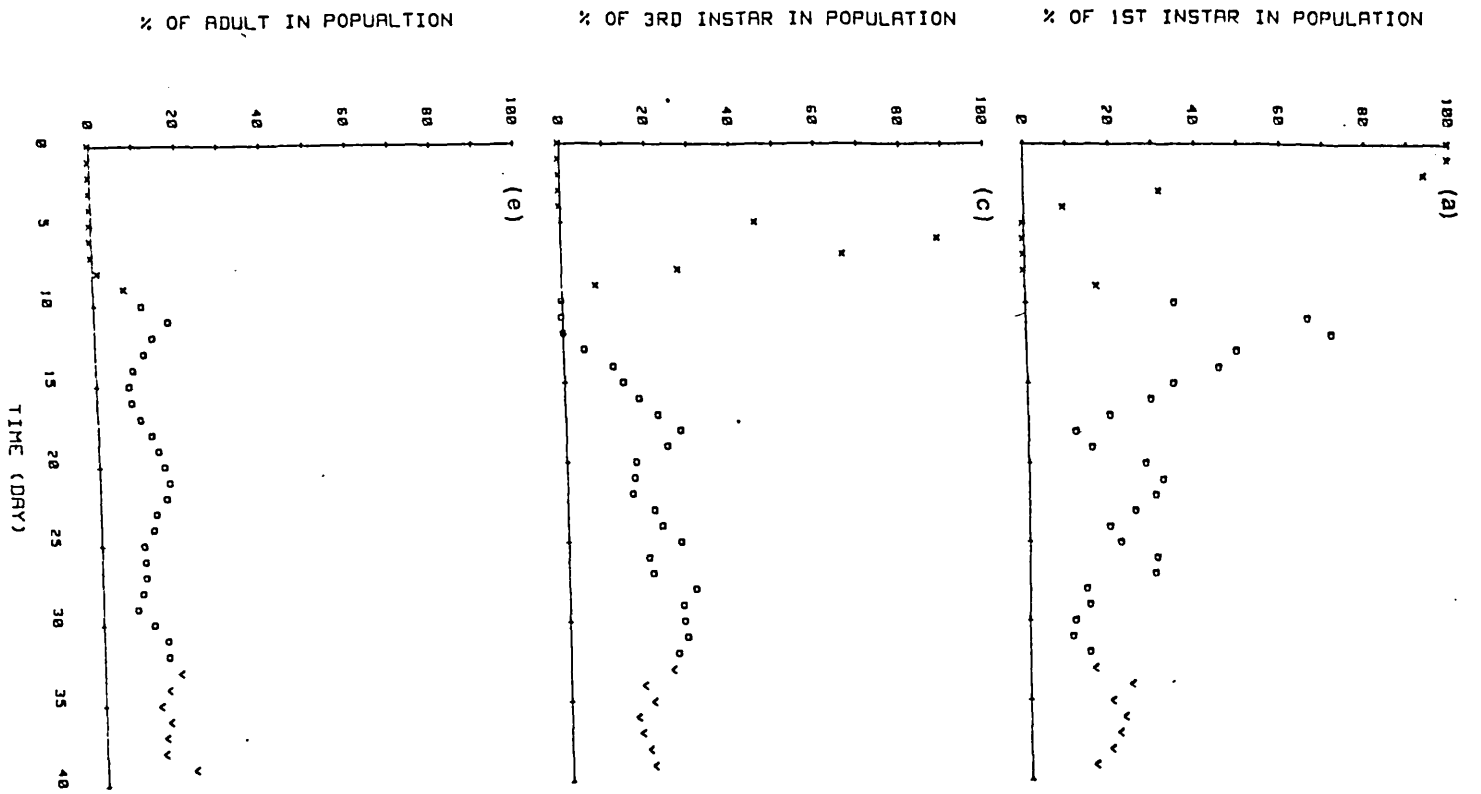


Figure 2.7

As figure 2.6, but now the stage distributions over time of B. brassicae populations on Brussels sprouts are obtained from field cages.

The symbols are the same as in Figure 2.6.

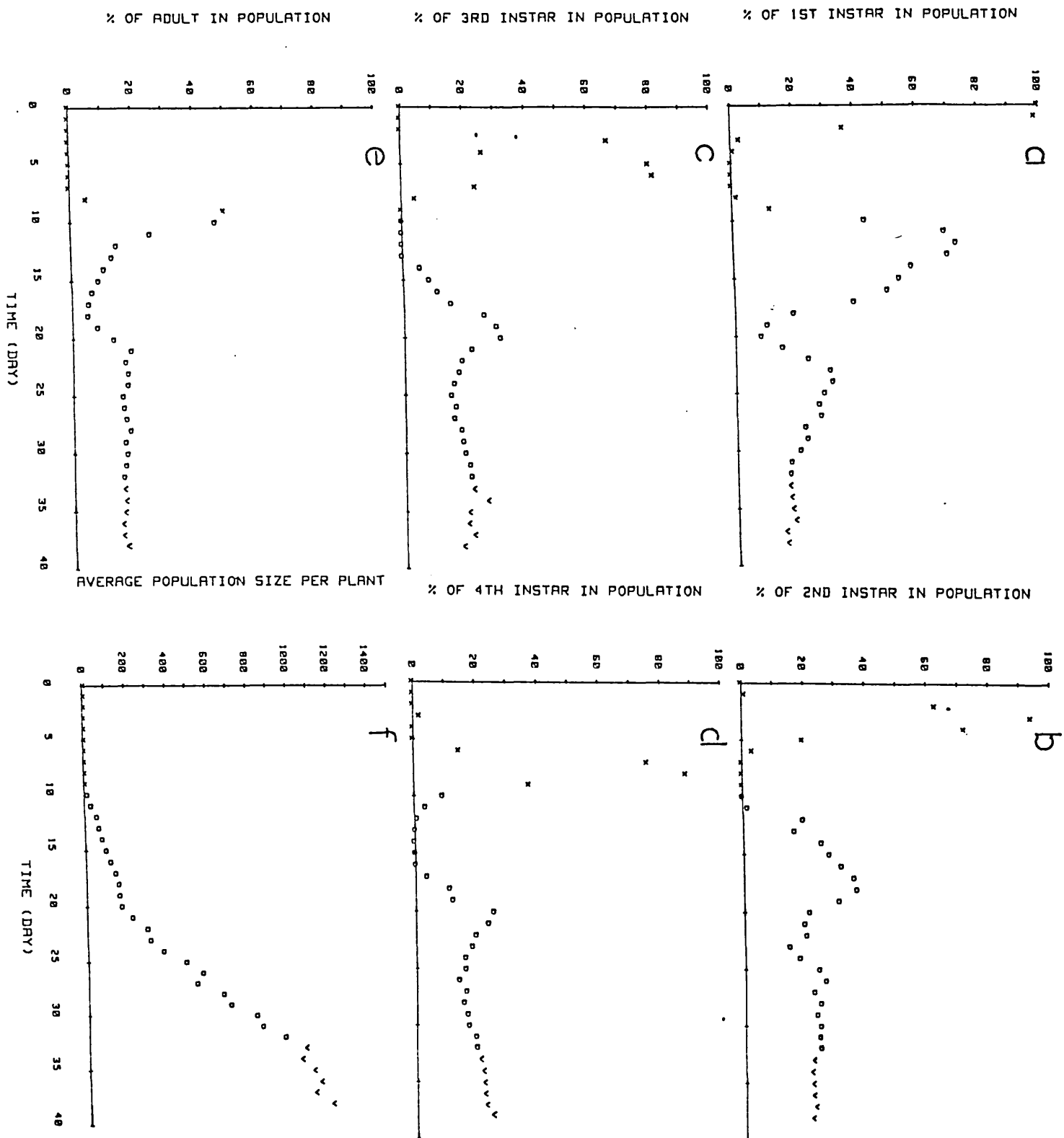
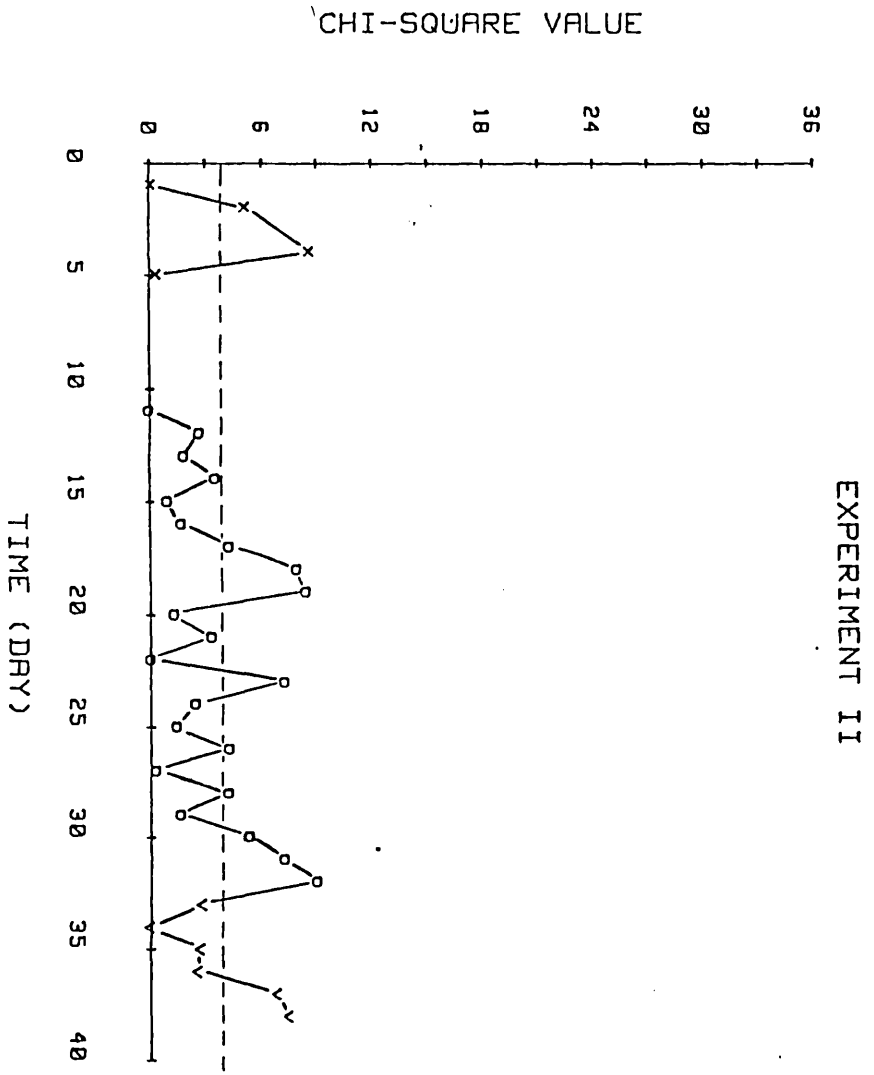
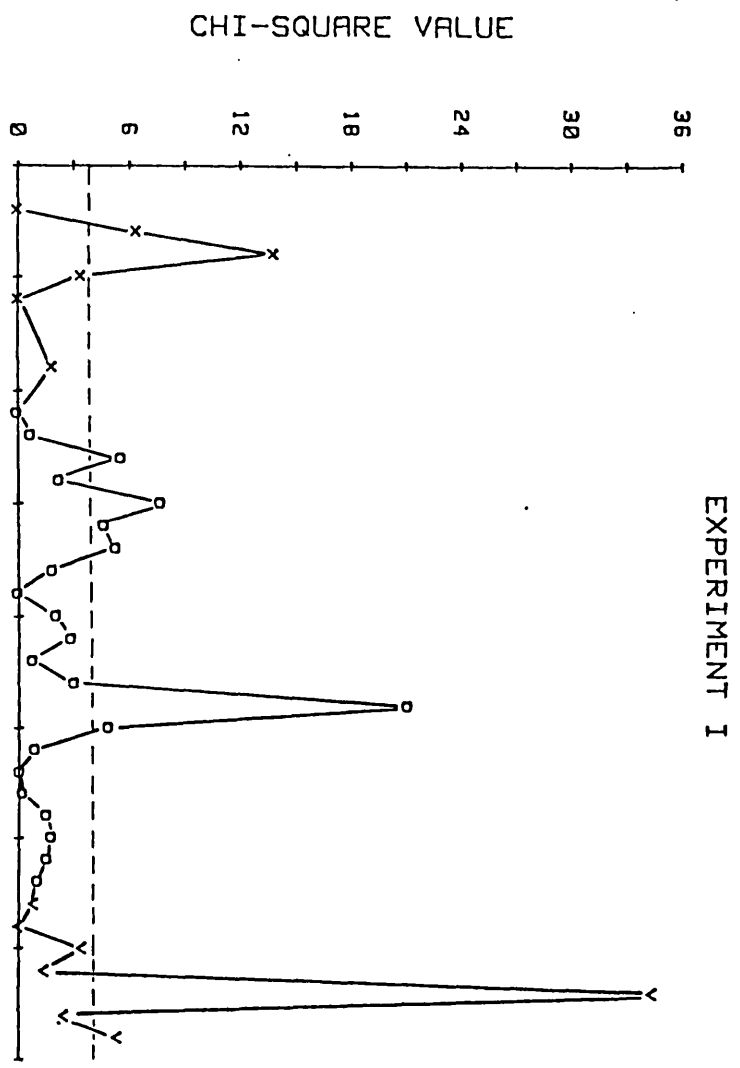


Figure 2.8

χ^2 values obtained from Expt. I (C.T. room) and Expt. II (field cages).
 $p > 0.05$ when $\chi^2 > 3.84$.

The symbols are the same as in Figure 2.6.



over all the samples, should be acceptable. In this study the results from both experiments reject this assumption:

Experiment I, $\chi^2 = 144.24$ with 34 degree of freedom, $p < 0.01$;

Experiment II, $\chi^2 = 115.99$ with 31 degree of freedom, $p < 0.01$.

Thus, as a set, the data fail to confirm a geometric relation, although most of the individual sample values for χ^2 did not. It can therefore be concluded statistically that the stage distribution of the cabbage aphid populations in these two experiments were unstable based on the geometric relation assumption. Carter et al. (1978) suggest that a possibly more reliable estimate could be based on the numbers present in all instars rather than in the numbers in the first three instars only. However, when this is done, the aphid populations do not achieve a statistically acceptable SSD.

Stage distributions of B. brassicae field populations in 1981 and 1982 are shown in Fig. 2.9 and 2.10, respectively. The variability of the data from the field populations in 1981 and 1982 does not suggest that any significant trend exists.

2.3.3 Population density and stage distribution of B. brassicae populations

The percentages of the aphid populations in each stage versus population size for Expts. I, II, 1981, and 1982 are shown in Fig. 2.11, 2.12, 2.13, and 2.14, respectively. Comparison of the four figures shows one interesting feature: most of the data points are concentrated on the lower right hand side of the figures. This is made clearer when each figure can be divided into six sections by drawing two horizontal lines running through 40% and 10% (for 1st and 2nd instars), 30% and 10% (for 3rd and 4th instars), 20% and 10% (for adult stages) on the Y-axis, and one vertical line running through an arbitrarily chosen

Figure 2.9

The stage distributions of B. brassicae field populations on Brussels sprouts in 1981, (a) first instar, (b) second instar, (c) third instar, (d) fourth instar and (e) adult stage.

Proportion of instar in B. brassicae population

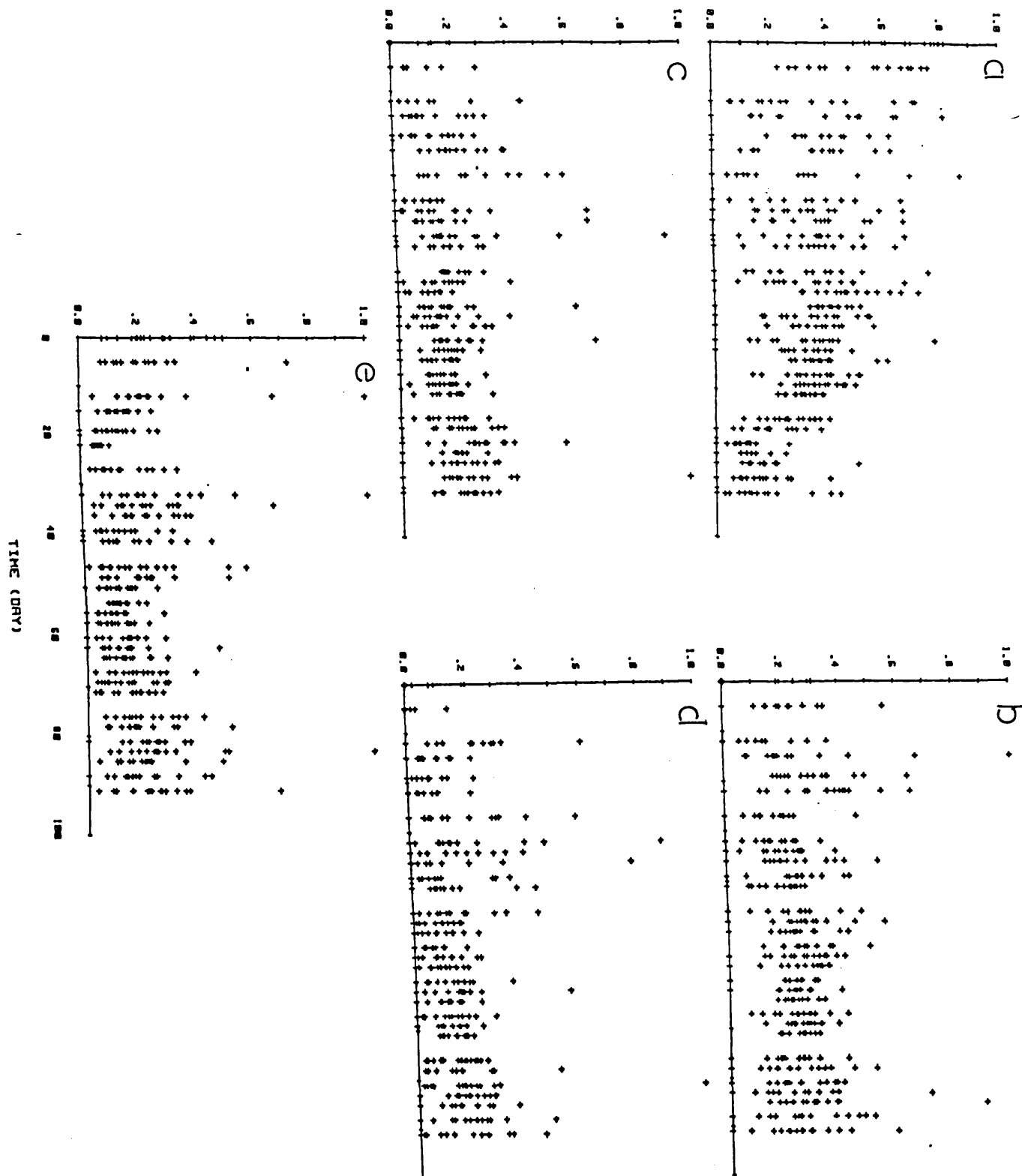


Figure 2.10

As Figure 2.9, but for stage distributions of B. brassicae field populations on Brussels sprouts obtained in 1982.

Proportion of instar in B. brassicae population

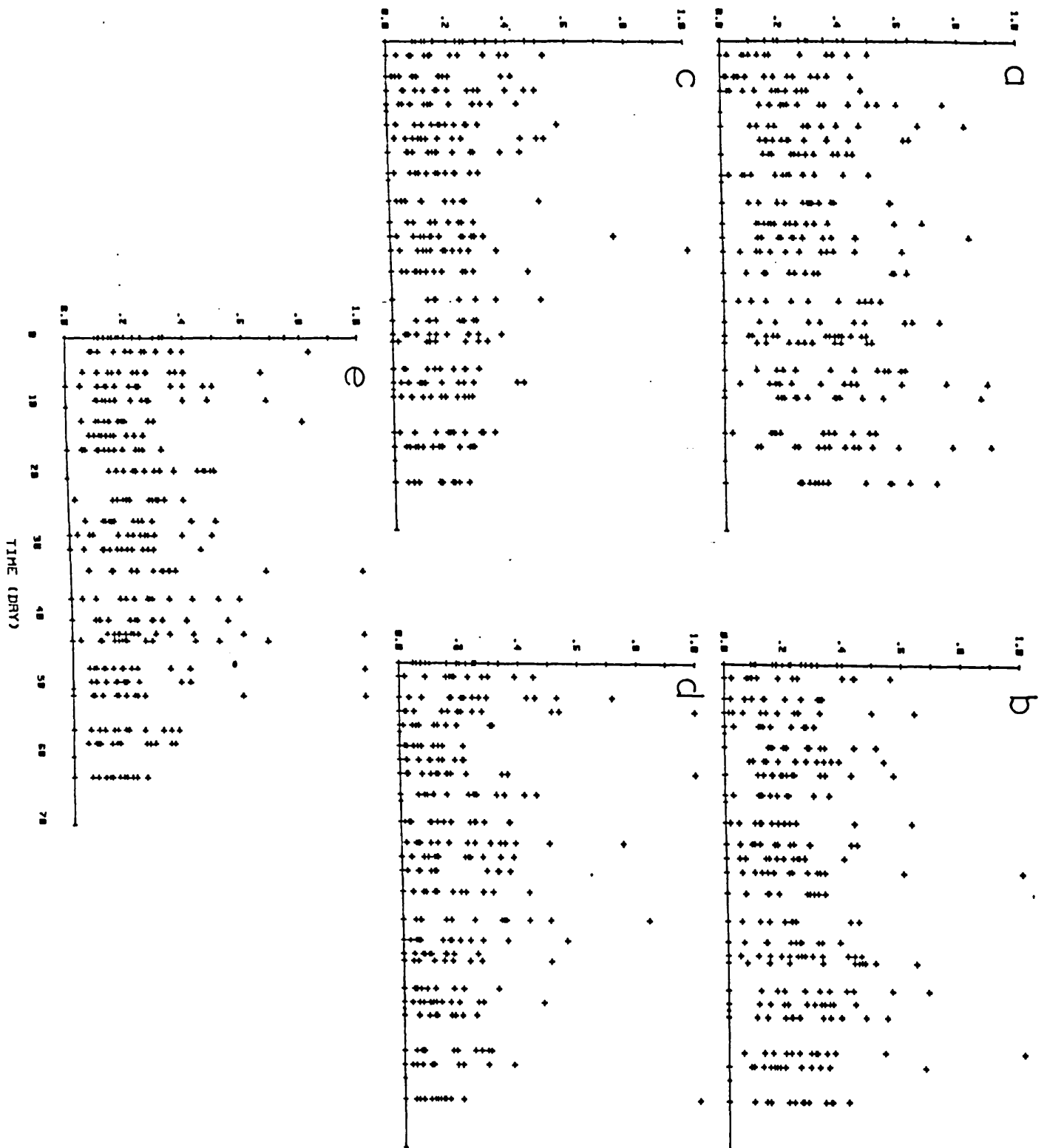


Figure 2.11

Stage distributions of the aphid populations (lumped total data) on Brussels sprouts plants in C.T. room, for first, second, third, fourth and adult stages plotted with respect to the population size in log scale.

The symbols "v", "*" and "o" represent the data points obtained during the experimental period from the first ten days, the final seven days, and the days between.

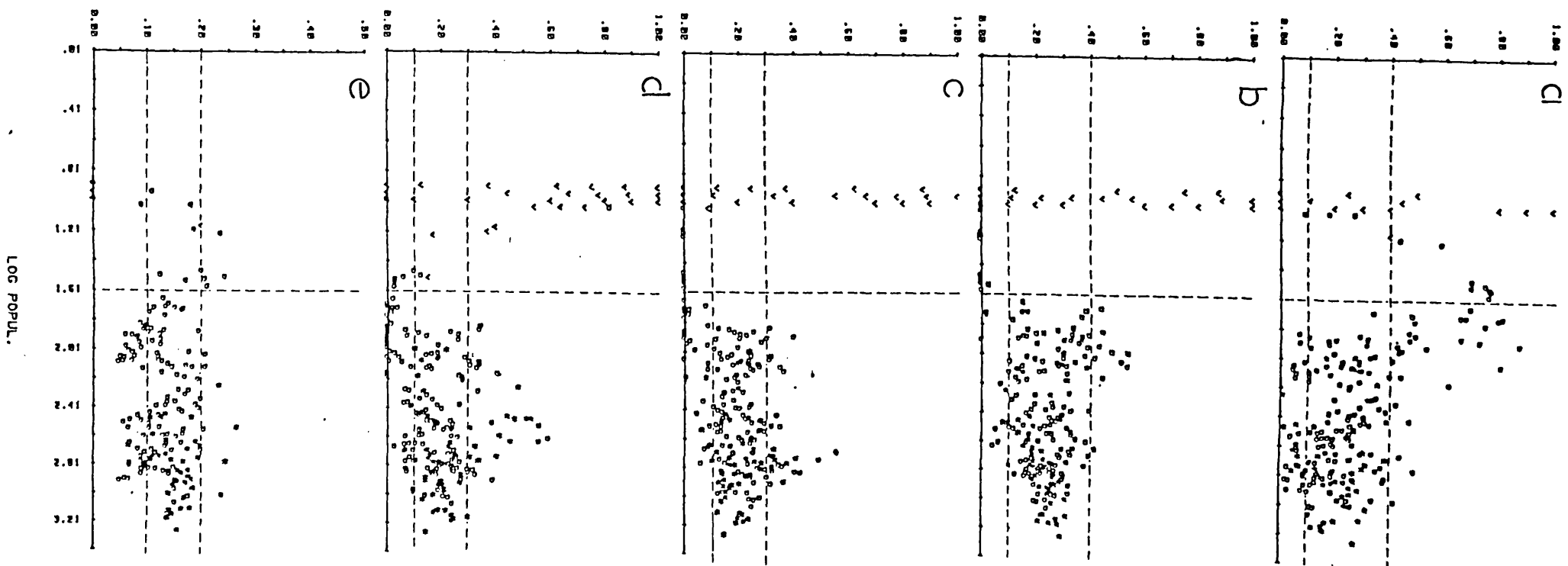
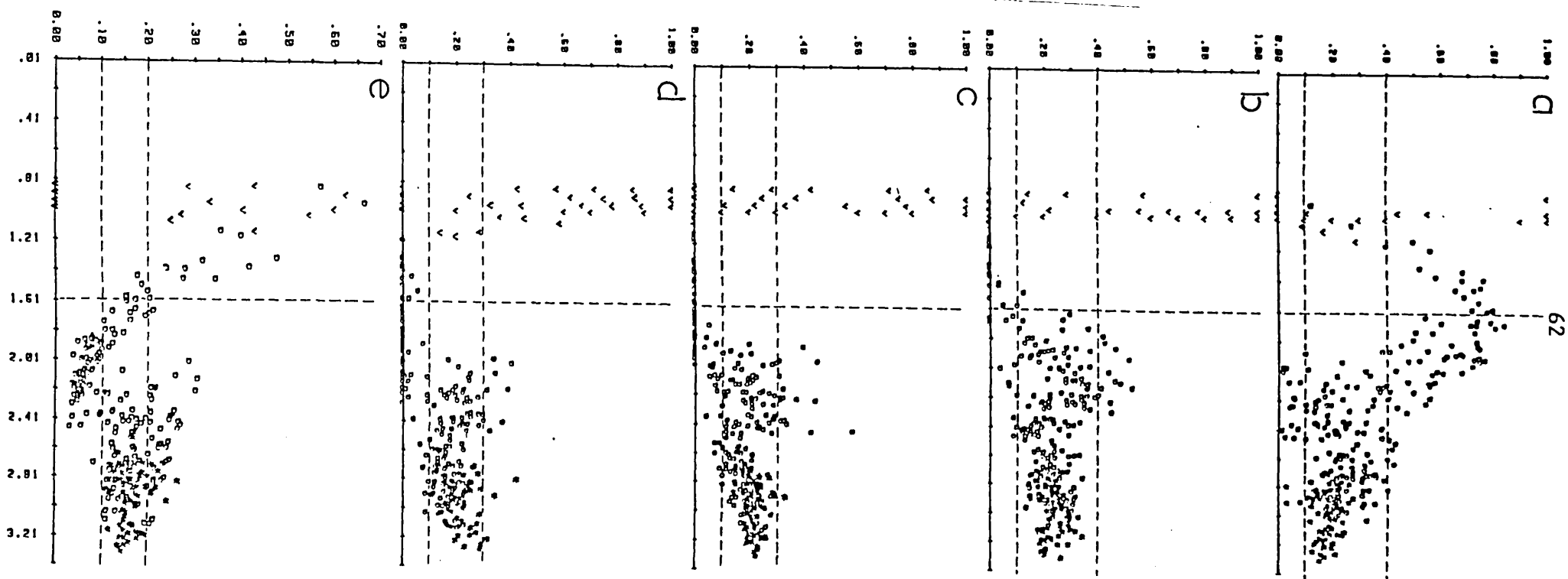
Proportion of instar in B. brassicae population

Figure 2.12

As Figure 2.11, but for the stage distribution over population size of B. brassicae on Brussels sprouts obtained from field cages.

The symbols are the same as in Figure 2.11.

Proportion of instar in B. brassicae population



LOG POPUL.

Figure 2.13

As Figure 2.11, but for the stage distribution over population size of B. brassicae on Brussels sprouts plant obtained from the field in Silwood Park from July to October 1981.

The symbols are the same as in Figure 2.11.

Proportion of instar in B. brassicae population

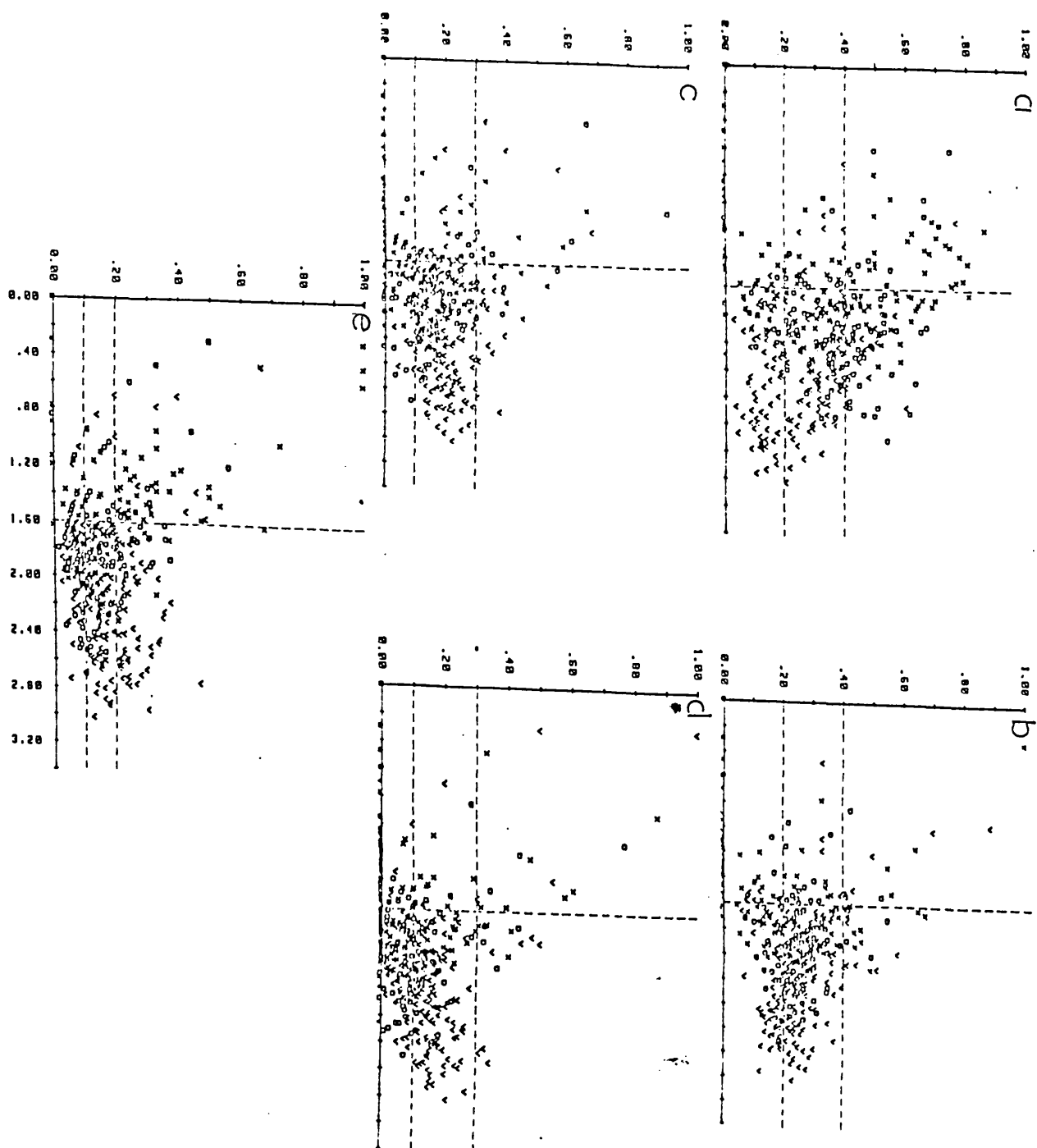
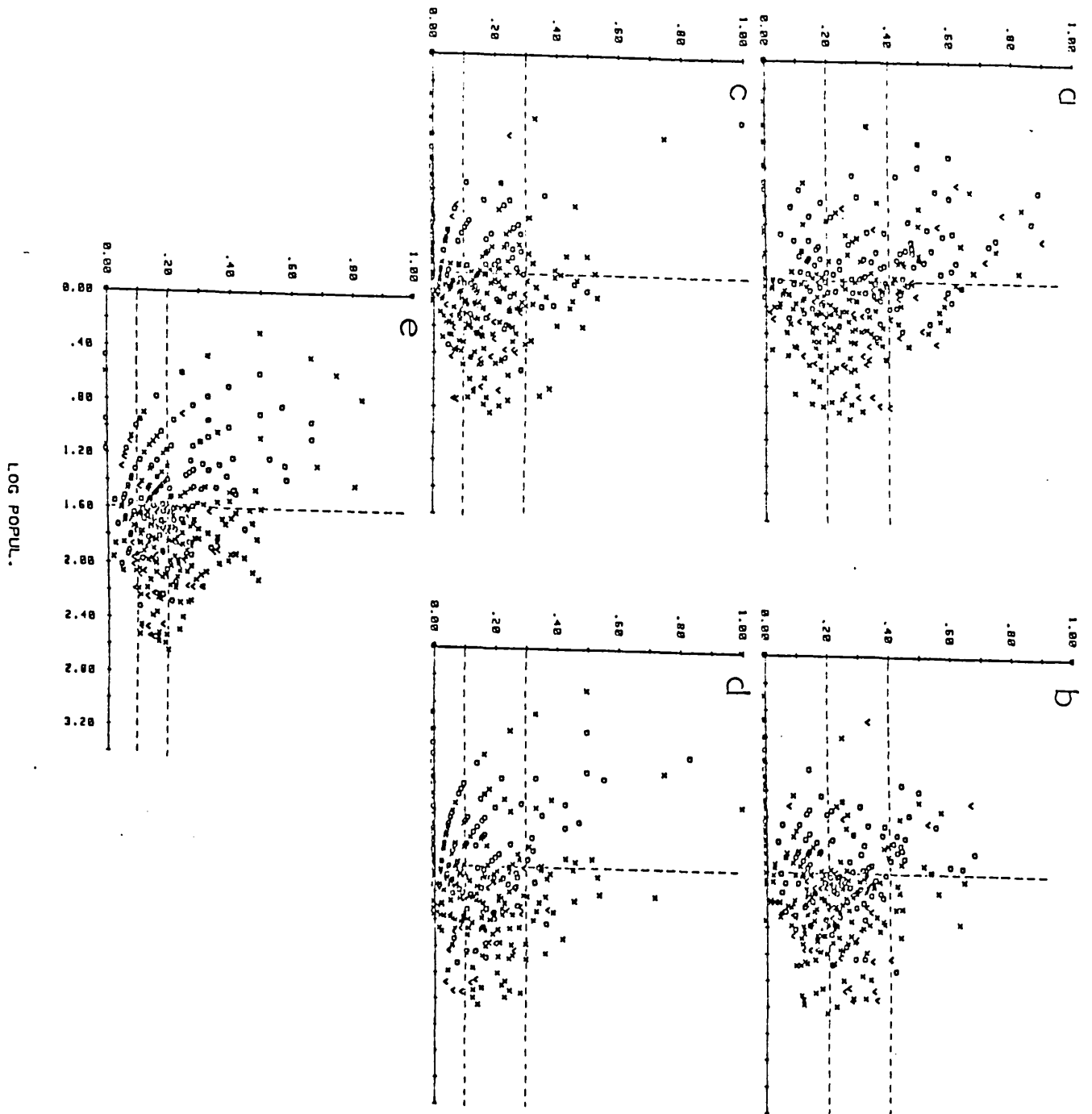


Figure 2.14

As Figure 2.13, but for the stage distribution over population size of B. brassicae on Brussels sprouts plant obtained from the field in Silwood Park from July to September 1982.

The symbols are the same as in Figure 2.11.

Proportion of instar in B. brassicae population



value of 1.6 on the X-axis. Most of the data points now appear to be concentrated in the middle right hand section. A similar trend is shown for Expts. I, II, 1981, and 1982. The percentage of the data points in the section for each Expt. is shown in Table 2.2.

In Expt. I the percentages of the data points located in the section are generally higher than the other experiments, as the variation of the population density in Expt. I is lower and more steady than the others. Although the percentages of 1st and 2nd instar stages in the section are higher than the 3rd, 4th instar, and adult stages, it does not imply the degree of concentration of the data points is higher. On the contrary the degree of concentration in 1st and 2nd instar is lower than the other stages.

However, there is a strong suggestion of a relationship between the aphid population density and stage distribution. The relationship can be explained quantitatively: When the population density of the aphid increases higher than 40 aphids per plant, its stage distribution will tend to fall within the boundaries of 10% and 40% for 1st and 2nd instars, 10% to 30% for 3rd and 4th instars, and 10% to 20% for the adult stage. Thus, it is reasonable to conclude that the aphid populations are tending to approach a steady state, but the convergent process is very sensitive to population density.

2.4 Conclusions

During July and August when temperature was at its most suitable for aphid population growth there was no subsequent increase in the population level. When the physiological rates of the aphids were reduced, as a result of decreasing temperatures, in September, the

Table 2.2

The percentage of the data points of Figures 2.11, 2.12, 2.13, 2.14 located in middle right section. Data in bracket are the proportion of the points in the section.

Stage Expt.	1st	2nd	3rd	4th	adult
I	60.36% (¹⁶⁹ /280)	62.14% (¹⁷⁴ /280)	57.5% (¹⁶¹ /280)	43.21% (¹²¹ /280)	46.43% (¹³⁰ /280)
II	50.26% (¹⁹⁶ /390)	62.05% (²⁴² /390)	53.33% (²⁰⁸ /390)	47.95% (¹⁸⁷ /390)	40.26% (¹⁵⁷ /390)
1981	48.60% (²²⁶ /465)	68.81% (³²⁰ /465)	54.62% (²⁵⁴ /465)	40% (¹⁸⁶ /465)	34.62% (¹⁶¹ /465)
1982	40.83% (¹⁴⁷ /360)	46.11% (¹⁶⁶ /360)	34.44% (¹²⁴ /360)	30.56% (¹¹⁰ /360)	26.11% (⁹⁴ /360)

population size showed an increase. This suggests that temperature and other climatic factors are unlikely to be major factors influencing the role of aphid population growth during the summer, other factors having a strong suppressing role. The results of the laboratory experiments can, as a result, be used to explain the growth pattern observed in the field.

The intrinsic rate of increase is defined as the actual rate of increase of a population with stable age-distribution (Andrewartha and Birch, 1954; Lotka, 1922). Since the SSD has not been statistically confirmed in the current study, and as the distribution of stages varies with time, it is unlikely that the intrinsic rate of increase can be accurately calculated. The use of an alternative realistic parameter, such as age-specific fecundity, rather than the theoretical intrinsic rate of increase is therefore necessary in the construction of a population model.

The aphid population density in this study has been found to play an important role in the stage distribution of the aphid population, the distribution of stages tending to approach a steady state when the density exceeds 40 aphids per plant. It has been observed that the compact aggregations of B. brassicae are very significant (Hayamizu, 1982), improving the nutrition of the leaves they colonize and enhancing the growth and reproduction of the aphids up to a certain density level (Way and Cammell, 1970). When this level is approached, this aggregative behaviour may be the cause of intra-specific competition which decreases fecundity, increases mortality and results in the production of alate individuals. In this way intra-specific competition can regulate local population densities (Dixon and Wratten, 1971; Way and Banks, 1967;

Way, 1968; Way and Cammell, 1970).

In the light of these conclusions, it is suggested that population density is a crucial factor in the population dynamics of B. brassicae and is an important component of any population model constructed for the species. The degree of density dependence and its importance in B. brassicae populations is considered further in the following chapters.

Chapter Three

Intraspecific Competition I

3.1 Introduction

The negative feedback mechanisms that regulate the growth of many biological populations (i.e. density dependent processes) have long been recognized as being important controlling factors in the dynamics of natural populations. The majority of population models are developed in terms of birth and death rates, but for age-structured populations, development is a crucial process in the growth of a population. It is, therefore, essential to understand fully the precise effects of these processes on the quantity and quality of individuals within a population.

In this study, the cabbage aphid, Brevicoryne brassicae, is examined as an example of a species whose net population growth is frequently controlled by density dependent processes. By making a detailed investigation of the way in which the properties of individuals determine the dynamics of an age-structured population, a model can be developed for the population as a whole. First, a simple situation is considered where the total aphid population is considered irrespective of age structure. The effect of density on the primary demographic parameters of the population (i.e. survival, fecundity and developmental rates) is determined using laboratory populations. Using these data a number of age-specific demographic functions have been developed to describe these rates and how they are influenced by changes in the population density.

The chapter has three main aims:

- (1) to detect the severity of density dependence,
- (2) to consider how these age dependent effects influence the demographic processes of the population, and
- (3) to show how these processes are fundamentally related to population density and age.

3.2 Density Dependent Processes in Brevicoryne brassicae

The following experiments were conducted in order to determine the effect of density on reproduction, survival, and development in age-homogeneous populations of B. brassicae. Highly fecund, parthenogenetic, virginoparous apterae of B. brassicae (10-12 days old) were collected from the standard stock cultures. Varying numbers of adults (3, 5, 10, 20, 40 and 80) were placed on Brussels sprouts plants which had been kept for at least two days at 25°C (C.T. room conditions as described earlier) and covered by leaf cages (15cm high and 3.0cm diameter). The leaf cages were similar to those described by Murdie (1965), consisting of two clear perspex rings supported by a spring clip and lined with foam rubber to ensure a complete seal. Each ring was fitted with a muslin covered cap. After 24 hours, the leaf cages and adults were removed and the progeny reduced to 1, 5, 10, 50, 100 and 200 per plant. Each plant was then placed in the polythene cylindrical insect cages described previously, each density being replicated between four and ten times.

Throughout the experimental period changes in the aphid populations were recorded daily. Such observations enabled time of moulting, number of nymphs produced, and the time of death to be recorded on a cohort basis. Any numbers produced were removed to ensure that the age-structure of the aphid populations remained reasonably homogeneous. The number of alate produced were too low to obtain reliable data, and consequently have not been included in the analysis.

An extensive review of the graphical methods used to detect the presence and effect of density dependence has been made by Bellows (1981). Plotting the number surviving, S_t , against the initial population

density, $\underline{N}$, provides the simplest method, any deviation from a straight line through the origin with slope of unity indicating density dependence. If proportionate survival, S/N , is plotted against the initial density $\underline{N}$ any deviation from a line with zero slope will point towards density dependence. A positive deviation from a line with zero slope when k -values ($= -\log_{10}(S/N)$, Varley and Gradwell, 1960) are plotted against the logarithm of the whole population density also indicates density dependence. The statistical problems of detecting density dependence have been considered by many authors (e.g. Varley and Gradwell, 1963; Eberhardt, 1970; Maelzer, 1970; St. Amant, 1970; Itô, 1972; Kuno, 1973; Royama, 1977, 1981a, 1981b).

Bellows (1981) also reviews several mathematical models describing density dependent effects and concludes that the model developed by Maynard Smith and Slatkin (1973) is of particular value in being flexible enough to apply to species with quite different density dependent responses. The general form of the model is

$$S = C \cdot N \cdot [1 + (a \cdot N)^b]^{-1} \quad (3.1)$$

where $\underline{a}$ denotes a scaling constant which determines the density at which proportionate mortality begins to increase rapidly, $\underline{b}$ is the severity of the density dependence, and $\underline{C}$ is the proportionate density-independent factor. This model has been used to investigate the presence and the degree of density dependence in the data collected from the aphid populations.

3.3 Some Models for Age-Specific Demographic Processes

3.3.1 Survival Models

Since Pearl and Miner's (1935) unsuccessful attempt to find a

mathematical model which describes survival curves for a variety of species, a number of such models have been constructed (e.g. Johnson, 1963; Burch, 1967; Siler, 1979; Hogg and Nordheim, 1983). However, these only deal for the most part with senescent mortality. Although the Weibull distribution has shown some attractive features (David, 1974; Pinder, Weiner, and Smith, 1978), its usefulness as a survivorship model is limited to situations where mortality rate is a monotonic function of age. When this is not the case, it is preferable to use a Gompertz-like distribution (Gompertz, 1825) or a mixture of distributions (Siler, 1979). Any such distributions, as long as non-negative, are possible candidates. However, only a few specific distributions, which preliminary analyses of the cabbage aphid's survivorship data has suggested could provide appropriate fits, have been considered in this section. The distributions to be discussed are all continuous (Table 3.1). The symbol t always has the dimensions of time (or age); the other symbols a , b , c , --- are used to denote adjustable parameters. The precise interpretation of these parameters differs for the various distributions. Some of the model's properties have been listed in Table 3.1 in which the survivorship function S , the survival probability density function f , and the age-specific mortality function H , are presented. The equivalence of these three functions is discussed in Appendix I.

Model 1, the power function,

$$S(t) = 100 \cdot \left(1 - \frac{t}{a}\right)^b \quad (3.2)$$

represents the probability, that given a maximum life span of a , an individual survives to age t . Figure 3.1(a) illustrates the variation

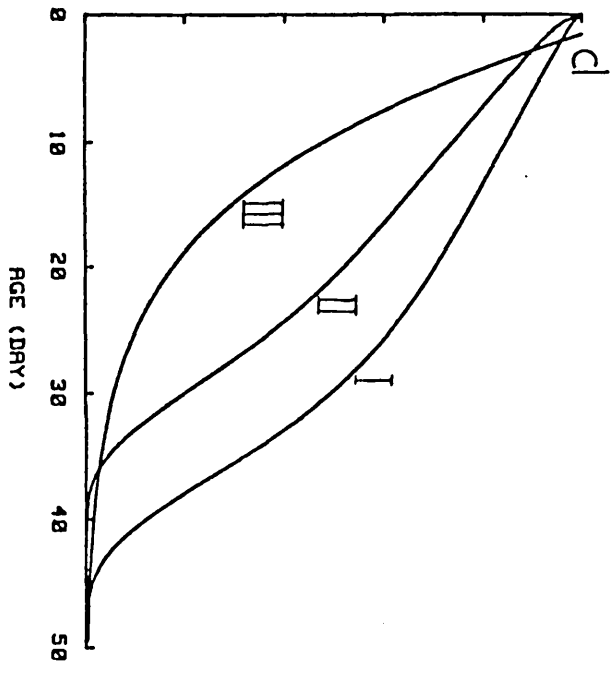
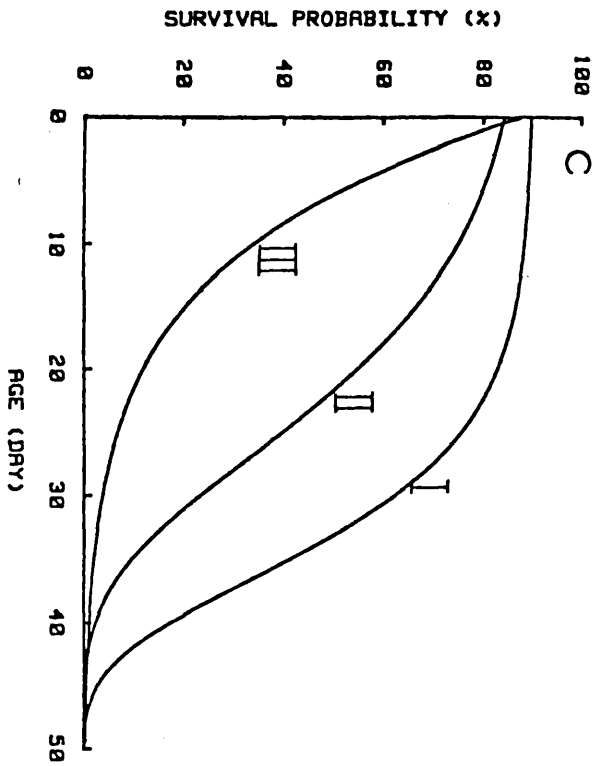
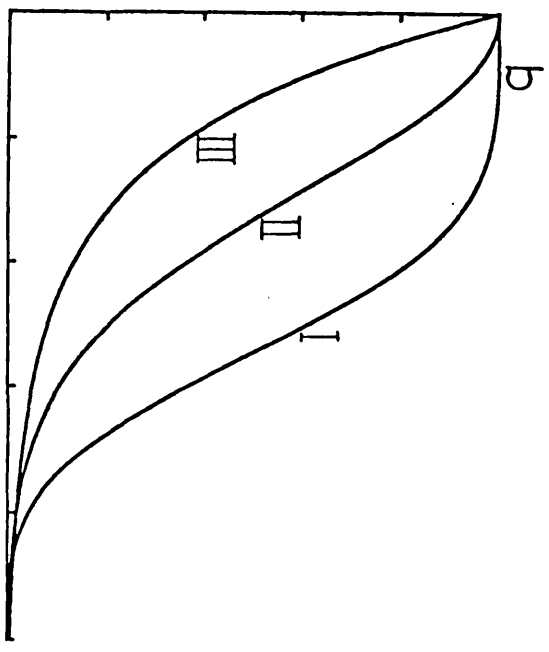
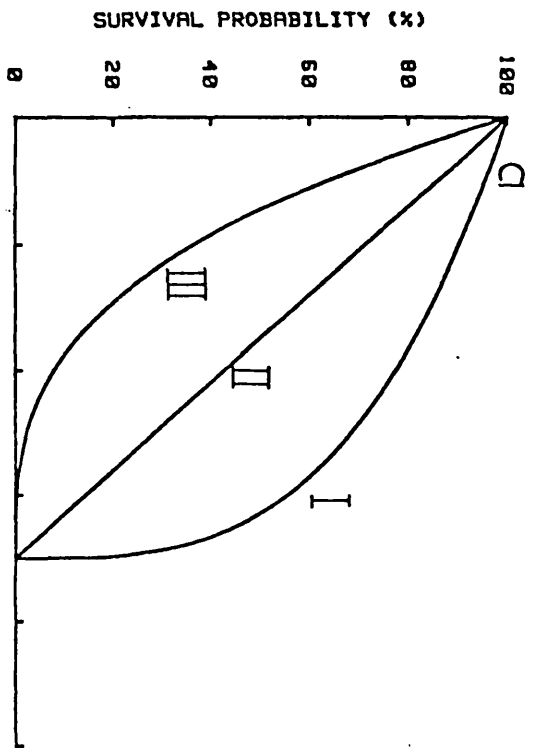
Table 3.1 The form of the four survival distributions of $S(t)$ discussed in the text, and the corresponding age-specific survival functions, $f(t)$, and age-specific mortality, $H(t)$. A more complete list of such distributions is given by Cox and Oakes (1984). The equivalence of the three functions is given in Appendix I.

Model	$S(t)$	$H(t)$	$f(t)$	No. of Parameters	Authors
1	$100 \cdot (1 - t/a)^b$	$b/(a - t)$	$100 \cdot (b/a) \cdot (1 - t/a)^{b-1}$	2	Zachmann & Logan (1984)
2	$100 \cdot \text{Exp}(-(t/a)^b)$	$(b/a) \cdot (t/a)^{b-1}$	$100 \cdot \text{Exp}(-(t/a)^b) \cdot (b/a) \cdot (t/a)^{b-1}$	2	Pinder, Wiener & Smith (1978)
3	$\text{Exp}(a) \cdot (-\text{Exp}(b - c \cdot t))$	$c \cdot \text{Exp}(a) \cdot (-\text{Exp}(b - c \cdot t))$	$\text{Exp}(a) \cdot (-\text{Exp}(b - c \cdot t)) \cdot c \cdot \text{Exp}(a) \cdot (-\text{Exp}(b - c \cdot t))$	3	Gompertz (1825)
4	$\text{Exp}((-a/b) \cdot (1 - \text{Exp}(-b \cdot t))) \cdot \text{Exp}(-c \cdot t) \cdot \text{Exp}((d/e) \cdot (1 - \text{Exp}(e \cdot t)))$	$a \cdot \text{Exp}(-b \cdot t) + c + d \cdot \text{Exp}(e \cdot t)$	$H(t) \cdot S(t)$	5	Siler (1979)

Figure 3.1

Examples of the survivorship models in Table 3.1

- (a) Model 1 (Eq. 3.2) : curve I, $a = 35$, $b = 0.3$; curve II,
 $a = 35$, $b = 1$; curve III, $a = 35$, $b = 30$.
- (b) Model 2 (Eq. 3.3) : curve I, $a = 30$, $b = 4$; curve II,
 $a = 20$, $b = 2$; curve III, $a = 10$, $b = 1$.
- (c) Model 3 (Eq. 3.4) : curve I, $a = 4.5$, $b = -5.5$, $c = -0.15$;
 curve II, $a = 4.5$, $b = -2.75$, $c = -0.01$; curve III,
 $a = 13.5$, $b = 2.2$, $c = -0.01$.
- (d) Model 4 (Eq. 3.6) : curve I, $a = 0.034$, $b = 3.0$, $c = 0.015$, $d = 0.0002$,
 $e = 0.18$; curve II, $a = 0.073$, $b = 2.3$, $c = 0.0258$, $d = 0.0004$,
 $e = 0.20$; curve III, $a = -0.5$, $b = 4.0$, $c = -0.04$, $d = 0.12$,
 $e = 0.01$.



of $\underline{S}$ with respect to the parameter $\underline{b}$. For curve III large values of $\underline{b}$ give a high initial mortality rate while small values of $\underline{b}$ give curve I in which most individuals survive near to age $t = a$. Finally, when $b = 1$ (curve II) there is a constant probability of survival, $f(t) = 1/a$, through the life span.

Model 2, the Weibull frequency distribution, is given by:

$$S(t) = 100 \cdot \text{Exp}(-(t/a)^b), \quad (3.3)$$

where $S(t)$ is the probability, at birth, of an individual surviving to age t , a is a scaling parameter, and b governs the shape of the curve. Figure 3.1 (b) shows three basic types of survivorship curves obtained from this model which have comparable patterns to those for model 1. The convenience of the Weibull distribution for empirical work stems from the simplicity of its three equivalent functions given in Table 3.1.

Model 3, a modified Gompertz distribution, can be written as:

$$S(t) = \text{Exp}(a) \cdot (-\text{Exp}(b - c \cdot X)), \quad (3.4)$$

where a is a scaling parameter, b determines whether the curve is concave or convex in the initial stage, and c determines the severity of the mortality. This somewhat older model (Gompertz, 1825), as for models 1 and 2, can show a fair degree of flexibility when fitted to different data sets (Fig. 3.1(c)).

Model 4, with five parameters, incorporates a mixture of distributions. It is well known that many empirically obtained survivorship curves decline initially, tend to level off, and then decline. Siler

(1979) suggests that these characteristics occur as a result of the risk faced by three different stage groups, i.e., juveniles, adults, and those that are senescent. Siler uses Gompertz's distribution to describe the age-specific mortality rates of the juvenile and senescent stages; and for the adults, the conventional constant mortality model. The total age-specific mortality model is written as

$$H(t) = a \cdot \text{Exp}(-b \cdot t) + c + d \cdot \text{Exp}(e \cdot t), \quad (3.5)$$

For simplicity, it is assumed that for each stage the risk arises as a result of intrastage competition and that there are no interactions between the three stages. By differentiating $H(t)$ with respect to time t , it is seen that the mortality will eventually increase monotonically. The survival model $S(t)$ is

$$S(t) = \text{Exp}((-a/b) \cdot (1 - \text{Exp}(-b \cdot t))) \cdot \text{Exp}(-c \cdot t) \cdot \text{Exp}((d/e) \cdot (1 - \text{Exp}(e \cdot t))) \quad (3.6)$$

where $\underline{a}$, $\underline{c}$, and $\underline{d}$ are the initial mortalities of juvenile, adult and senescent stages, respectively and $\underline{b}$ and $\underline{e}$ are the adjustment coefficients of the juvenile and senescent stages. This combined model, obtained by the simple addition of the three component mortalities, declines sharply during the initial and juvenile period, levels off during adulthood, and finally slopes downwards sharply during senescence. The three basic types of the survivorship curves are shown in Figure 3.1(d).

The flexibility and behaviour of these models of $S(t)$, established for each model and illustrated in Figure 3.1 by the three basic types of curve, cater for many of the commonly hypothesized survivorship curves (e.g. Pearl and Miner, 1935; Deevey, 1947; Slobodkin, 1962).

All the four models are used to describe the experimental data in the ensuing sections. In the next section the model provides the most flexible empirical fit, preferable with relative simple statistical analysis, will be chosen.

3.3.2 Fecundity Models

In studying population growth it is important to quantify the shape of the curve representing the number of offsprings produced as a function of time. Although there is a complex density dependent model for insect fecundity (Watt, 1960), a parametric distribution for describing age-specific fecundity is still lacking (Bellows, 1979). An attempt has been made here to find a simple and reliable model. Examination of a scatter diagram of the fecundity pattern of B. brassicae shows that the relationship increases sharply at first, passes a peak, then declines smoothly. Firstly, for simplicity, a normal (symmetric) distribution is considered where

$$F(t) = a'_F \cdot \text{Exp} (-b'_F \cdot (t - c'_F)^2) \quad (3.7)$$

a'_F being the maximum fecundity rate, b'_F , relates to the spread of the distribution curve, and c'_F to the time when the maximum fecundity rate occurs (Fig. 3.2(a)).

Secondly, when the data on fecundity rates are considered a positive skewed curve with age is obtained. The product of two modified power functions can thus be used, an increasing one:

$$Y_1 = u \cdot t_1^b,$$

and a decreasing one:

$$Y_2 = v \cdot t^{-c}$$

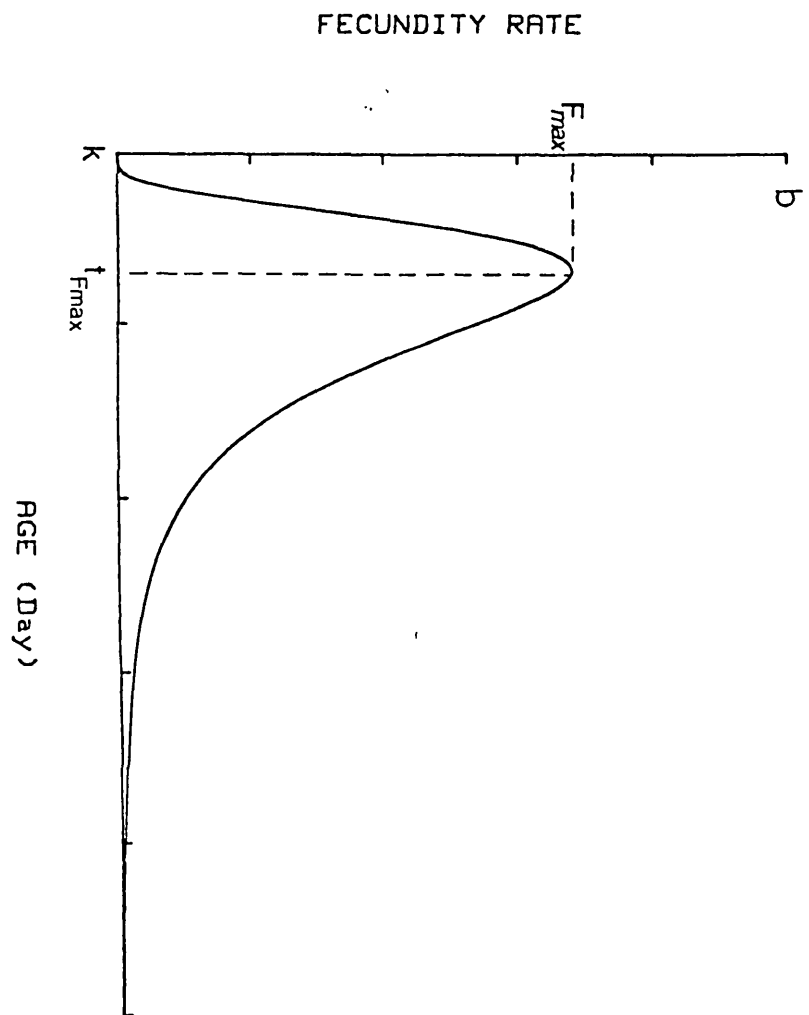
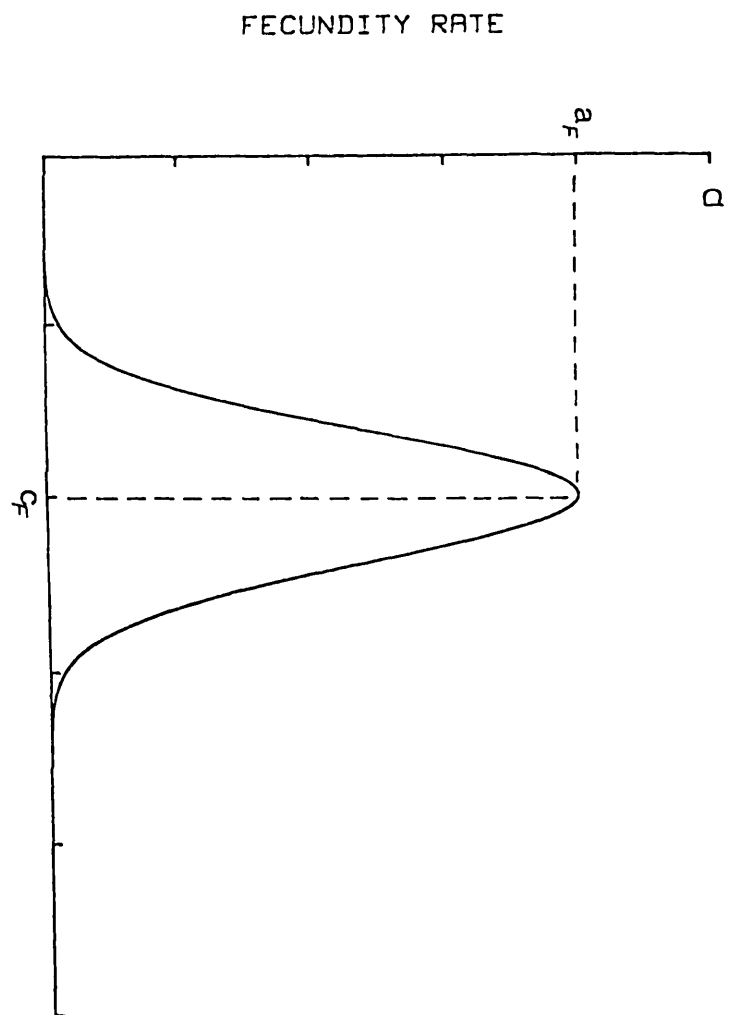
As the curve begins at age, k , the time at which the first offspring are

Figure 3.2

Two age-specific fecundity curves described by

- (a) a normal (symmetric) distribution, equation 3.7, and
- (b) a mixture of distributions, equation 3.8, where $\underline{k}$ is the age at which first reproduction occurs.

See text for discussion.



produced, it is necessary to transfer $\underline{t}_1$ to $\underline{t-k}$. For convenience, the two parameters, $\underline{u}$ and $\underline{v}$ are assumed to take the form $\underline{\text{Exp}}(\underline{a})$, making

$$F(t) = Y_1 \cdot Y_2 = \text{Exp}(a_F) \cdot (t-k)^{b_F} \cdot t^{-c_F}, \quad (3.8)$$

where $\underline{a}_F$, $\underline{b}_F$ and $\underline{c}_F$ are the three parameters of the function. Equation 3.8 gives a curve of the type shown in Fig. 3.2(b). The maximum fecundity rate can now be estimated as:

$$F_{\max} = \text{Exp}(a_F) \cdot k^{(b_F-c_F)} \cdot (c_F-b_F)^{(c_F-b_F)} \cdot b_F^{b_F/(c_F-b_F)}. \quad (3.8a)$$

The time when $F_{\max}$ is reached, $\underline{t}_{F\max}$, can be calculated from Eq. 3.8.

3.3.3 Developmental Models

The developmental period of an instar is variable, different individuals developing at different rates depending on factors such as temperature, food quality, moisture conditions, and population density. Such variable rates can, as a result, form a distribution through time of the way in which individuals from a single cohort complete a specific instar stage. These distributions of the developmental rate may be described by a set of functions suitable to fit the development curves of the insect's instars.

A number of distributions have been used to describe the development of insects, such as the gamma distributions (Howe, 1966), special Erlangian distributions (Ashford, Read and Vicker, 1970), a normal (symmetric) distribution (Manly, 1974), the beta distributions (Stinner, Butler, Bacheler and Tuttle, 1975), the time-varying distributed delays (Goudriaan, 1973), and a skewed normal distribution (Sharpe, Curry, DeMichele and Cole, 1977). These models are used to describe frequency distributions of development (Fig. 3.8). When a cohort is initiated from the same age, however, the probability of individuals remaining

in the first developmental stage decreases sharply but smoothly (Fig. 3.3a). For such a case, a modified Gompertz equation should fit most data:

$$P_1(t) = a_1 \text{Exp}(-b_1 \cdot \text{Exp}(c_1 \cdot t)) \quad (3.9)$$

where $P_1(t)$ is the probability of individuals remaining in the first developmental stage at time t . Although there are three parameters, a_1 , the initial percentage of the population in the first development stage, is the most powerful. Here b_1 is the scaling parameter, and c_1 governs the shape.

After a period of time the developmental curves of the aphid's successive stages became positively skewed (Fig. 3.8), and therefore, a skewed normal distribution (Sharpe *et al.*, 1977) has been chosen to describe the developmental rates of these stages (Fig. 3.3b). It is written as

$$P_i(t) = (a_i \cdot b_i \cdot \sqrt{2\pi})^{-1} \cdot \text{Exp}(-\frac{1}{2}((\frac{1}{t}c_i)/b_i)^2) \quad (3.10)$$

where $P_i(t)$ is the probability of individuals remaining in the stage i at time t , a_i is the scaling parameter, c_i is the mean developmental rate of stage i , and b_i is the standard deviation ($= \sigma$) of the developmental rate.

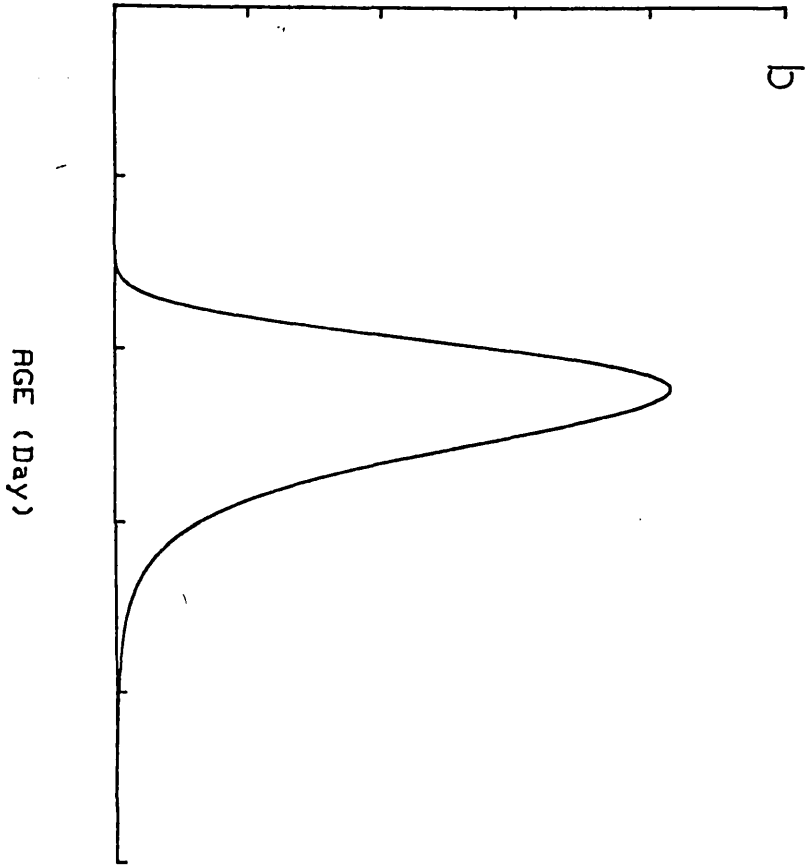
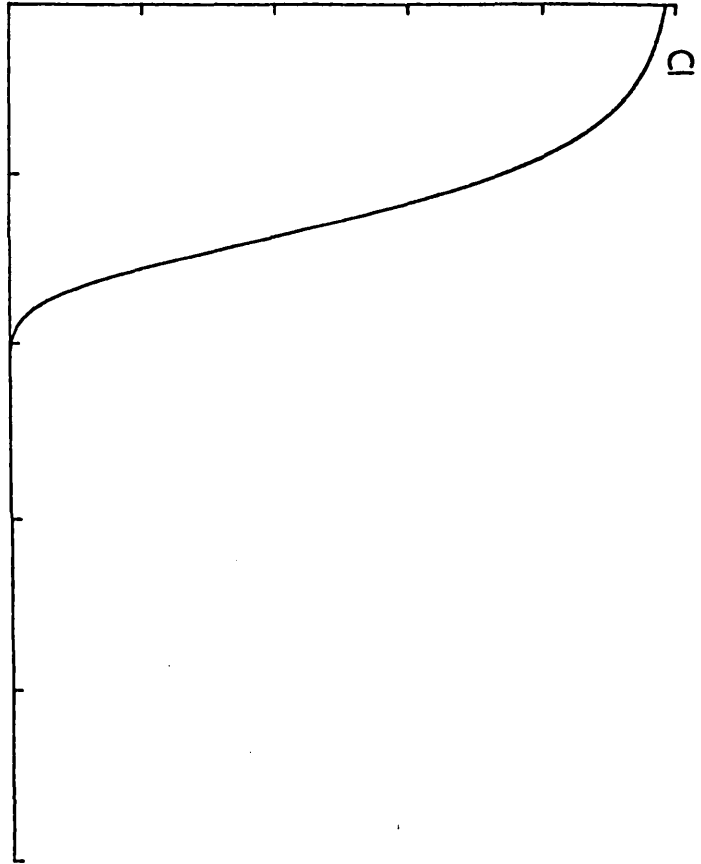
3.4 Validation of Models

In this study, validation is broadly defined as "the process of comparing the model's predictions with reality". The most straightforward and widely used method is a subjective comparison of model predictions with results obtained from experiments (e.g., Carter, 1978; Barlow and Dixon, 1980; Gutierrez, Baumgaertner, and Summers, 1984).

Figure 3.3

The developmental distributions of the initial stage (a) and the other successive stages (b). The distribution (a) shown arises from equation 3.9 where $a_1 = 100$, $b_1 = 0.001$, and $c_1 = 3$. The distribution (b) shown arises from equation 3.10 where $a_i = 0.08$, $b_i = 0.06$, and $c_i = 0.30$.

DEVELOPMENT PROBABILITY



A good test of models must include data that has not been used in the model's construction. The difficulty arises in obtaining a large volume of field data collected in both a statistically and biologically sound way. With statistical tests, such as the chi-squared test and the correlation coefficient method which compare sets of observed and predicted data representing a time series, it is impossible to assign significance levels (Barlow and Dixon, 1980).

The non-parametric Kolmogorov-Smirnov test (K-S test) (Lindgren, 1968; Sokal and Rohlf 1981) is used in this study to validate the model. It is applicable to continuous and discrete frequency distributions, and is more powerful than the conventional tests of goodness of fit, such as the chi-squared. The test is based on differences between an observed $\hat{F}$, and an expected, F , distribution, the largest difference, D , being found by computing the difference from the top of each step in the observed distribution. As this difference depends on the variable of distribution, x , the K-S statistic is taken to be the least upper bound of such differences:

$$D = \max | F(x) - \hat{F}(x) |.$$

The statistic D is essentially "two-sided", involving the absolute difference of $F(x)$ and $\hat{F}(x)$. The critical region $D > K(0.05, n) = 1.36/\sqrt{n}$ is used to test $F(x)$ against the alternative that the cumulative density function is not $F(x)$, where n is the number of data in F .

3.5 Results and Discussion

The primary objective of this section is to determine whether the population growth of the cabbage aphid is influenced by density dependent

factors, and also to see if this indicates contest or scramble competition (Nicholson, 1954; Varley, Gradwell and Hassell, 1973; Bellows, 1981). In addition, the influence of density of the age-specific demographic rates of the aphids is also considered.

3.5.1 Assessment of Density Dependence

The relationships between survival and initial population densities for the aphid have been plotted in Figure 3.4(a). The apparent deviation from a straight line through the origin obtained when equation 3.1 is fitted to the experimental data suggests that a density dependent dependent process does act on the aphid population. The same conclusion can be drawn from the inverse relationship in Figure 3.4(b) and the exponentially increasing curve in Figure 3.4(c). The goodness of fit of the curve was investigated using the nonparametric Kolmogorov-Smirnov test (Lindgren, 1968; Sokal and Rohlf, 1981). The test indicated that the proposed curve (Fig. 3.4(a)) did not differ significantly from the experimental data at the 5% level of significance ($D = 0.01606 < D(0.05, 36) = 0.2267$). The test, applicable to continuous and discrete distributions, is more powerful than the G- or chi-squared test for goodness of fit, and is especially advantageous with small sample sizes (Sokal and Rohlf, 1981). The overall survival rates (S/N) show no significant differences between densities 1, 5, 10, 50, and 100 ($P > 0.05$), while the rate at density 200 is significantly smaller than the others ($P < 0.05$) (Table 3.2 and Figure 3.4b).

3.5.2 Effects of Age and Density on Demographic Processes

(1) Survival

The graphical representation of the decline in survival - the survivorship curve, is the simplest description of a life budget.

Figure 3.4

The relationship between survival and density for B. brassicae.

(a) The number surviving, S against the initial population density N. The data have been described using equation 3.1 fitted by a non-linear least square procedure. The estimated values of parameters for the equation with 95% confidence interval are as follows:

$$a = 0.0050 \pm 0.0001, b = 3.0815 \pm 0.0868 \text{ and } c = 0.7606 \pm 0.1185.$$

(b) The data from (a) expressed as proportion surviving against density. The fitted line is obtained by transforming the predicted number of survivors to proportionate survival.

(c) The data from (a) expressed as k-value ($= \log (S/N)$) against density ($\log(N)$). The fitted line is obtained by transforming the predicted number of survivors to a k-value.

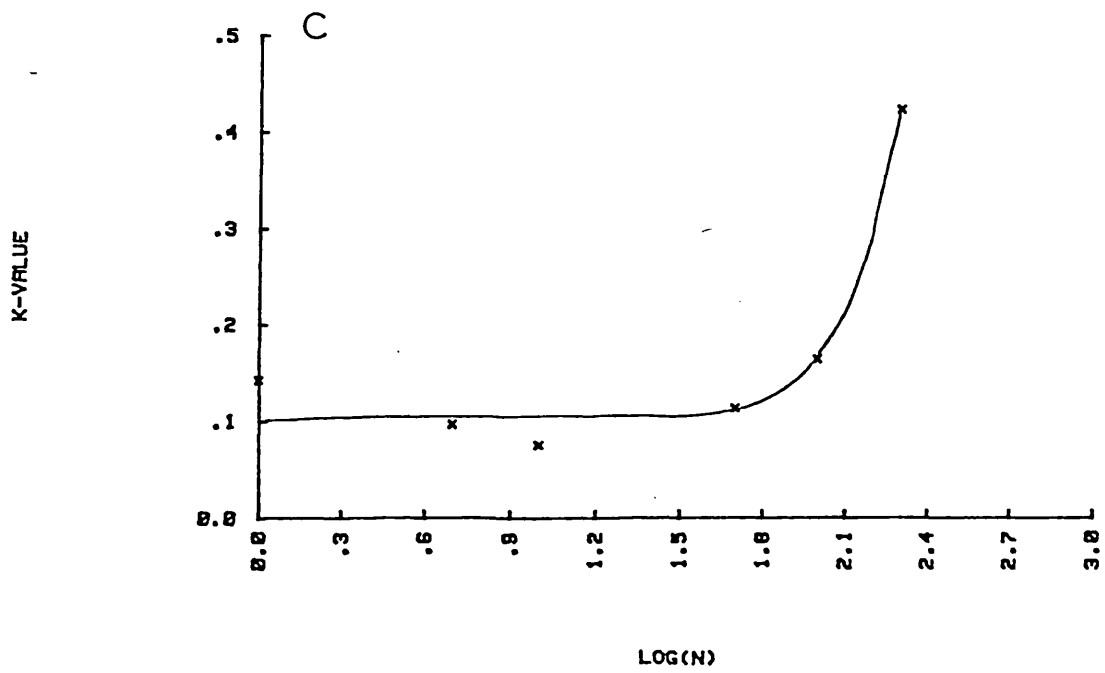
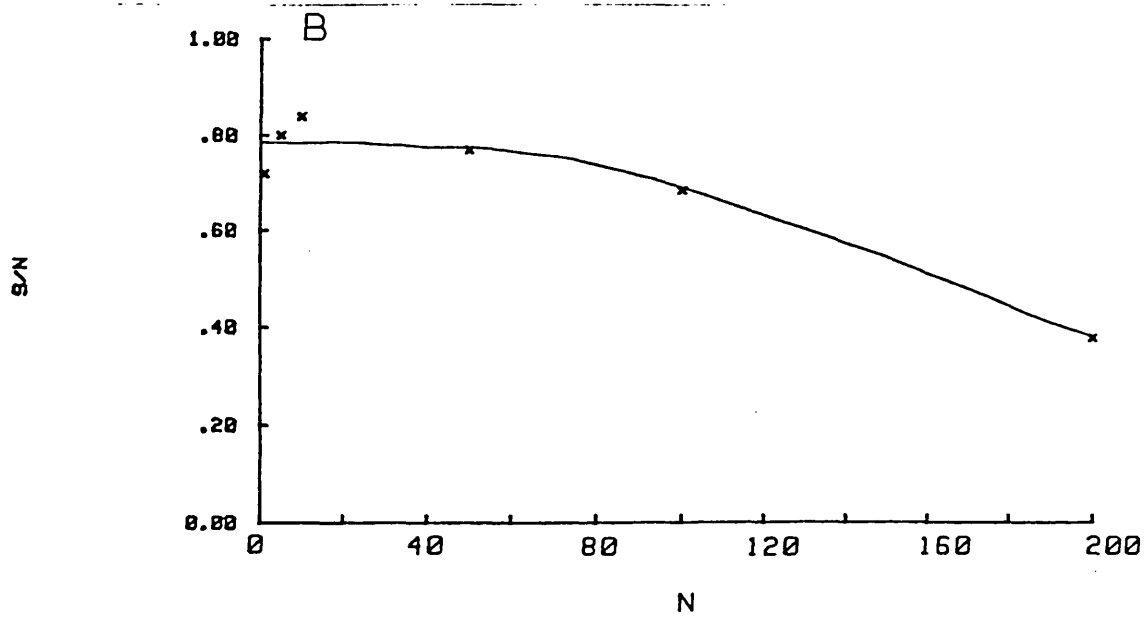
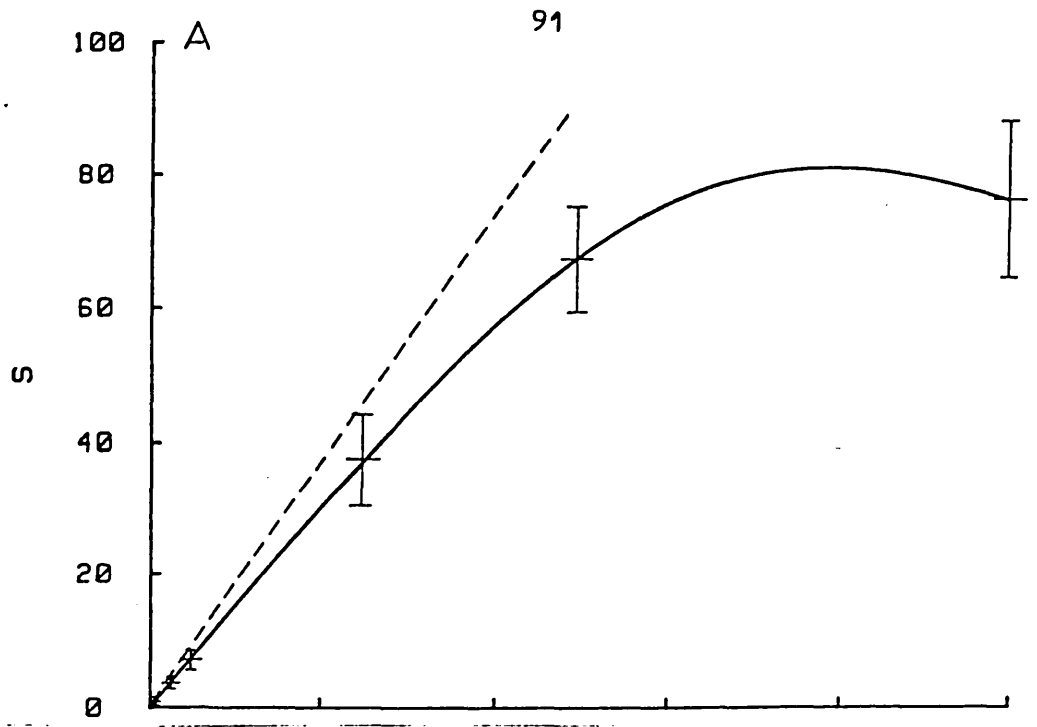


Table 3.2 Individual stage and overall survival rates of B. brassicae at various density conditions.

Density (No. Aphid/Plant)	Stage Survival Rate (%)				Overall Survival Rate (%)*
	I	II	III	IV	
1	88	93.18	95.12	92.31	72.0 ± 8.4 a
5	98	85.91	95.23	100.0	80.0 ± 9.4 a
10	97	92.78	97.75	96.55	84.0 ± 7.0 a
50	94	92.55	97.13	91.12	77.0 ± 8.4 a
100	94.5	90.21	93.26	85.85	68.2 ± 5.2 a
200	86.6	83.95	73.73	70.52	37.8 ± 5.6 b

*: Data followed by the same letter in each column are not significant at $P = 0.05$, according to LSD.

The survivorship curves of aphids at six different densities are plotted against age in Figure 3.5. The different survival models do not appear to show any substantial difference in their effect on the population dynamics of the interaction. All the models show similar ability to describe the various survivorship curves obtained in the experiment. However, it is necessary to test the agreement between the expected values and the experimental data, to investigate the similarity between the models, while also considering their simplicity in the context of the present study.

All the models have been fitted to the survival curves using a non-linear least-square procedure. Their estimated parameters with 95% confidence limits and sum of squared residuals (SSR) are presented in Table 3.3. All four models have been tested using the Kolmogorov-Smirnov test at each density, and there is no significant difference between the observed and the expected data at the 5% level of significance (Table 3.4). Of the four models, models 1 and 2 have relatively simple forms with only two parameters each, while model 4 is the most complex with five parameters. However, it is with this latter model that the total sum of squared residuals is least, suggesting that model 4 describes the data sets relatively well. Model 2 has the highest SSR. As a result, it is only Model 1 and 4 that are analysed further to determine whether there is any significant difference between them.

The two-sample Kolmogorov-Smirnov test (or the Smirnov test) (Lindgren, 1968) has been applied and the statistic $\underline{D}$, defined as

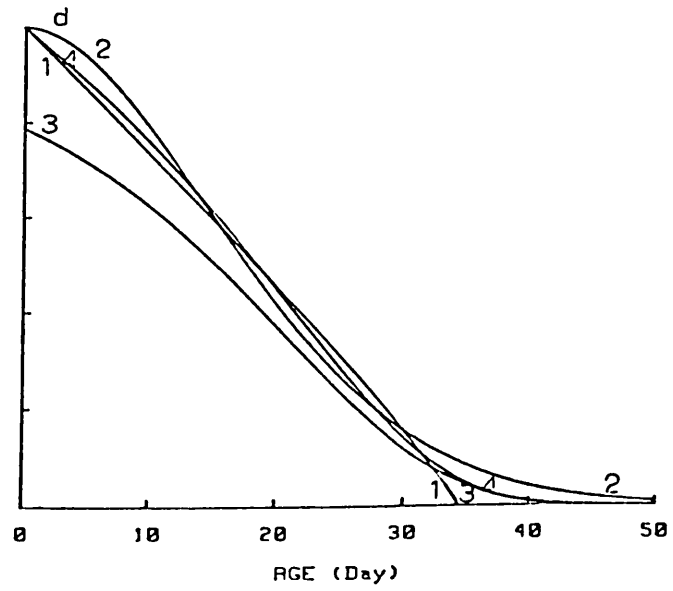
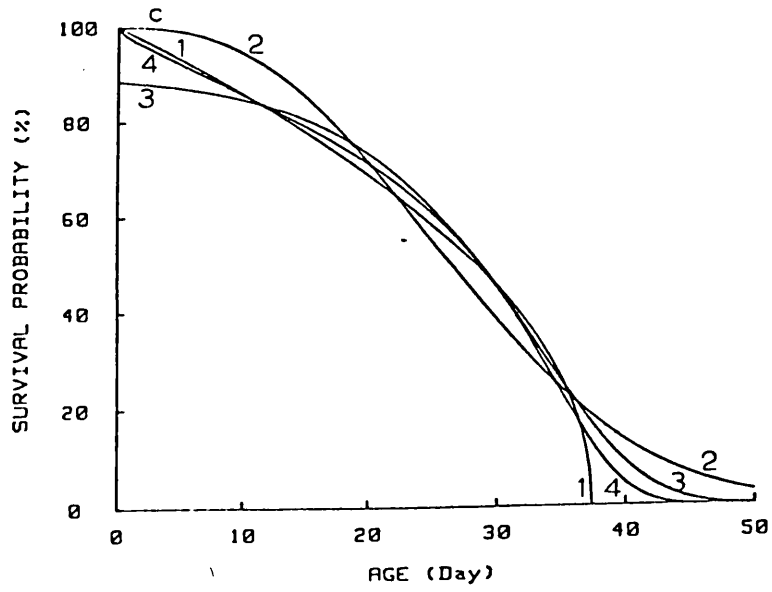
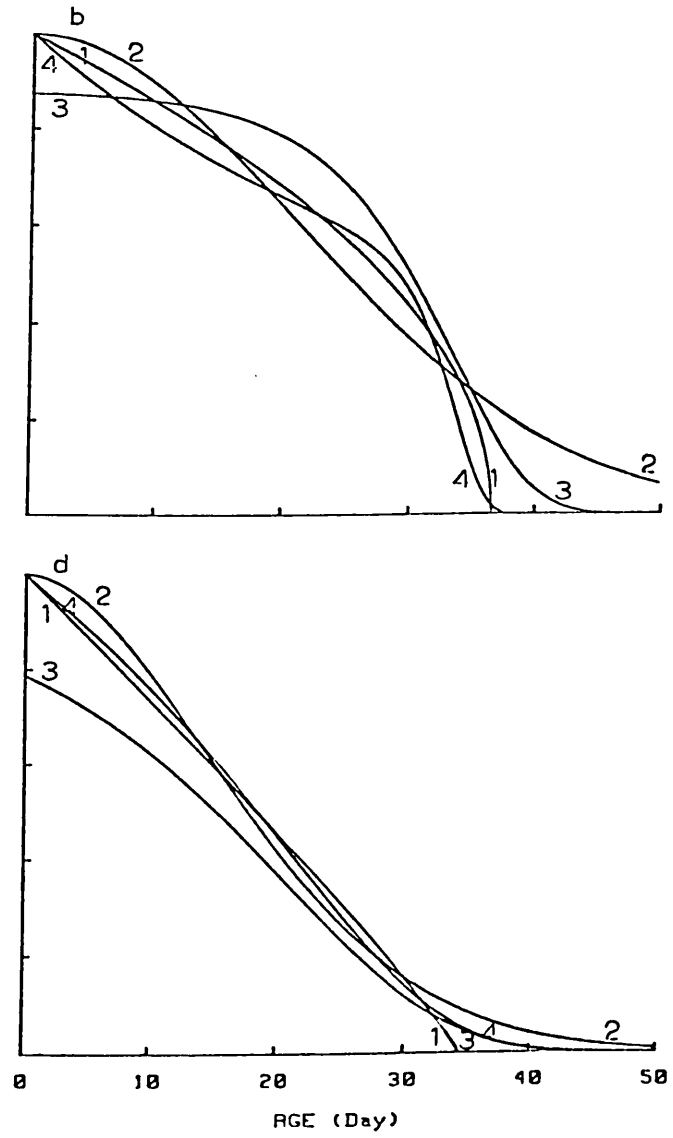
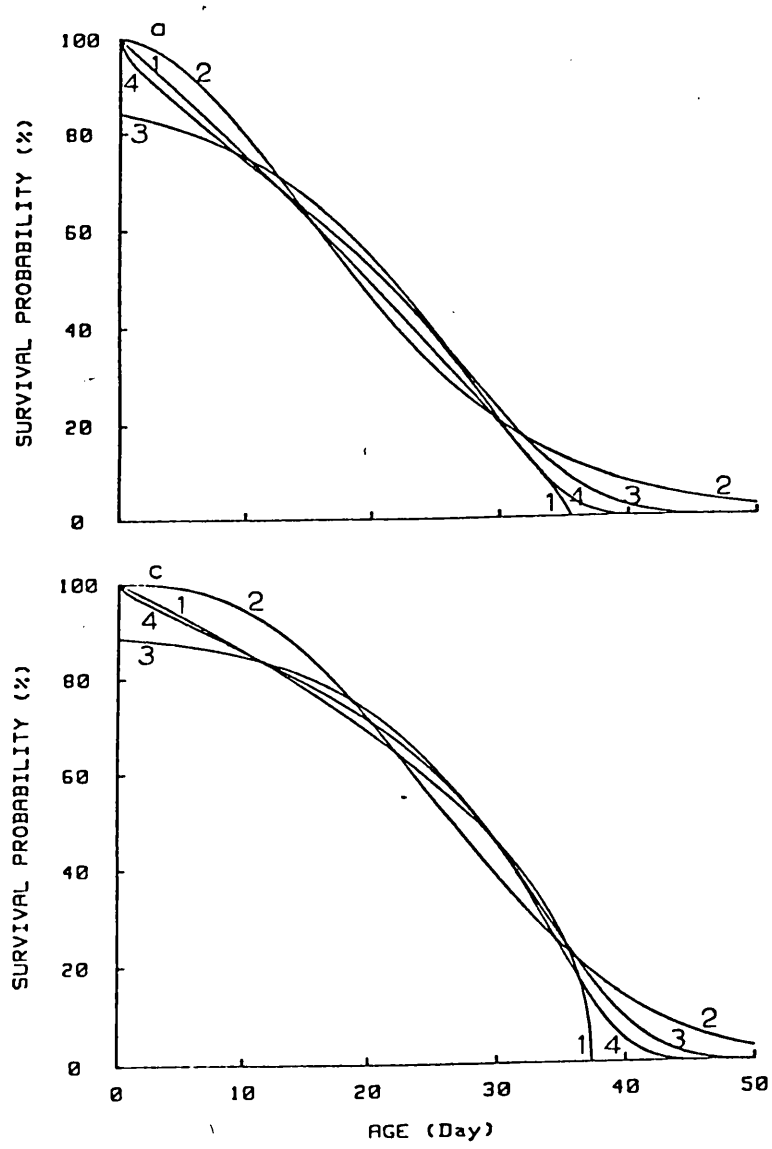
$$D = \max | F_m(x) - G_n(x) | , \text{ is calculated.}$$

$\underline{F_m}(x)$ is the sample distribution function of a sample of size $\underline{m}$ from

Figure 3.5

The simulated age-specific survivorship curves for B. brassicae at different densities : (a) 1, (b) 5, (c) 10, (d) 50, (e) 100, and (f) 200, and the experimental data (g). Numbers 1, 2, 3 and 4 in Figures (a) - (f) represent the curves fitted using models 1, 2, 3 and 4, respectively. The parameter values and confidence intervals of each model are given in Table 3.3. The symbols "+", "o", "x", "v", "●" and "*" in Figure (g) represent the density 1, 5, 10, 50, 100 and 200, respectively.

Cont.



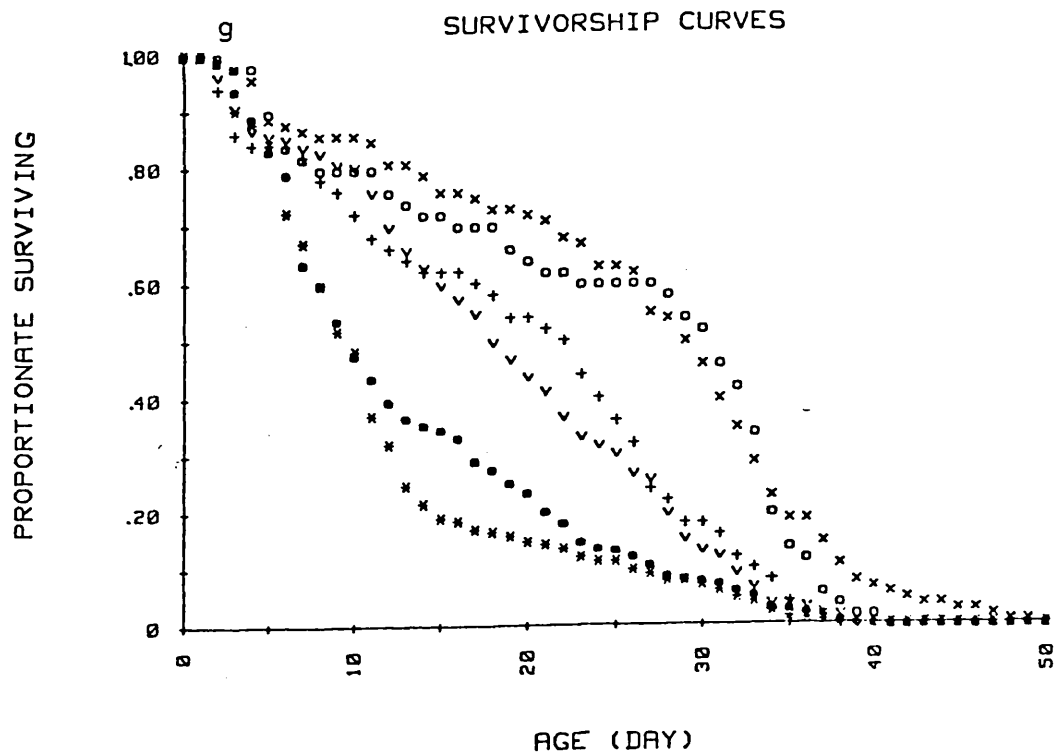
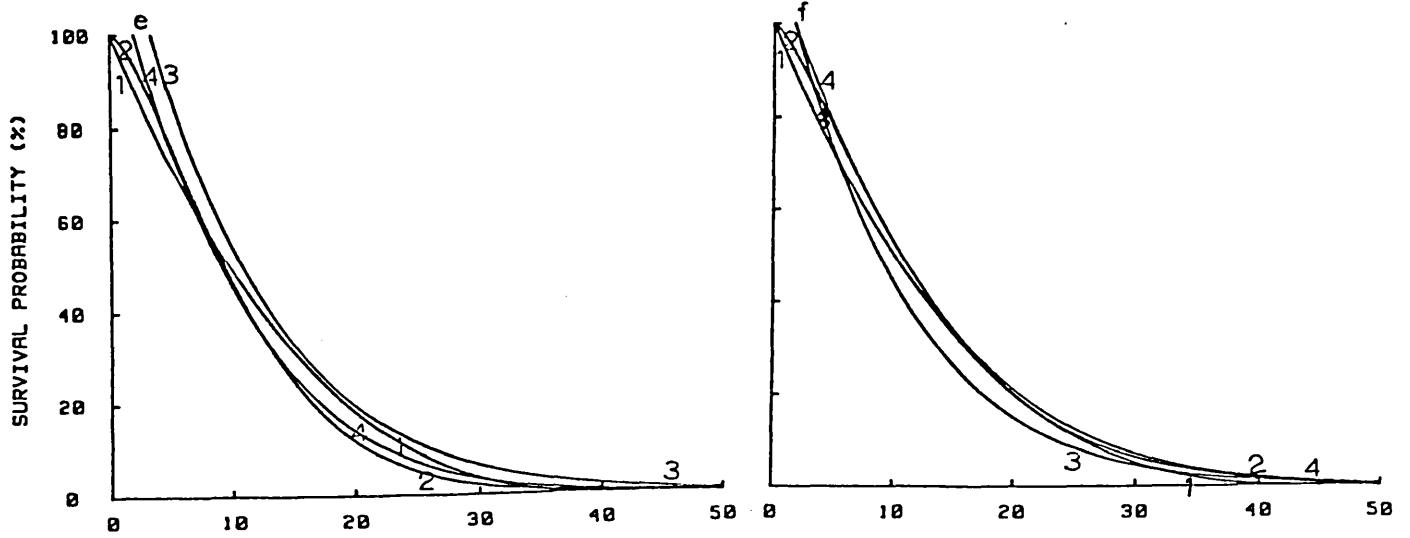


Table 3.3 Estimated parameters ($\pm$ 95% confidence limits) obtained by fitting the models (1) - (4) to the survivorship curves in Figure 3.5 using a non-linear least-squares procedure, and their sum of squared residuals (SSR)

(a) Model 1

Density	Parameter		SSR
	a	b*	
1	35.52 $\pm$ 1.22	0.87 $\pm$ 0.07 b	424.94
5	36.50 $\pm$ 0.93	0.49 $\pm$ 0.05 a	1153.28
10	37.35 $\pm$ 0.54	0.49 $\pm$ 0.04 a	753.70
50	34.27 $\pm$ 0.90	0.90 $\pm$ 0.05 b	253.17
100	41.53 $\pm$ 16.37	2.59 $\pm$ 0.78 c	1385.65
200	45.87 $\pm$ 10.42	2.80 $\pm$ 1.41 c	673.64
			Total SSR = 4644.38

*: Same as Table 3.2, according to t test.

(b) Model 2

Density	Parameter		SSR
	a	b	
1	22.99 $\pm$ 0.01	1.75 $\pm$ 0.22	1804.93
5	29.90 $\pm$ 0.009	1.99 $\pm$ 0.40	4236.58
10	30.43 $\pm$ 0.92	2.58 $\pm$ 0.29	1992.53
50	21.50 $\pm$ 0.006	1.88 $\pm$ 0.13	508.74
100	12.01 $\pm$ 0.02	1.48 $\pm$ 0.13	678.62
200	14.02 $\pm$ 0.02	1.34 $\pm$ 0.08	406.58
			Total SSR = 9627.98

Cont.

Table 3.3 (Cont.)

(c) Model 3

Density	Parameter			SSR
	a	b	c	
1	4.51 ± 0.06	-2.67 ± 0.34	-0.10 ± 0.01	265.16
5	4.39 ± 0.04	-5.36 ± 0.87	-0.16 ± 0.03	1301.09
10	4.51 ± 0.03	-3.96 ± 0.33	-0.12 ± 0.01	267.75
50	4.76 ± 0.05	-1.66 ± 0.19	-0.08 ± 0.006	103.86
100	13.63 ± 0.64	2.16 ± 0.07	-0.01 ± 0.001	378.01
200	14.07 ± 10.73	2.23 ± 1.14	-0.01 ± 0.008	223.11
				Total SSR = 2538.98

Cont..

Table 3.3 (Cont.)

(d) Model 4

Density	Parameter					SSR
	a	b	c	d	e	
1	0.070±0.060	2.320±0.26	0.0260±0.0075	0.0004±0.0002	0.1991±0.0216	231.64
5	0.008±0.0005	0.045±0.0001	0.0157±0.0002	0.00000001±0.00000001	0.4529±0.0013	301.64
10	0.034±0.0657	3.020±0.4500	0.0136±0.0051	0.00026±0.0001	0.1878±0.0136	247.05
50	0.009±0.068	3.652±2.521	0.0121±0.0064	0.0091 ±0.0020	0.0964±0.0084	121.04
100	-0.722±0.097	4.164±0.022	-0.0354±0.0037	0.1219 ±0.0034	0.0149±0.0005	614.78
200	-0.509±0.105	4.079±0.051	-0.0377±0.0062	0.1068 ±0.0055	0.0128±0.0008	290.87
						Total SSR = 1807.02

Table 3.4 The Kolmogorov-Smirnov statistics of the four survival models. The acceptance limit for the test of goodness of fit is 0.19* (sample size, n = 50; significance level, $\alpha = 0.05$).

Model	K - S Statistic of Density Treatment					
	1	5	10	50	100	200
1	0.0018	0.0045	0.0044	0.0033	0.0108	0.0063
2	0.0065	0.0077	0.0052	0.0033	0.0089	0.0051
3	0.0034	0.0090	0.0035	0.0022	0.0096	0.0066
4	0.0029	0.0032	0.0026	0.0027	0.0077	0.0057

*: $D_{(0.05, 50)} = 1.36/\sqrt{50} = 0.1923$

$\underline{F}$, and $\underline{G}_n(x)$ is the sample distribution function of a sample of size n from $\underline{G}$. When the maximum absolute difference, $\underline{D}$, is less than the five percent rejection limit, $D_{(0.05,m,n)} = (1.36)\sqrt{(m+n)/m \cdot n}$, the null hypothesis of identical distributions, $H_0: F = G$, is accepted. The null hypothesis of identical distribution, i.e. that model 1 equals that of model 4, is accepted, the statistics at each density (Table 3.5) being less than the rejection limit, $D_{(\alpha,m,n)}$. Consequently, the simple, flexible and adequately descriptive model 1 has been considered as the age-specific survival model for this study.

Figure 3.5 shows the fit of model 1 to the survivorship curves of B. brassicae at densities of 1 (Fig. 3.5(a)), 5 (b), 10 (c), 50 (d), 100 (e), and 200 (f). The fitted parameters from the data in Table 3.3 may be used to characterize the nature of the survivorship curves shown at various densities. The maximum life span, $\underline{a}$, at the six densities show no significant difference between each other (t test, $p > 0.05$). While the parameter $\underline{b}$ of each density is significantly different from that of the others (t test, $p < 0.05$).

In this latter case, as density increases from 1 to 50, the value of the parameter decreases from near one to a value far lower than unity. There is subsequently an increase to its original position. For densities higher than 50, values of $\underline{b}$ become progressively higher. Survivorship curves, therefore, show a comparable variation to the types of the survivorship curve suggested by Pearl (1928), Deevey (1947) and Slobodkin (1962), on increasing from low to high density, the curve change from a type II, to a type I, followed by a return to a type II, and finally type III (Fig. 3.5).

Table 3.5 The statistics of the two-sample Kolmogorov-Smirnov of Model 1 and 4. The acceptance limit for the test of goodness fit is 0.2720*. (Sample size, $m = n = 50$, significance level, $\alpha = 0.05$).

D	Density					
	1	5	10	50	100	200
	0.0014	0.0036	0.0043	0.0026	0.0112	0.0057

*: $D_{(0.005, 50, 50)} = (1.36) \cdot \sqrt{(50 + 50)/50 \cdot 50} = 0.2720$

Comparable survivorship curve patterns arise from aphids reared on different cultivated hosts (Root and Olsen, 1969), and at various temperatures (DeLoach, 1974) to those resulting from the effects of density. It implies that host plant, temperature, and population density can all influence the mortality of the aphid and cause the changing pattern in survivorship curves.

Itô (1961) has shown that insect mortality often occurs in distinct stages resulting in the survivorship curves showing a number of distinct steps. Such a stepwise trend, although slight, can be observed in the present study, particularly at density 5 and 10 (Fig. 3.5). This pattern is also clear when the stage survival rates are calculated (Table 3.2). This helps to explain the larger SSR occurring in those curves in Figure 3.5.

(2) Fecundity

Each of the six aphid density treatments examined in the fecundity experiments produced nymphs. The highest average fecundity was recorded from density 10 (Table 3.6), but it has no significant difference to the fecundity at density 5 (t-test; $p > 0.05$). The smallest average fecundity occurred when the density was higher than 100. The numbers of offspring obtained in the present experiment are lower than values of average fecundity reported by earlier workers, (e.g. 26-29 by Elze (1944), Markkula (1953), and Hafez (1961); 34.3 ± 10.7 at 23.8°C by Hughes (1963); 47-63 at a temperature alternating between 17° and 24°C by Bonnemaïson (1951); 40.7 ± 1.18 at 20°C by Ra-worth (1984)). These values were obtained by rearing individual aphids on single leaves, single plants or on leaf-discs suspended in water. As different food plants, temperature, and rearing techniques were used in these studies,

Table 3.6 The survival and fecundity data for B. brassicae at six densities.

Initial Density	No. of	Surviving adult		Proportional	Reproduction	Total Fecundity	Average
(N)	Replicate	(ΣS)	$\bar{S}$	Survival ($\bar{S}/N$)*	Duration (day)	(ΣF)	Fecundity ($\Sigma F/\Sigma S$)*
1	50	36	0.72±0.08	0.72±0.08 a	19 (day 10–28)	446	12.29±1.47 b
5	10	40	4.00±0.47	0.80±0.09 a	23 (day 9–31)	725	17.67±5.47 a
10	10	84	8.40±0.70	0.84±0.07 a	23 (day 9–31)	1639	19.51±2.56 a
50	4	154	38.50±4.20	0.77±0.08 a	21 (day 9–28)	2086	13.51±0.67 b
100	4	273	68.25±5.19	0.68±0.05 a	27 (day 8–34)	2565	9.51±0.68 c
200	5	378	75.60±11.19	0.38±0.06 b	26 (day 10–35)	3145	8.33±0.88 c

*: Same as Table 3.2, according to LSD

it is not to be expected that the data obtained in the present study should correspond with these values.

In general, the total fecundity of an insect, or average fecundity during its life span has less influence on the rate of increase than the rate of reproduction (Howe, 1953). In the present study it is the age-specific fecundity of the aphid which is of crucial importance to the population growth. Regardless of population density every aphid cohort has started producing offspring by 9 ± 1 days (Table 3.6).

By fitting the two proposed 3-parameter models, the symmetric normal (Equation 3.7) and the skewed distribution (Equation 3.8), using a non-linear least square procedure, the age-specific fecundity curves of B. brassicae have been described at the six densities (Fig. 3.6 and 3.7, respectively), and the estimated parameters with 95% confidence levels calculated (Table 3.7 and 3.8, respectively). However, the total SSR of the skewed distribution model (Eq. 3.8) is less than one third of the total SSR of the symmetric normal distribution model (Eq. 3.7). This implies that the former has a better descriptive ability, although the Kolmogorov-Smirnov statistics for the two fecundity models in Table 3.9 showed both to provide good fits to the age-specific fecundity data obtained during the experiment ($p < 0.005$). The skewed model has thus been chosen for the development of the age-specific fecundity model. Empirically, the time at which the first offspring is produced is set as seven ($k = 7$) in this model.

The pattern of increasing $F_{\max}$ up to density 10 followed by a decline with increasing density (and the reverse for $t_{F_{\max}}$) suggests an "Allee" effect may be operating (Table 3.10). Such an effect could be mediated

Figure 3.6

The age-specific fecundity curves of B. brassicae at different densities : (A) 1, (B) 5, (c) 10, (D) 50, (E) 100 and (F) 200. The fitted curves refer to equation 3.7 in text.

FECUNDITY CURVES

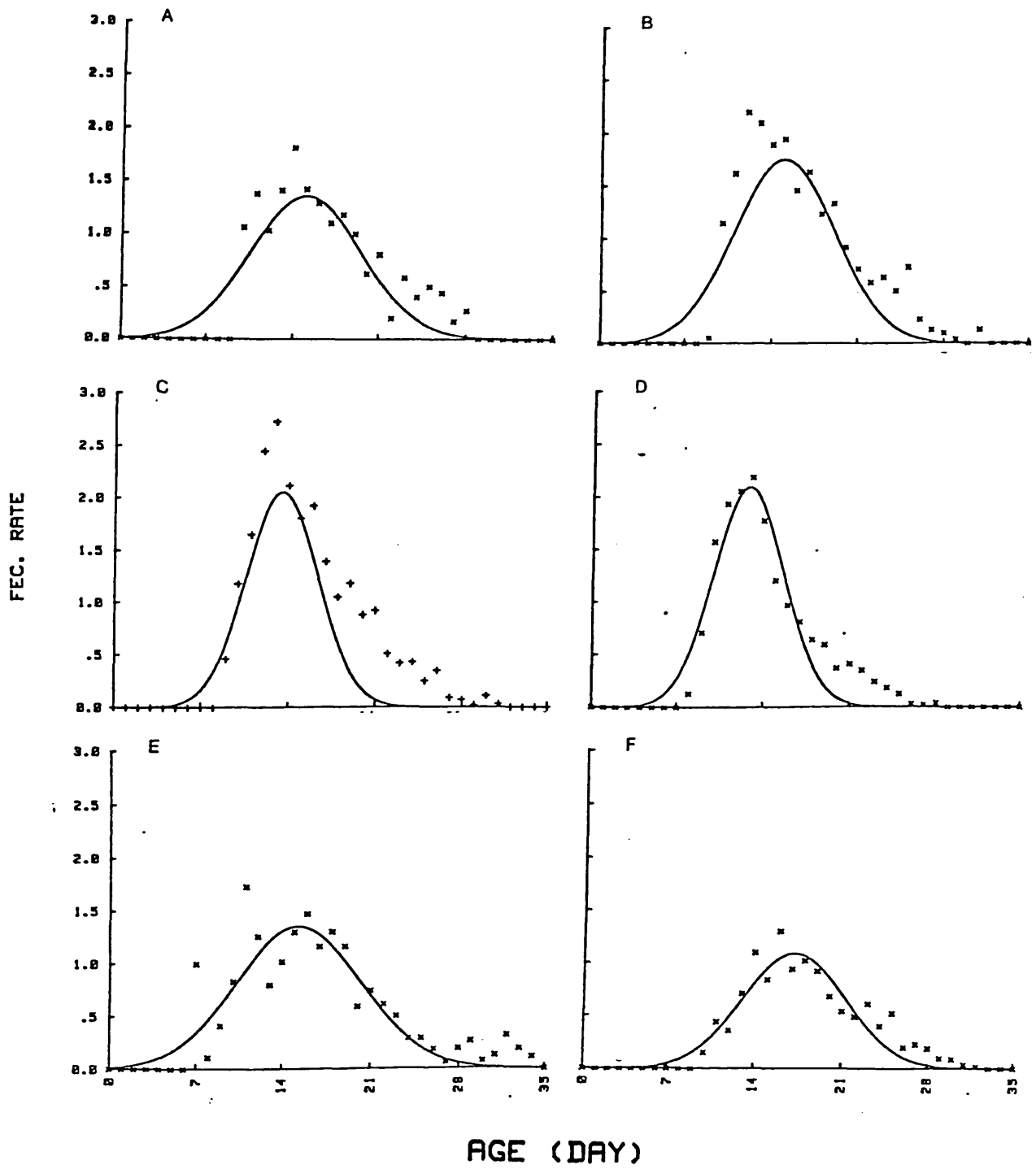


Table 3.7 Estimated values ($\pm$ 95% confidence limits) of parameters and sums of squared residuals obtained by fitted equation 3.7 to the curves in Figures 3.6 (a) - (f).

Density	Parameters			SSR
	a	b	c	
1	1.3543 $\pm$ 0.0001	0.0245 $\pm$ 0.0001	15,0000 $\pm$ 0.0001	1.8697
5	1.7545 $\pm$ 0.0001	0.0299 $\pm$ 0.0001	14.6724 $\pm$ 0.0001	2.9749
10	2.0200 $\pm$ 0.0001	0.0600 $\pm$ 0.0001	13.5500 $\pm$ 0.0001	4.6503
50	2.0755 $\pm$ 3.0167	0.0605 $\pm$ 1.8875	12.7889 $\pm$ 0.0016	1.2262
100	1.3530 $\pm$ 0.0001	0.0202 $\pm$ 0.0001	15.2559 $\pm$ 0.0001	2.0269
200	1.0893 $\pm$ 0.0001	0.0300 $\pm$ 0.0001	17.1400 $\pm$ 0.0001	0.5821
				Total SSR =
				13.3301

Figure 3.7

The age-specific fecundity of B. brassicae at the six densities:
(a) 1, (b) 5, (c) 10, (d) 50, (e) 100 and (f) 200. The fitted
curves refer to equation 3.8 in text.

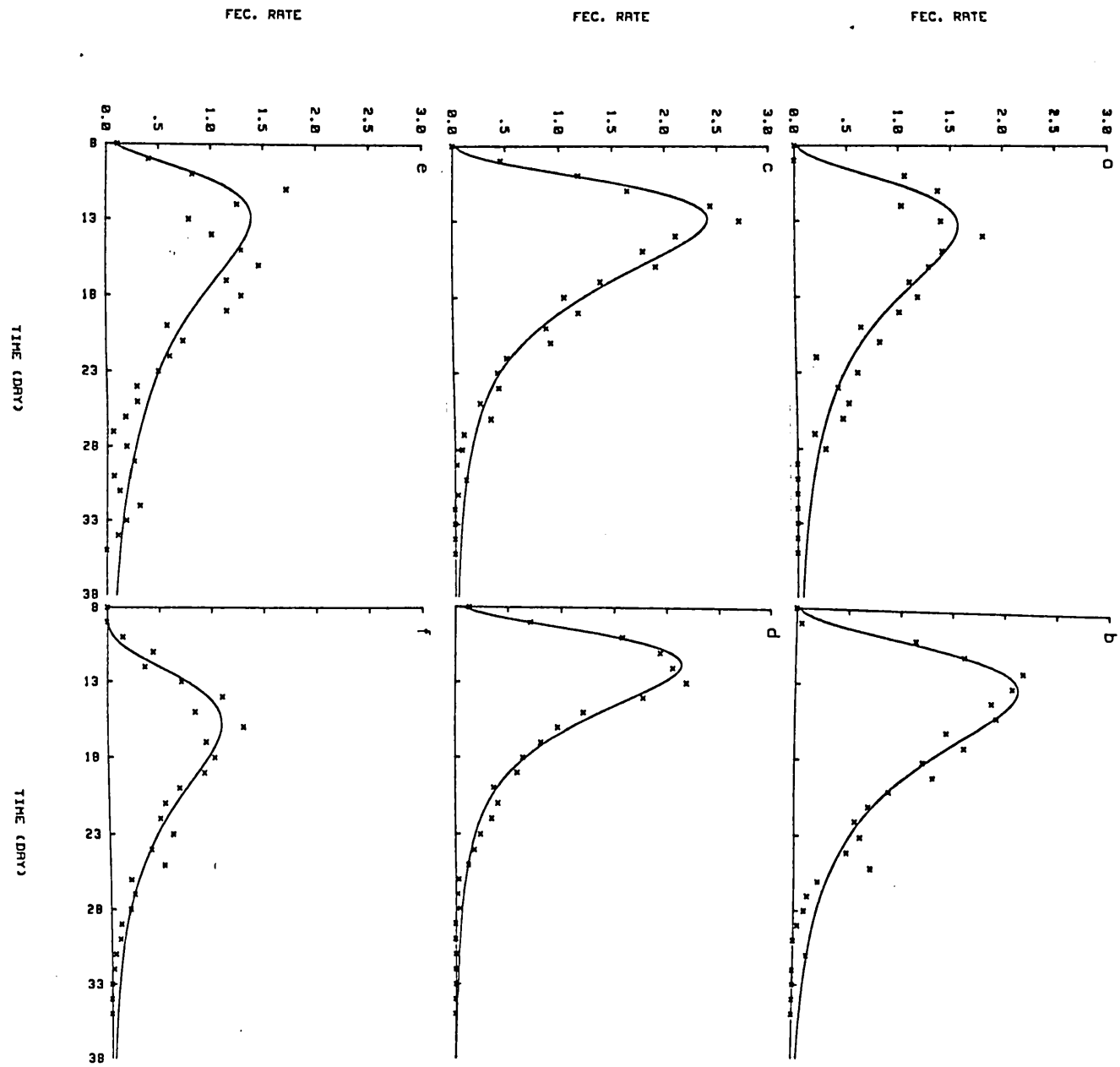


Table 3.8 Same as Table 3.7, but obtained by fitted equation 3.8 to the curves in Figures 3.7(a) - (f).*

Density	Parameter			SSR
	a	b	c	
1	19.8954 ± 1.5349 b	5.3653 ± 0.5145 a	11.3311 ± 0.8888 a	0.8751
5	22.1114 ± 0.9765 b	5.7628 ± 0.3222 ab	12.3504 ± 0.5607 ab	0.5870
10	24.8327 ± 0.8572 c	6.2486 ± 0.2761 b	13.7038 ± 0.4861 b	0.4920
50	25.4099 ± 0.6626 c	5.4363 ± 0.1878 a	13.4415 ± 0.3614 b	0.1704
100	14.7501 ± 5.4781 a	3.7804 ± 1.6698 a	8.2632 ± 3.2459 a	1.3312
200	30.2256 ± 1.2290 d	10.7918 ± 0.4895 c	19.4254 ± 0.7321 c	0.3022
				Total SSR =
				3.7579

* : Same as Table 3.2, according to t-test.

Table 3.9 The Kolmogorov-Smirnov statistics of the two fecundity models. The acceptance limit for the test of goodness of fit is 0.2267* (sample size, $n = 36$; significance level, $\alpha = 0.05$).

Model	Density					
	1	50	10	50	100	200
Symmetric (Eq. 3.7)	0.0375	0.0350	0.0369	0.0268	0.0400	0.0728
Skewed (Eq. 3.8)	0.0248	0.0174	0.0156	0.0144	0.0358	0.0193

*: $D = 1.36/\sqrt{36} = 0.2267$

Table 3.10 The maximum fecundity rate, $F_{\max}$ at six densities and the predicted time at which maximum fecundity rate occurred, $t_{F_{\max}}$, calculated using Eq. 3.8a and 3.8, respectively.

Density	$F_{\max}$ (No. Nymph/♀/day)	$t_{F_{\max}}$ (day)
1	1.57	13.30
5	2.14	13.12
10	2.41	12.86
50	2.15	11.75
100	1.39	12.90
200	1.09	15.73

by the aggregation of the aphid (Way, 1968; Way and Banks 1967; Way and Cammell, 1970) which enhances reproduction.

(3) Development

The development of B. brassicae on Brussels sprouts plants in the laboratory at the six densities mentioned are shown in Figure 3.8 in terms of the percentage of the initial cohort in each stage against age. Each cohort is initiated from first instar nymph(s) born within 24 hours of each other. The percentage of the individuals remaining at the first instar stage declines sharply but smoothly. Empirically, a modified Gompertz equation (Eq. 3.9) has been used to describe the distribution of the first instar development and the curves obtained by fitting the model to the experiment data are shown in Figure 3.9. The estimated parameters with 95% confidence limits and SSR for each density are presented in Table 3.11. No significant difference have found between each density for parameters a and b (t-test; $p > 0.05$), so that the Kolmogorov-Smirnov test was used as a test of goodness of fit. This showed good correspondence between the predictions of the Gompertz distribution and experimental data (Table 3.12). As parameters a and b do not differ significantly at the six densities, a further investigation has been made to test whether there are any differences as a result of the density treatments. Using the two-sample Kolmogorov-Smirnov test, all the statistics are less than $D_{(0.05,16,16)} = 1.36 \cdot (\sqrt{(16+16)/16 \cdot 16}) = 0.48$ (Table 3.13). The six distributions are, therefore, indistinguishable and agreement with the modified Gompertz distribution is accepted at the 95% acceptance level. This implies that density has no significant influence on the developmental rate of the first instar aphids. It is thus convenient to pool the data and find a set of parameters to describe the developmental rate of the first

Figure 3.8

The development of a cohort of B. brassicae at different densities:

(a) 1, (b) 5, (c) 10, (d) 50, (e) 100 and (f) 200. The symbols

"I - IV" represent instars 1 - 4.

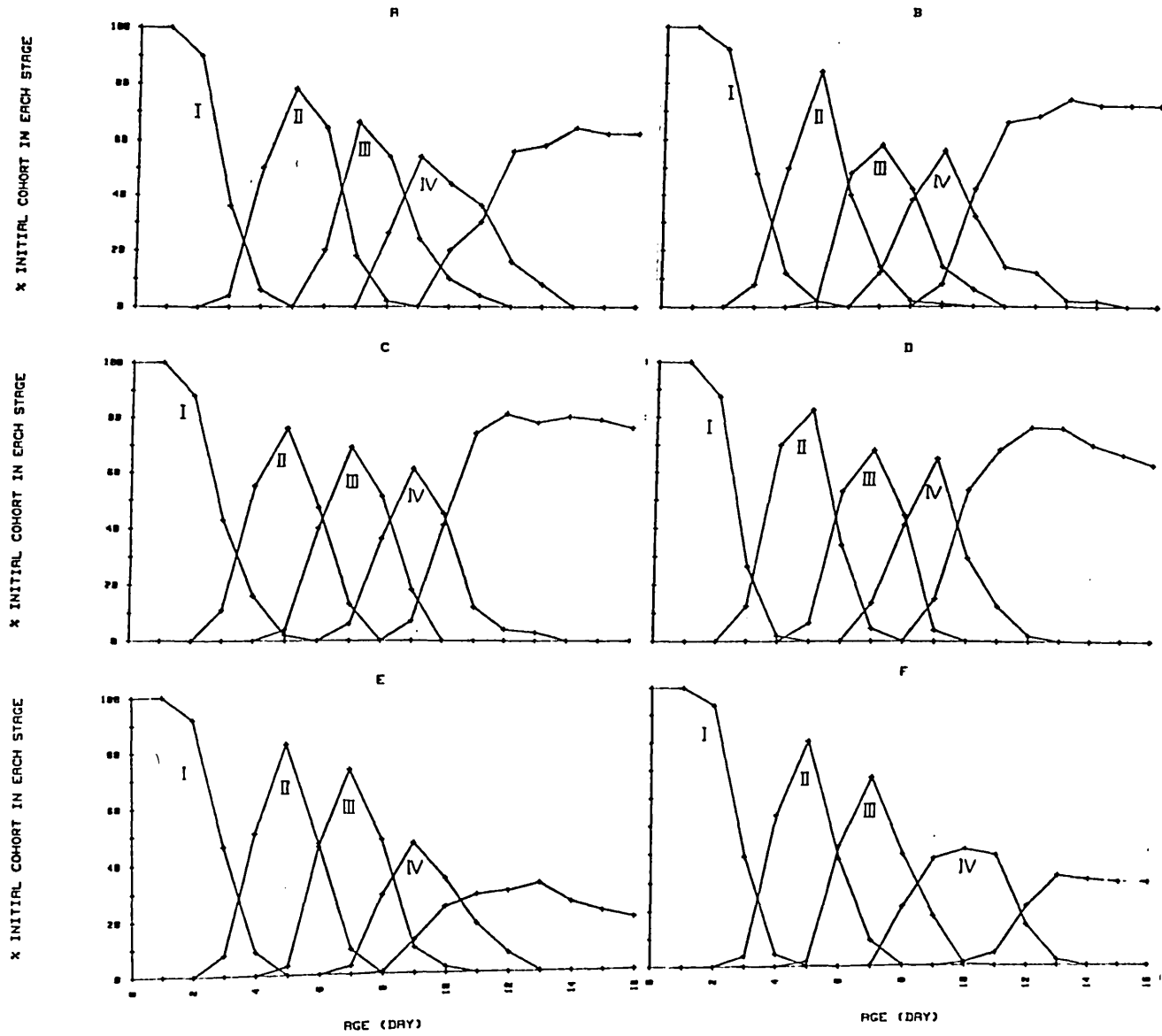


Table 3.11 Estimated parameters ($\pm$ 95% confidence limits) and sums of squared residuals obtained by fitted the equation 3.9 to the curves of development probability in Figure 3.9 using a non-linear square procedure.

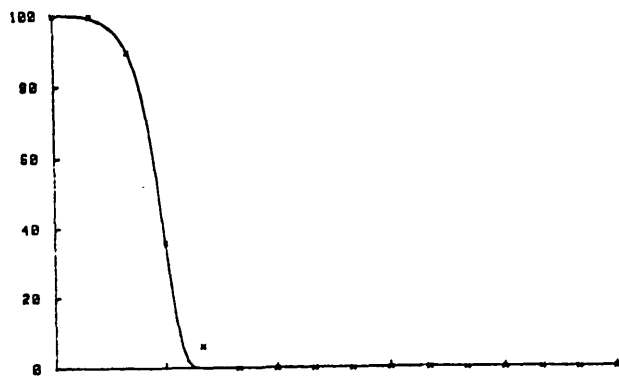
Density	Parameter			SSR
	a	b	c	
1	100.6239 $\pm$ 2.9244	0.0013 $\pm$ 0.0008	2.2278 $\pm$ 1.2627	36.49
5	104.4925 $\pm$ 4.9622	0.0137 $\pm$ 0.0115	1.3057 $\pm$ 0.2489	76.17
10	107.1691 $\pm$ 7.8213	0.0307 $\pm$ 0.0275	1.0627 $\pm$ 0.2562	128.68
50	100.7359 $\pm$ 1.0686	0.0015 $\pm$ 0.0006	2.2618 $\pm$ 0.1404	4.87
100	100.6749 $\pm$ 4.1154	0.0012 $\pm$ 0.0027	2.1965 $\pm$ 0.7363	72.07
200	100.1360 $\pm$ 2.3282	0.0002 $\pm$ 0.0001	2.8960 $\pm$ 0.5731	34.93

Figure 3.9

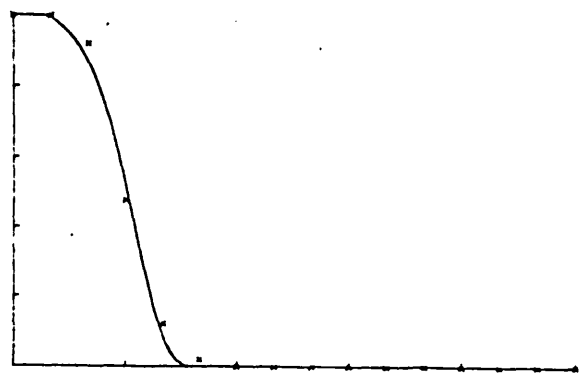
The development of the first instar stage of B. brassicae at six densities. The curves are fitted using the modified Gompertz equation (see Eq. 3.9 in text).

DEVELOPMENT PROBABILITY (%)

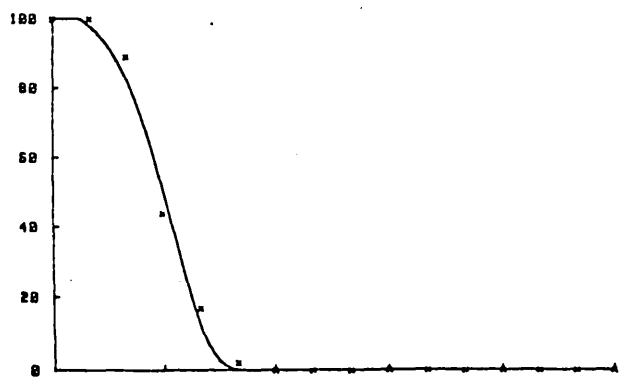
a DENSITY DEPENDENT DEVELOPMENT - 1.



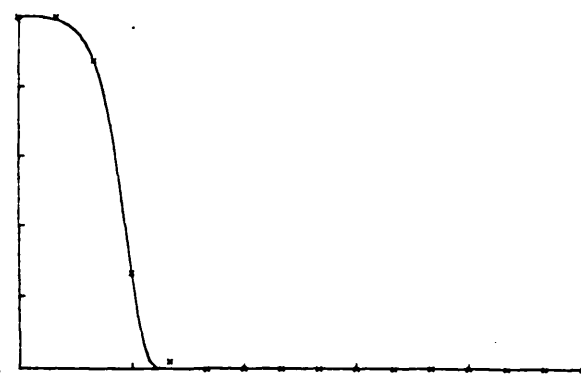
b DENSITY DEPENDENT DEVELOPMENT - 5.



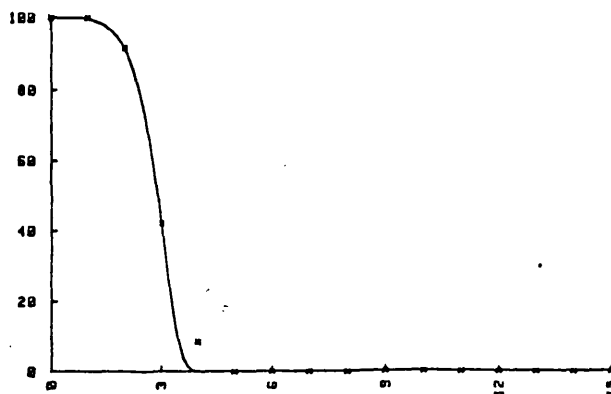
c DENSITY DEPENDENT DEVELOPMENT - 10.



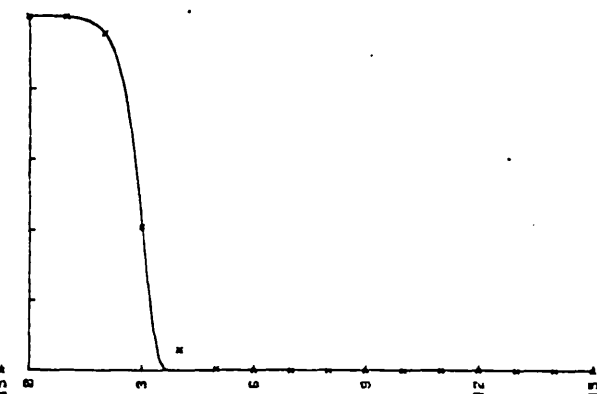
d DENSITY DEPENDENT DEVELOPMENT - 50.



e DENSITY DEPENDENT DEVELOPMENT - 100.



f DENSITY DEPENDENT DEVELOPMENT - 200.



AGE (DAY)

Table 3.12 The Kolmogorov-Smirnov statistics of the model (Eq. 3.9) for the development of the first instar aphids. The acceptance limit for the test of goodness of fit is 0.34.
(sample size, $n = 16$; significance level, $\alpha = 0.05$).

	Density					
	1	5	10	50	100	200
D	0.0180	0.0121	0.0211	0.0063	0.0247	0.0192

Table 3.13 The statistics of the two-sample Kolmogorov-Smirnov of the models of the first instar development for the six densities. The acceptance limit for the null hypothesis $H_0: F_1 = F_2$ is 0.48; for significance level = 0.05, sample size $n = 16$.

Density	Density				
	5	10	50	100	200
1	0.0180	0.0356	0.0261	0.0166	0.0072
5		0.0120	0.0658	0.0231	0.0282
10			0.0617	0.0355	0.0456
50				0.0617	0.0456
100					0.1518

instar irrespective of density.(Fig. 3.10a).

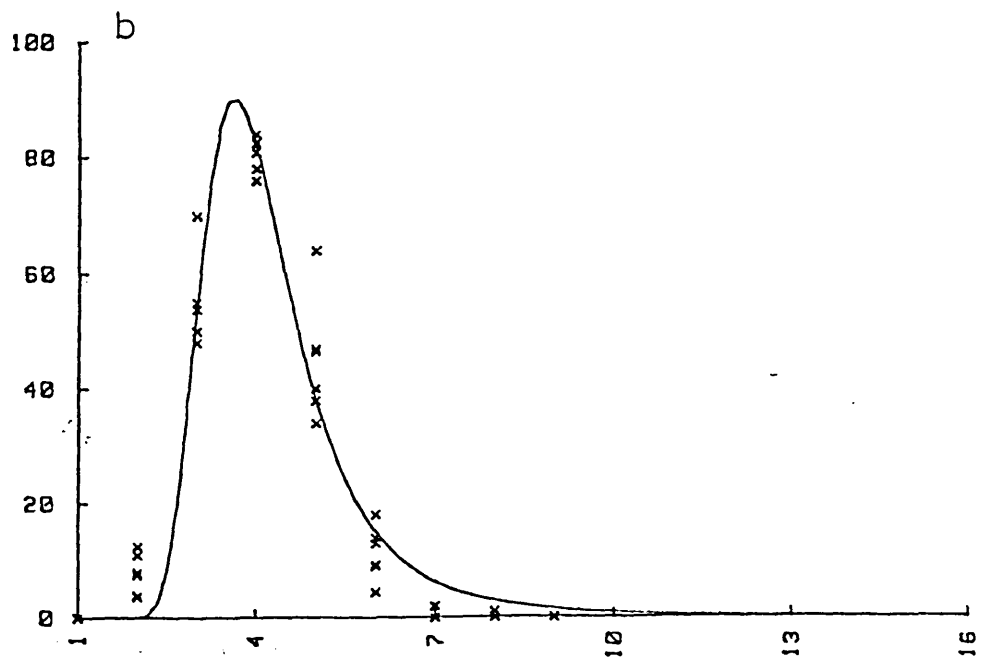
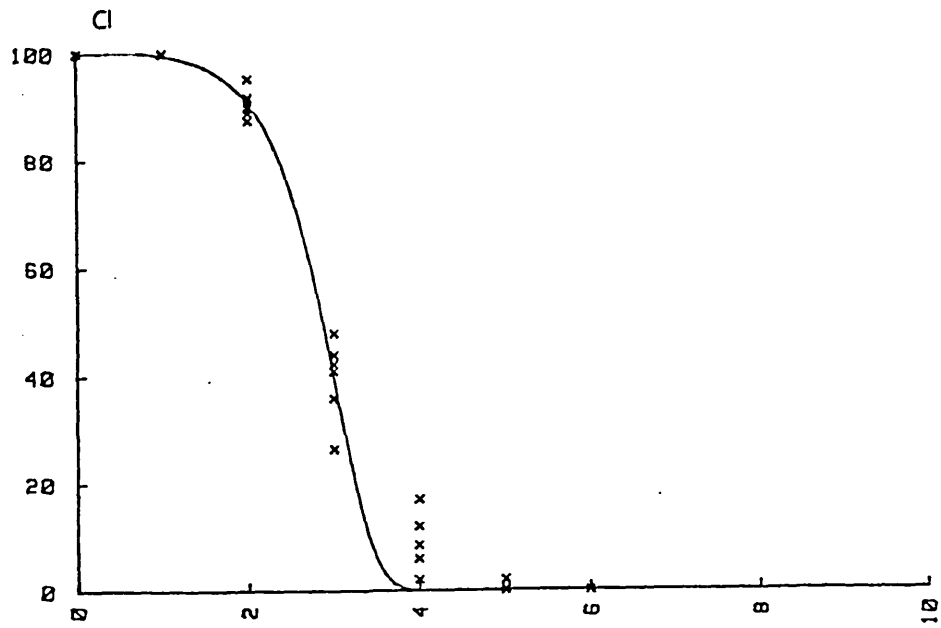
The curves for the developmental rates of the second, third and fourth instar aphids have been obtained by fitting the skewed compound distribution (Eq. 3.10) to the experimental data. The statistics of the K-S test show good correspondence between the predictions of the model (Eq. 3.10) and experimental data (Table 3.14). For the second instar, the difference of the parameters a, b and c between each density treatment is not significant (t-test; $p > 0.05$). A general condition can, therefore, be obtained from the pooled data by using the same procedure as for the first instar (Fig. 3.10(b)). In the third and fourth instar, the difference between the densities is significant (t-test; $p < 0.05$; Table 3.15a & b). For the parameter C₃, the average developmental rates of the third instar stage increase as density increases from one to five, before tending to level off. The fourth instar stage shows the same trend except now there is a significant decrease in C₄ as density increases from 100 to 200. The trend of increasing deviation at low densities, implies an "Allee" effect that may influence the development of the third and fourth instars, but has not been found in the younger stages.

The results of the experiment suggest that density dependent factors acting on population of B. brassicae are intense enough to cause high mortality, affect the fecundity of the adult stage at low and high density conditions, and influence the development of the third and fourth instar stages. The experiment has, in general, confirmed that these demographic rates show an "Allee type" response to density. The inverse effect of low density on these vital rates of B. brassicae is suggested to be caused principally by the "sink effect", i.e. an inflow of important nutrients such as soluble nitrogen compounds induced by the feeding of a certain population level of aphid aggregated on certain parts of

Figure 3.10

The general development curves of the first (a) and the second (b) instar stages of B. brassicae. The fitted curves were obtained by fitting Eq. 3.9 and 3.10 to the pooled development data of the first and second instars, respectively. In (a), equation 3.9: $a = 100.64 \pm 3.26$, $b = 0.0012 \pm 0.0021$, $c = 2.2059 \pm 0.5593$ and $SSR = 909.9408$. In (b), equation 3.10: $a = 0.0773 \pm 0.0044$, $b = 0.0572 \pm 0.0036$, $c = 0.2751 \pm 0.0036$ and $SSR = 2123.5$.

DEVELOPMENT PROBABILITY (%)



AGE (DAY)

Figure 3.11

The development probability of the third (III) and the fourth (IV) instar stages of B. brassicae at six densities : (a) 1, (b) 5, (c) 10, (d) 50, (e) 100 and (f) 200. The curves have been fitted using equation 3.10. The estimated parameters of Eq. 3.10 are given in Table 3.15.

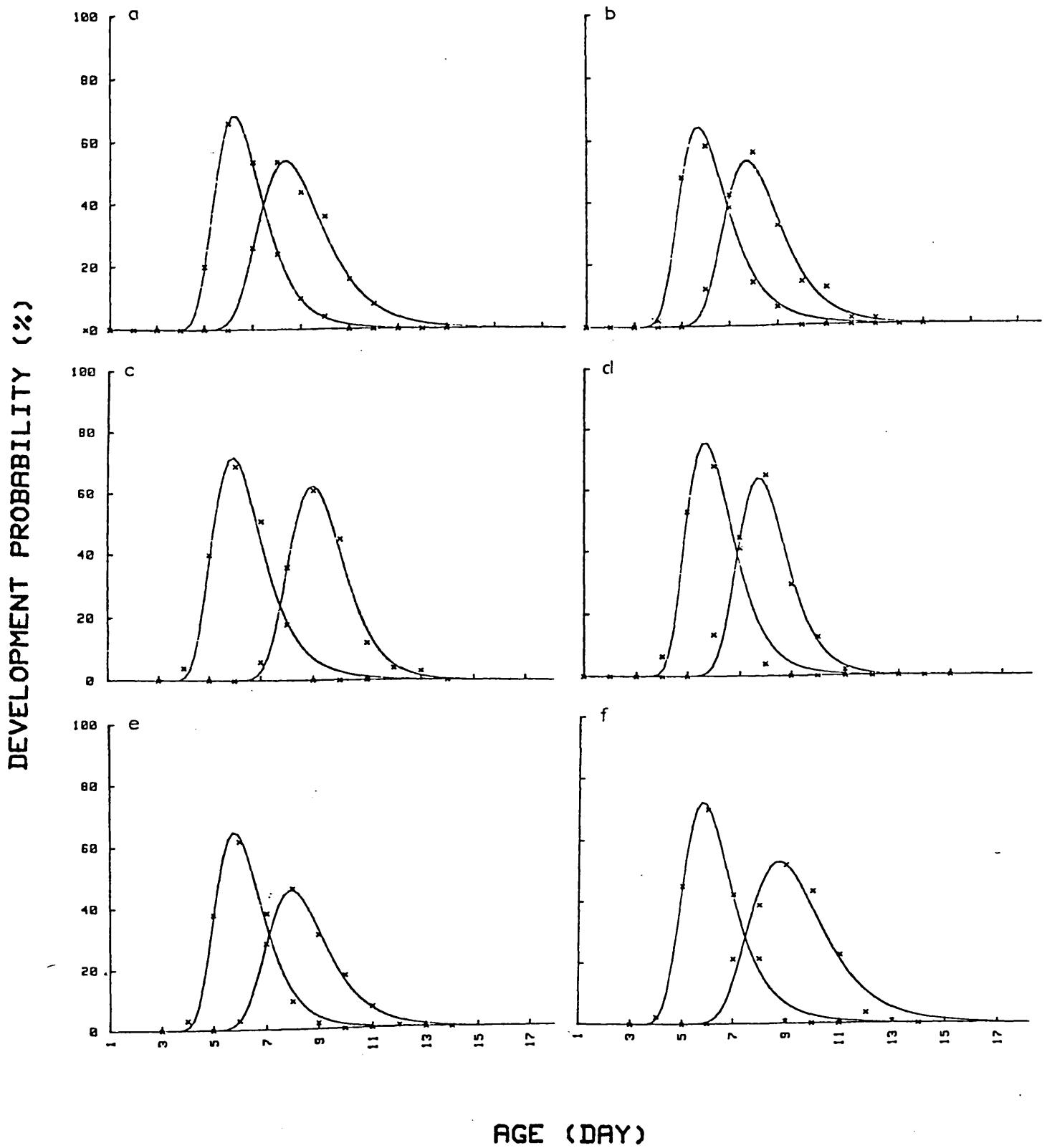


Table 3.14 The K-S statistics of the model (Eq. 3.10) for the development of the second, third, and fourth instar aphids.

$\alpha = 0.05$.

Instar	Sample size (n)	Density					
		1	5	10	50	100	200
2	9	0.0794	0.0401	0.0573	0.0612	0.0492	0.0239
3	9	0.0078	0.0404	0.0393	0.0511	0.0283	0.0323
4	10	0.0337	0.0240	0.0185	0.0587	0.0132	0.0420

Table 3.15 Estimated parameters ($\pm$ 95% confidence limits) and sums of squared residuals obtained by fitted the equation 3.10 to the curves of development probability in Figure 3.11 using a non-linear least square procedure.*

(a) The third instar

Density	Parameters			SSR
	a_3	b_3	c_3	
1	0.2334 $\pm$ 0.0062 a	0.0250 $\pm$ 0.0007	0.1605 $\pm$ 0.0009 a	3.8227
5	0.2029 $\pm$ 0.0241 b	0.0308 $\pm$ 0.0043	0.1755 $\pm$ 0.0042 c	66.7221
10	0.2054 $\pm$ 0.0038 b	0.0271 $\pm$ 0.0042	0.1694 $\pm$ 0.0045 b	123.1553
50	0.1921 $\pm$ 0.0051 b	0.0274 $\pm$ 0.0062	0.1766 $\pm$ 0.0057 c	209.5045
100	0.2031 $\pm$ 0.0022 b	0.0262 $\pm$ 0.0025	0.1725 $\pm$ 0.0027 bc	40.7424
200	0.1959 $\pm$ 0.0196 b	0.0281 $\pm$ 0.0032	0.1724 $\pm$ 0.0032 bc	60.0349

(b) The fourth instar

	a_4	b_4	c_4	
1	0.3921 $\pm$ 0.0451 ab	0.0195 $\pm$ 0.0017 c	0.1199 $\pm$ 0.0024 a	75.4528
5	0.3772 $\pm$ 0.0015 a	0.0187 $\pm$ 0.0024 bc	0.1293 $\pm$ 0.0020 c	84.0622
10	0.3426 $\pm$ 0.0338 a	0.0159 $\pm$ 0.0017 a	0.1266 $\pm$ 0.0018 bc	78.6517
50	0.3836 $\pm$ 0.0023 a	0.0157 $\pm$ 0.0027 a	0.1294 $\pm$ 0.0027 c	137.4512
100	0.4336 $\pm$ 0.0814 ab	0.0174 $\pm$ 0.0037 abc	0.1256 $\pm$ 0.0010 b	9.7526
200	0.4969 $\pm$ 0.0262 b	0.0176 $\pm$ 0.0010 ab	0.1145 $\pm$ 0.0038 a	193.4907

*: The same as Table 3.2, according to t-test.

host plants (Way and Banks, 1967; Way and Cammell, 1970). Other possible mechanisms, such as hormone control (Way and Banks, 1967), however, cannot be ruled out.

During the experiment, it was observed that the aphids shows a defensive kicking behaviour to any minor disturbance such as a gust of wind or when touching each other. This kind of disturbance may be a factor in reducing physiological rates. As the population density increases and the population aggregates as a dense pack, the frequency of defensive kicking increases, and it is assumed that the level of disturbance increases accordingly. If the food resource is unlikely to be a limiting factor, the disturbance caused by aggregation and crowding in local populations may be important in reducing the demographic rates. However, the possibility also exists of other mechanisms being involved, such as, limited quantity of food resource (Crombie, 1943), and declining quality of food (Dixon, 1963).

3.6 Conclusion

Quantitative information of the functional form and magnitude of density dependent constraints on cabbage aphid population growth is very limited (Hughes, 1963; Raworth et al., 1984). In qualitative terms, however, such effects are known to operate on the survival, fecundity, and development of aphids (e.g. Dixon, 1963, 1966, 1970, 1975; Chambers, 1982). The experiment and analyses in this chapter stress the importance of considering the age-specific demographic rates in relation to density dependence.

Some non-linear models describing the age-specific demographic parameters have been proposed and tested. The models chosen are general in that they are flexible and can be applied to various densities simply

by changing the value of their parameters, as shown for the various types of survivorship curves.

It has been shown experimentally that several types of survivorship curves can be generated by the same organism, merely by changing density. The form of the curves is comparable to the survivorship curve types considered by Pearl and Miner (1935), Deevey (1947), and Slobodkin (1962).

During aphid development, the effect of density acts mainly on the older nymphal stages, i.e. the third and fourth instars. At high densities the effect causes the development rates to be reduced and inevitably the duration of developmental time lengthened. The inversely density dependent process acting on development at low densities shows a similar effect as on the fecundity of the aphid, particularly in the fourth instar. These results all suggest that the demographic rates may be influenced by an "Allee type" density effect.

This chapter has been concerned with the processes of density dependent demographic rates for age homogeneous populations of the aphid. The models of age-specific and density-dependent demographic parameters and the processes including age heterogeneous population will be discussed in the following chapter.

Chapter Four

Intraspecific Competition II

4.1 Introduction

In general, competition in stage-structured populations can be partitioned into two categories: intra- and inter-stage competitions. The importance of competition in structuring ecological communities has long been recognized. However, there is one aspect of this widespread phenomenon that has received relatively little attention, that of competition between stage-classes within a population, i.e. inter-stage competition. Depending on the degree of niche overlap inter-stage competition in natural populations may range from being virtually non-existent to being relatively severe (Price, 1975). Like most exopterygote insects, cabbage aphids have only a small degree of divergence of stage-class morphologies, and during the summer the developmental stages share a common resource base.

Numerous studies have been attempted to introduce density dependence into age structural models of population growth (e.g. Leslie, 1948; Pennycuik, Compton and Beckingham, 1968; May, Conway, Hassell, and Southwood, 1974; Gurtin & MacCamy, 1974; Lee, 1974; Beddington, 1974; Oster and Takahashi, 1974; Guckenheimer, Oster, and Ipaktchi, 1977; Bellows and Hassell, 1984). Of these, only May et al. (1974) and Bellows & Hassell (1984) have explicitly considered inter-stage competition. Using a similar approach to that of the two stage-class population model, Tschumy (1982) has examined the configuration of the zero growth isoclines of adult and juvenile densities, the shape of these isoclines, and the number of equilibria which result. Unfortunately, there are no parameters in their vital functions.

In the previous chapter, certain functions which provide simple descriptions of the age-specific demographic parameters of the aphid

at various densities were established. This chapter sets out to describe these rates in more detail, using previously described equations, with the purpose of predicting changes in population size and age from one day to the next. The models are also expanded to include interactions between stage classes in the aphid population. These functions will be primarily concerned with the stage-structured aphid populations.

The chapter is divided into three sections. First, the age-specific demographic models with density dependence are considered, models being constructed to describe the relationships between parameter values and population density. Secondly, the models are modified and stage classes incorporated into the demographic functions. An experiment designed to determine how changes in stage structure effect these demographic functions is also described, and results are presented that allow the quantification of the models' parameters. The sub-models are validated by simulation.

4.2 Age-Specific Demographic Models with Density Dependence

The method used in this section to incorporate the effect of density is based on describing the parameters of the age-specific demographic models in relation to the density of the stage homogeneous population. The resulting mathematical description can then be used to estimate the parameters of the demographic model at various population densities. A correlation test and the Kolmogorov-Smirnov test will then be applied to validate the models, as referred to in the previous chapter.

4.2.1 Survival

The model and parameters considered are those of the age-specific survival model described in the previous chapter (see Eq. 3.2 and Table

3.3a). As no significant difference has been shown to exist in the maximum life span at various densities (see Table 3.3a), the mean value of the parameter over all densities has been used as a constant ($a_s = 38.51$). The relationship between parameter b_s (governing the shape of the curve) and population densities of cabbage aphids reared on Brussels sprouts was also considered (Fig. 4.1a). When tested with a second-degree polynomial regression model, parameter b_s of equation 3.2 was affected significantly by the population density N ($\gamma^2 = 0.9041$; d.f. = 3; $p < 0.01$) to give

$$b_s(N) = 0.9068 - 1.4795 \cdot \log_{10} N + 1.0294 \cdot (\log_{10} N)^2 \quad (4.1a)$$

By replacing b_s in Eq. 3.2 with the above equation (4.1a), the age specific survival model can also be written as a function of population density,

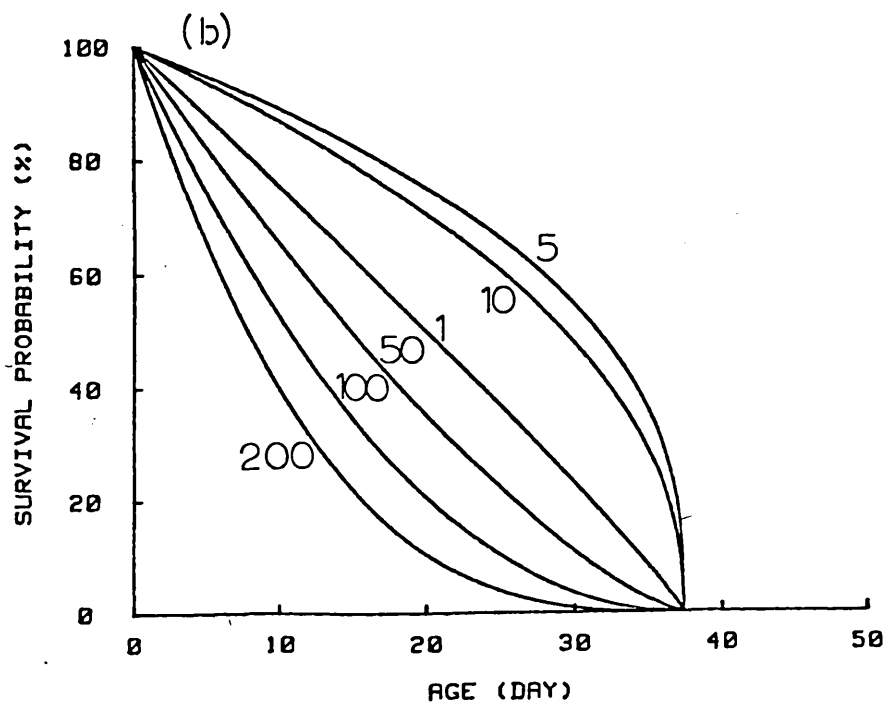
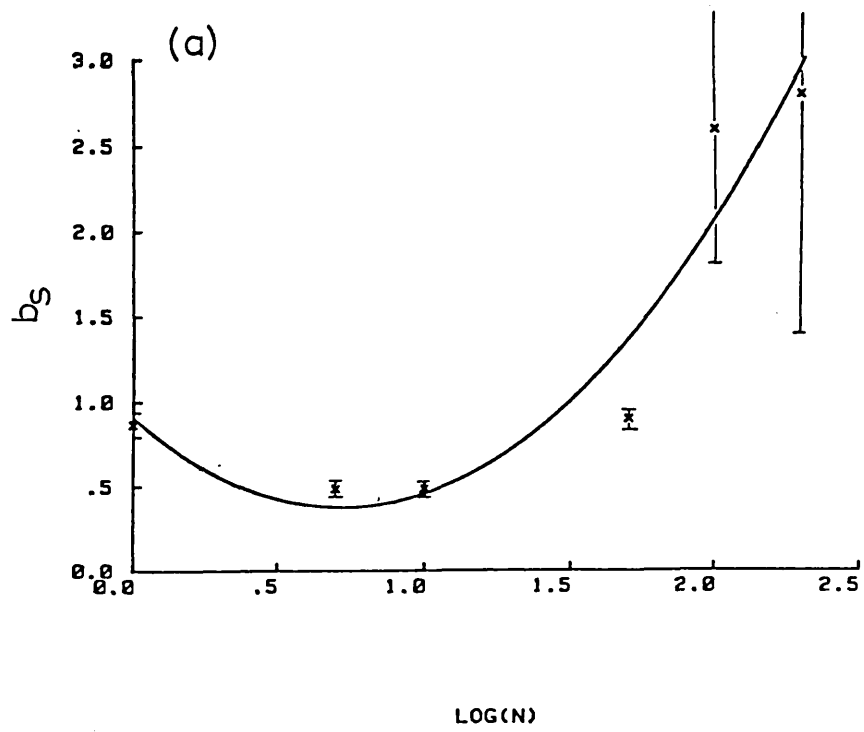
$$S(t, N) = 100 \cdot \left(1 - \frac{t}{38.51}\right)^{b_s(N)} \quad (0 \leq t \leq 38.51; 0 \leq N) \quad (4.1b)$$

where $S(t, N)$ denotes the survival probability of the population with initial density N at age t . The behaviour of the model at various densities is presented in Fig. 4.1(b). The correlation between the model (Eq. 4.1) and the pooled experimental data given in the previous chapter is good ($\gamma^2 = 0.9556$; d.f. = 238; $p < 0.01$), and furthermore the statistic of the Kolmogorov-Smirnov test for goodness of fit showed that the agreement of the model to the experimental data was significant ($D = 0.0038$; $p < 0.05$). This suggests that the model is an adequate description of the experimental data, and that it can be used to predict the probability of survival at various densities. The model predictions at various densities are presented in Figure 4.1b.

The survivorship curves described in the previous chapter may be

Figure 4.1

- (a) Relationship between parameter $\underline{b_s}$ of equation 3.2 and population density ($\log(N)$). The fitted curve is described by equation 4.1(a).
- (b) Behaviour of the age-specific survival model with density dependence (equation 4.1). Values on lines are the initial population densities. See text for discussion.



shown as a continuum starting at a density of one and increasing to 200, as shown in Figure 4.1b. This confirms that the types of the survivorship curves obtained for B. brassicae can be generated by changing the initial density.

4.2.2 Fecundity

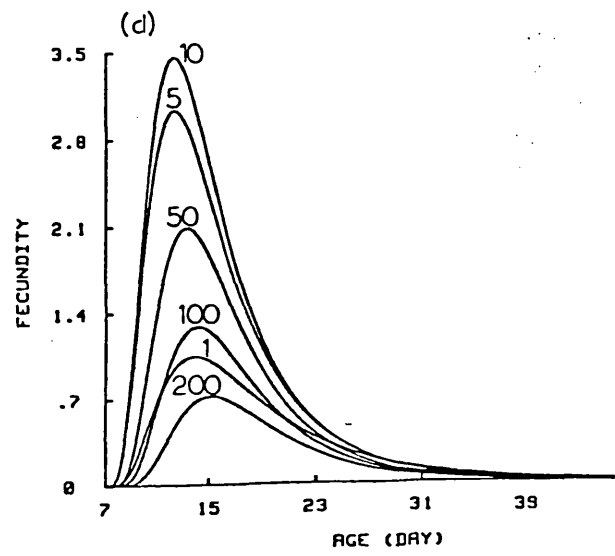
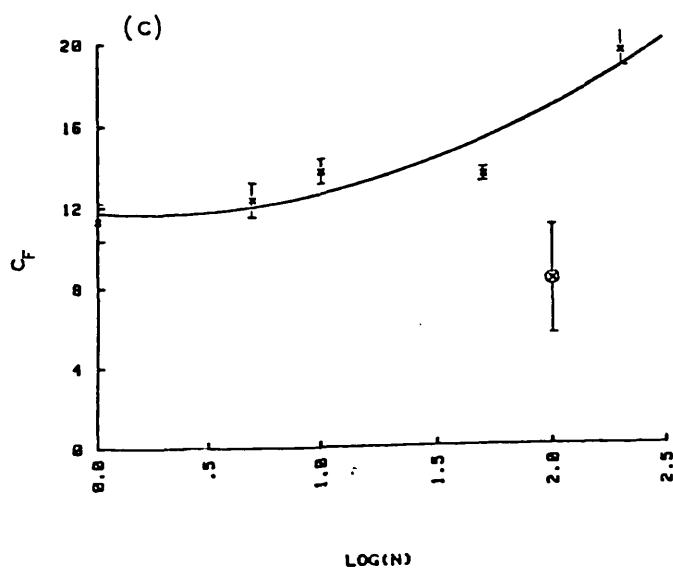
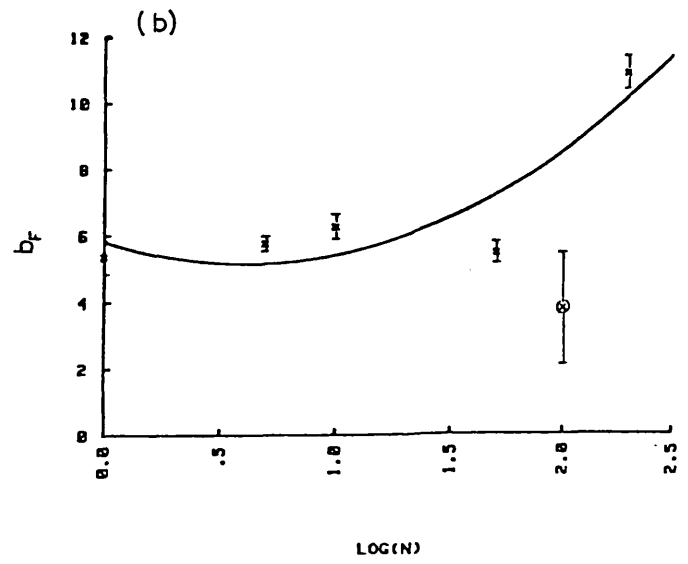
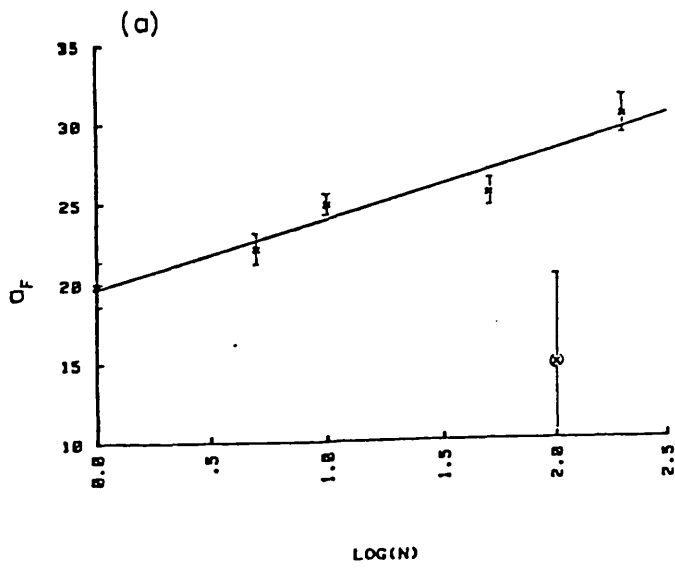
Similar steps were used, as for the survival model, to expand the age-specific fecundity model (see Eq. 3.8) into a density dependent one. The values of parameters $\underline{a_F}$, $\underline{b_F}$ and $\underline{c_F}$ in the fecundity model (see Table 3.8), although variable, were not consistently affected by initial population densities of B. brassicae (Figure 4.2). When tested with high-order polynomial regression models, the relationships between the parameters $\underline{a_F}$, $\underline{b_F}$ and $\underline{c_F}$ and the initial population densities became impractical as the degrees of freedom were reduced to one. Furthermore, if we replace the three parameters in equation 3.8 with these high-order polynomial regression models, the validation test of the fecundity model showed that the difference between the experimental data and the model's predictions are significant at densities 10, 50, 100, and 200 ($p < 0.01$).

A problem in deducing trends in the parameters $\underline{a_F}$, $\underline{b_F}$ and $\underline{c_F}$ is the apparently drifting data point at density 100. The relationships shown in Figure 4.2 are those omitting these points, a questionable procedure, but in part can be justified by the very much larger confidence limit about these points compared to all the others.

If we ignore the data points occurred at density 100, parameter values estimated from the other density will show a significant relationship to the initial population densities, $\underline{N}$, and the relationships can be described by relatively simple regression equation. Parameter $\underline{a_F}$, was estimated with a linear regression equation,

Figure 4.2

Relationship between parameters $\underline{a_F}$, $\underline{b_F}$ and $\underline{c_F}$ of Equation 3.8 and initial population density ($\log(N)$) for (a), (b) and (c) respectively (lines given by Equation 4.2a, 4.2b and 4.2c). (d) Behaviour of the age-specific fecundity model (Equation 3.8) with density dependent parameters $\underline{a_F}$, $\underline{b_F}$ and $\underline{c_F}$ given by Equations 4.2a, 4.2b and 4.2c at various densities. Values on peak of curve are the initial population densities. See text for discussion. Points " $\otimes$ " in (a), (b) and (c) represent the parameters obtained at density 100.



$$a_F(N) = 19.6788 + 4.2255 \cdot \log_{10} N, \quad (4.2a)$$

$$(\gamma^2 = 0.9348; \text{d.f.} = 3; p < 0.01).$$

parameter $\underline{b}_F$ with a second-degree polynomial regression equation

$\gamma^2 = 0.7719; \text{d.f.} = 2; p < 0.05$),

$$b_F(N) = 5.8097 - 2.1420 \cdot \log_{10} N + 1.7336 \cdot (\log_{10} N)^2, \quad (4.2b)$$

and similarly parameter $\underline{c}_F$ ($\gamma^2 = 0.8726; \text{d.f.} = 2; p < 0.05$),

$$c_F(N) = 11.7247 - 0.7473 \cdot \log_{10} N + 1.6430 \cdot (\log_{10} N)^2. \quad (4.2c)$$

The curves are presented in figures 4.2a, 4.2b, and 4.2c, respectively.

As for the survival model, the age-specific fecundity model, which is also a function of initial density, was obtained by replacing Eqs. 4.2a, 4.2b and 4.2c for $\underline{a}_F$, $\underline{b}_F$ and $\underline{c}_F$ respectively in Eq. 3.8. Therefore the final expression for fecundity becomes:

$$F(t, N) = \text{Exp}(a_F(N)) \cdot (t-k)^{b_F(N)} \cdot t^{-c_F(N)}. \quad (4.2d)$$

The behaviour of the model is presented in Figure 4.2d. The correlation between these numerical examples and the pooled experimental data was very significant ($\gamma^2 = 0.7649; \text{d.f.} = 160; p < 0.001$), and the statistic of the Kolmogorov-Smirnov test for the simulation shows a good fit to the data ($D = 0.0047; p < 0.05$). The results support the belief that the model developed in this subsection can be accepted and applied to describe the age-specific and density-dependent fecundity of B. brassicae.

From the simulation results it is predicted that the highest fecundity occurs at a density of ten, the peak of the curve declining rapidly as density is either increased or decreased, as referred to in Section 3.5.2.

4.2.3 Development

A similar approach is used to develop expressions for the parameters of the development models for the third and fourth instars described by Equation 3.10. First, by considering the parameters of the model for the third instar stage given in Table 3.15(a), it was found, using a t-test, that the values of parameter $\underline{b}_3$ (standard deviation of developmental rate) at various densities did not differ significantly from each other at the 5% level, while the values for parameters $\underline{a}_3$ (adjusting constant) and $\underline{c}_3$ (mean developmental rate) differed significantly between densities. A second-degree polynomial regression equation is used to describe the relationship between $\underline{a}_3$ and $\underline{N}$ (see Figure 4.3a):

$$\begin{aligned} a_3(N) &= 0.2320 - 0.0429 \cdot \log_{10} N + 0.0125 \cdot (\log_{10} N)^2, & (4.3a) \\ (\gamma^2 &= 0.8931; \text{d.f.} = 3; p < 0.01), \end{aligned}$$

$\underline{b}_3$ can be considered as a constant, given by the mean value, 0.0274, while the relationship between $\underline{c}_3$ and $\underline{N}$ (see Figure 4.3b) can be expressed as:

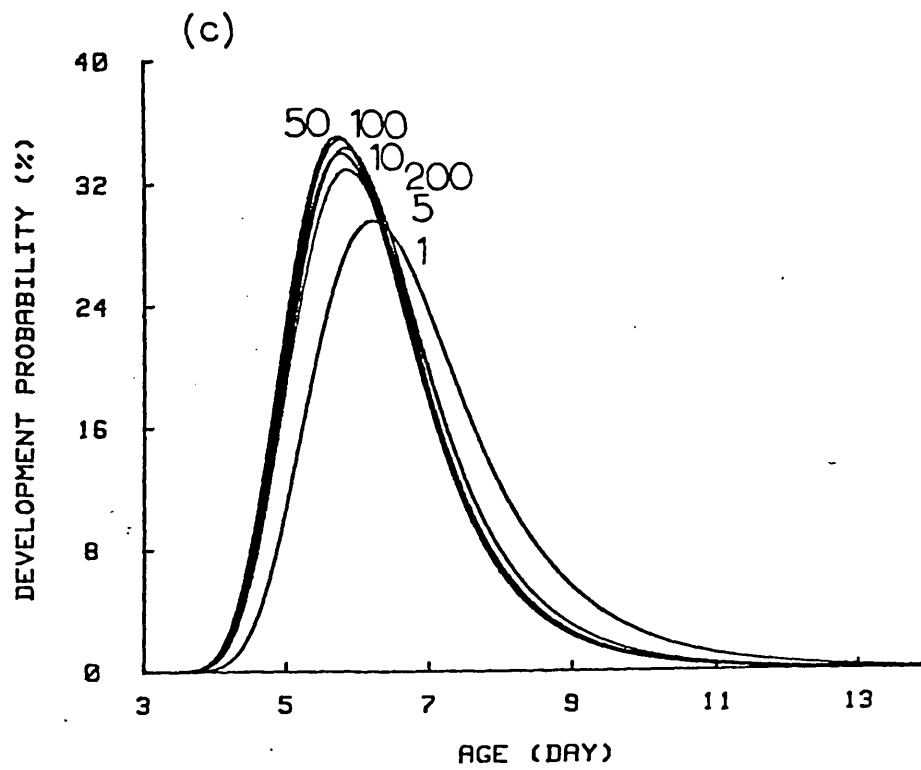
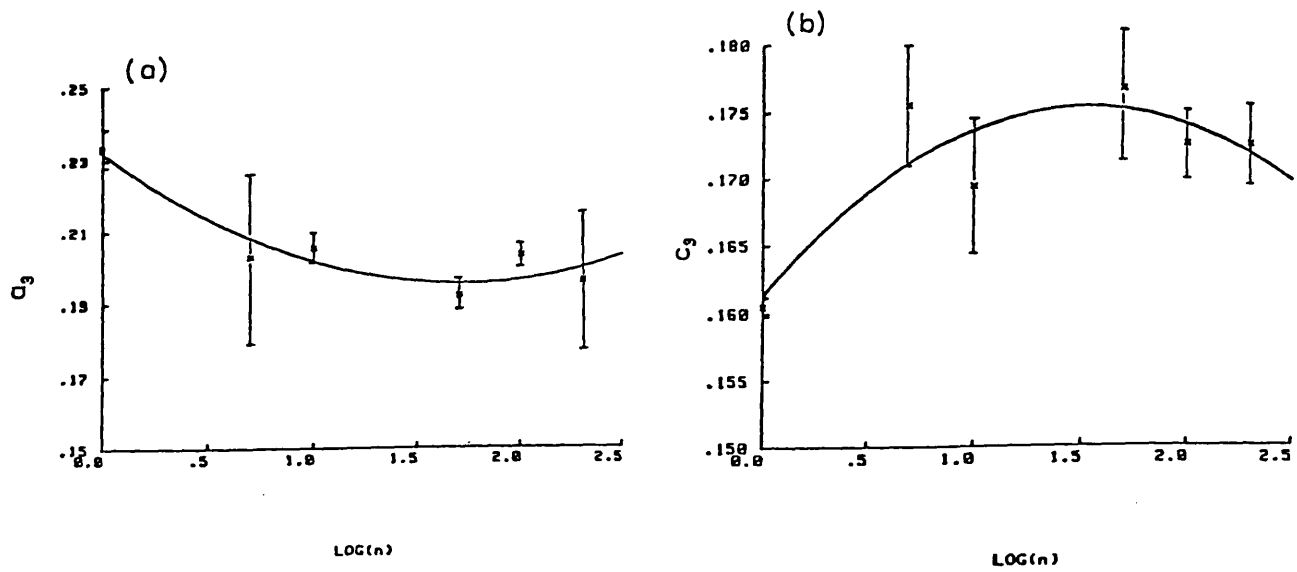
$$\begin{aligned} c_3(N) &= 0.1613 + 0.0183 \cdot \log_{10} N - 0.0060 \cdot (\log_{10} N)^2, & (4.3b) \\ (\gamma^2 &= 0.7509; \text{d.f.} = 3; p < 0.01). \end{aligned}$$

From this approach it was again found that the developmental model for third instar aphids was a function of density. This function can be described by replacing $\underline{a}_3$ and $\underline{c}_3$ in equation 3.10 with the expressions in Eqs. 4.3a and 4.3b, and replacing $\underline{b}_3$ by the constant 0.0274. This gives:

$$P_3(t, N) = (a_3(N) \cdot b_3 \cdot \sqrt{2\pi})^{-1} \cdot \text{Exp}(-\frac{1}{2}((\frac{1}{t} - c_3(N))/b_3)^2). \quad (4.3c)$$

Figure 4.3

Development of the third instar stage of B. brassicae. Relationships between parameters a_3 (a) and c_3 (b) of Equation 3.10 and initial population density ($\log(n)$). The fitted curves are given by Equations 4.3a and 4.3b for (a) and (b), respectively. (c) The behaviour of the age-specific and density-dependent development model for the third instar. See text for discussion. Values on line are the initial population densities.



The correlation between the model prediction and the experimental data was highly significant ($\gamma^2 = 0.9653$; d.f. = 52; $p < 0.01$), and the statistic of Kolmogorov-Smirnov test showed a good fit between data and model ($D = 0.2294$; $p < 0.05$).

The behaviour of the development model at various densities is presented in Figure 4.3c. The curves at densities 5, 10, 50 and 100 and 200 are relatively close and similar, their parameters not differing significantly at the various densities (c.f. Table 3.15(a), Fig. 4.3a and Fig. 4.3b). The curve of development probability at density one, in which the peak of the curve is lower and its timing later than at other densities, is the only curve significantly different from the others (Fig. 4.3c).

These results are consistent with those of the previous chapter (c.f. Table 3.15(a)).

The development model for the fourth instar is approached in a similar manner. However, all parameters now show significant differences at the various densities (Table 3.15(b)). The relationships between the three parameters and the initial density N can be written as:

$$a_4(N) = 0.4001 - 0.1145 \cdot \log_{10} N + 0.0664 \cdot (\log_{10} N)^2, \quad (4.4a)$$

$$(\gamma^2 = 0.9290; \text{d.f.} = 3; p < 0.01)$$

for parameter a_4 (in figure 4.4a),

$$b_4(N) = 0.0199 - 0.0048 \cdot \log_{10} N + 0.0016 \cdot (\log_{10} N)^2, \quad (4.4b)$$

$$(\gamma^2 = 0.6803; \text{d.f.} = 3; p < 0.05)$$

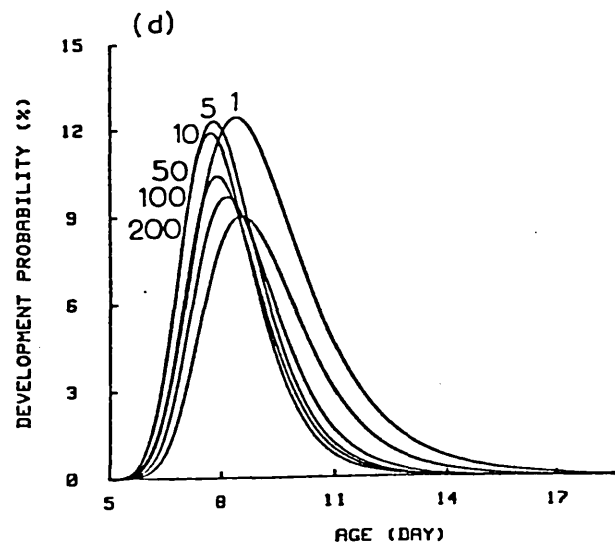
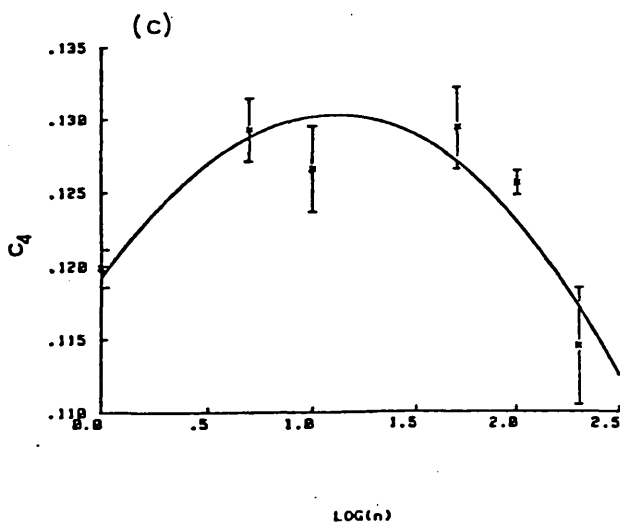
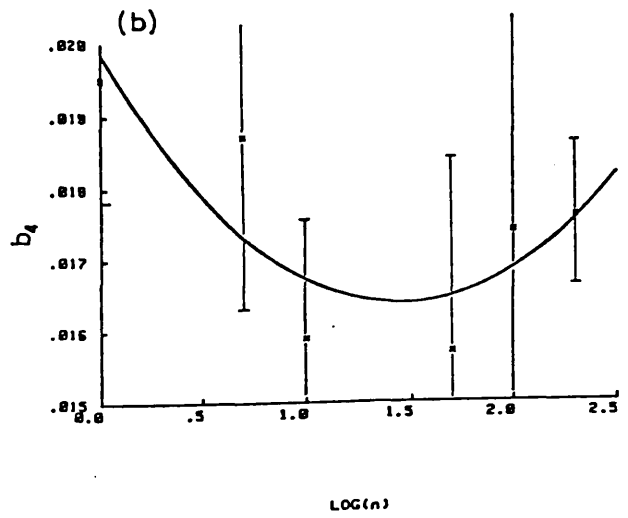
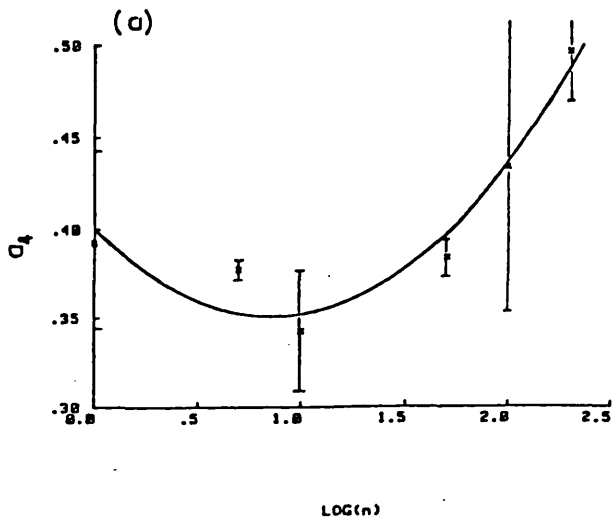
for parameter b_4 (in figure 4.4b) and

$$c_4(N) = 0.1192 + 0.0200 \cdot \log_{10} N - 0.0091 \cdot (\log_{10} N)^2, \quad (4.4c)$$

$$(\gamma^2 = 0.8069; \text{d.f.} = 3; p < 0.01)$$

Figure 4.4

Development of the fourth instar stage for B. brassicae. Relationships between the parameters in the model (see Equation 3.10 and Table 3.15) and initial population density ($\log(n)$) for parameters $\underline{a}_4$, (a), $\underline{b}_4$, (b) and $\underline{c}_4$, (c). (d) The behaviour of the age-specific and density-dependent development model for the fourth instar. Values on line are initial population densities. See text for discussion.



for parameter $\underline{c}_4$.

An age-specific and density-dependent development model for the fourth instar stage can be obtained by replacing $\underline{a}_4$, $\underline{b}_4$ and $\underline{c}_4$ in Eq. 3.10 by the expressions in Eqs. 4.4a, 4.4b, and 4.4c. This, then, has the form:

$$P_4(t, N) = (a_4(N) \cdot b_4(N) \cdot \sqrt{2\pi})^{-1} \cdot \text{Exp}(-\frac{1}{2}((\frac{1}{t} - c_4(N))/b_4(N))^2). \quad (4.4d)$$

The predictions of the model show a highly significant correlation ($\gamma^2 = 0.7430$; d.f. = 52; $p < 0.01$) and a good fit (K-S statistic, $D = 0.2050$; $p < 0.05$) to the pooled experimental data.

The predicted curves at various densities are presented in Figure 4.4d. The variance in the distribution of development probability is small at densities 10 and 50, becoming larger as the density either increases or decreases (c.f. Table 3.15(b)). The times at which the curve peaks at the various densities are consistent with the order in Table 3.15(b).

4.3 Extending the Demographic Models to Age Heterogeneous Populations

The previous section has outlined an approach for constructing age-specific and density-dependent demographic models where age-specific processes have been described by simple functions in which the parameters are then treated as functions of initial population density. In this section a brief outline of the development of a demographic model for age heterogeneous populations is presented. In the second part of this section experiments are described which were designed to investigate how changes in densities of different subpopulations (see below for definition), of the age heterogeneous total population affect the demographic rates of B. brassicae. The results are presented and discussed below.

4.3.1 The Modification of the Models

The demographic models discussed in the previous section can be modified to include interactions between the subpopulations which are comprised of young juveniles (first and second instars), old juveniles (third and fourth instars), and adults. Over the course of population growth it is assumed that the influences of various densities of different stages on demographic rates of the population are different. The effect of density can then be described by a linear combination of each subpopulation, written as

$$f(N) = \sum \alpha_i n_i, \quad (4.5)$$

where n_i is the subpopulation at stage i , and α_i is the weighting coefficient for stage i . The weighting coefficients reflect the per capita equivalence in density amongst other stages and are commonly called "competition coefficients" (c.f. Lokta, 1925; Volterra, 1926; Comins & Hassell, 1976; Hassell & Comins, 1976; Bellows & Hassell, 1984).

In the development of the survival model $S(N,t)$, the total population N in the model may be replaced in order to allow the inclusion of inter-stage interactions in a linear combination, A , of each tested subpopulation density n_i at stage i . The combination A is given as:

$$A = \sum u_i n_i, \quad (4.6)$$

where u_i is the competition coefficient of survival for stage i .

To expand the fecundity model to include these interactions a similar approach to that used for the survival model is employed. Thus for the fecundity model $F(N,t)$, the combination B to replace

total population $\underline{N}$ is written as,

$$B = \sum V_i n_i \quad (4.7)$$

where $\underline{V_i}$ is the competition coefficient for fecundity of stage $\underline{i}$ amongst other stages. For the development models $P_i(N,t)$, the combination $\underline{C}$ can be used to replace $\underline{N}$ as in the previous two models. It is thus given as,

$$C = \sum W_i n_i, \quad (4.8)$$

where $\underline{W_i}$ is the competition coefficient for development of stage $\underline{i}$ amongst other stages.

4.3.2 Experimental Materials and Methods

In any natural population of B. brassicae, several developmental stages will be observed during the summer. This makes a study of inter-stage-class effects important. To consider all possible interactions experimentally would, however, be too time consuming. The investigation has therefore been confined to three stages: young nymphs (first or second instars), old nymphs (third or fourth instars), and adults, using densities of 1, 10 and 100 individuals. A total of 27 combinations of different densities of the three stages was used, with each combination replicated five times as shown in Table 4.1.

The experiment was conducted using the same culture of standard cohorts of B. brassicae as in the previous chapters, and was conducted at 25°C, 60-70% relative humidity, and 16 h photoperiod. The general procedure of the experiment was as in experiment I (referred to in Section 2.12) but in this case the tested aphids were chosen from different age groups of the culture. The initial colonies of young and old nymphs

Table 4.1 The replicates and combinations of the three stage groups of B. brassicae

Young Juvenile	Old Juvenile	Adult Stage		
		1	10	100
1	1	5	5	5
	10	5	5	5
	100	5	5	5
10	1	5	5	5
	10	5	5	5
	100	5	5	5
100	1	5	5	5
	10	5	5	5
	100	5	5	5

of B. brassicae were taken from the culture on days 2 and 6 respectively. Newly emerged adult cohorts were obtained at day 10. The total number of offspring produced were counted and removed, and the time of death for the adults noted. In the case of the nymphs the time of moulting and death were also recorded. The experiment was terminated on the day when all the nymphal groups had developed to adults, and when the adult groups had stopped breeding. In general, the experiment lasted for 30 days.

A non-linear least squares method was used to estimate values of the model parameters derived from the experimental data. The method has been discussed briefly by Bellows (1981, 1982a, and 1982b) and Bellows & Hassell (1984). Following the same approach, the interstage competition coefficients $\underline{u}_i$, $\underline{v}_i$, and $\underline{w}_i$ for the survival, fecundity, and development models (Eqns. 4.6, 4.7 and 4.8) were estimated from the results of the experiment. Values of other parameters, i.e. $\underline{a}$, $\underline{b}$, and $\underline{c}$, used in the analysis were those previously estimated from stage homogeneous populations (referred to the previous section).

4.3.3 Results and Discussion

The results of the analysis of the inter-stage effect on survivorship are summarized in Table 4.2. The observation that in general the interaction coefficients for the various stage groups approached unity, suggests that, at least in terms of survivorship, no significant interactions occurred between the three stage groups. By applying a χ^2 test it was established that inter-stage competition was not making a significant impact on their survivorship ($p > 0.05$).

The analysis of inter-stage effects on fecundity of adults and on development for old juveniles are summarized in Table 4.3 and Table 4.4,

Table 4.2 The estimates of inter-stage competition coefficients of survivorship U_i (referred to in Eqn. 4.6), of B. brassicae. The values across each row give the effect on that stage by the stages identified at the top of each column.

<u>Stage</u>	<u>Young Juvenile</u>	<u>Old Juvenile</u>	<u>Adult</u>
Young Juvenile	1	1.0532±0.0931	1.2458±0.3822
Old Juvenile	0.9567±0.1427	1	1.1024±0.2075
Adult	0.8043±0.3152	0.9975±0.1028	1

Table 4.3 The estimates of inter-stage competition coefficients affecting fecundity V_i (referred to in Eqn. 4.7), of B. brassicae. Same as Table 4.2

Stage	Young Juvenile	Old Juvenile	Adult
Adult	0.7321 $\pm$ 0.4113	0.8941 $\pm$ 0.3221	1

Table 4.4 The estimates of inter-stage competition coefficients affecting development for old juveniles, W_i (referred to in Eqn. 4.8), of B. brassicae. Same as Table 4.2.

Stage	Young Juvenile	Old Juvenile	Adult
Old Juvenile	0.8896 $\pm$ 0.3373	1	1.1232 $\pm$ 0.2371

respectively. Following the same approach as above, a χ^2 test showed that the interaction coefficients did not differ significantly from unit ($p > 0.05$), suggesting that fecundity and development rate are affected equally by the three stage groups.

It would appear from the experimental results that inter-stage effects are unlikely to affect significantly the various demographic rates. Other factors may, however, play an important role. The young Brussels sprouts plants used in the experiment may be capable of compensating for damage arising from insect infestation (e.g. cabbage aphids). Over a short period of time, such as that used in the experiment, this extra growth might be able to provide a sufficient nutrient source for the aphids. This would reduce the effects of inter-stage interactions on the various demographic rates. The aphid does show a relatively strong tendency of aggregative behaviour (Hayamizu, 1982), and different stage groups of B. brassicae could have different responses. Young juvenile groups show considerable aggregation while old juveniles and adults are relatively mobile. Such difference could have important consequences, particularly when potentially mobile aphids have been disturbed by being transferred onto a plant while setting up an experiment. The mobility and scatter of old juveniles and adults could reduce mechanical interference between individuals, and be another factor in the reduction of inter-stage effects in the experiment. Because of limitation of time it was not possible to consider more than three densities for each stage group. This, however, may have been insufficient to give a true reflection of the effects mentioned.

4.4 Conclusions

The most important contribution made in this chapter to the modelling of the aphid demographic rates was the extension of the time-specific models to incorporate the density effects of Section 4.2. These models have been applied to data collected during this study, and both show considerable agreement. They allow the development of an age-specific population model incorporating density effects.

Population demographic rates do not appear to be influenced in any significant form by the density effects arising from inter-stage interactions. This may have been due to a number of factors, such as compensatory growth of the host plants, mobility of the aphid, and the experimental design and materials.

In the light of these considerations, the models developed in this chapter and in the previous chapter (Eqns. 3.9, 4.1, 4.2, 4.3, and 4.4) have been used to establish the population model of B. brassicae presented in the following chapter.

Chapter Five

A Population Model of Brevicoryne brassicae (L.)

5.1 Introduction

A theoretical model is an intellectual construction purporting to describe some general phenomenon. A mathematical model, however, contains a set of parameters and variables which are interrelated by specific functions. Models which enable the handling of changes in the age-structure of biological populations date from the eighteenth century (Euler, 1760) but, until relatively recently, their importance has been ignored. Lotka and his colleagues rekindled interest in the subject at the start of this century (Sharpe and Lotka, 1911; Lotka, 1922, 1925), and developed deterministic theories for human population growth. Over the subsequent decades rapid progress has been made in this field and the mathematical aspects of demography have been explored comprehensively (e.g. Keyfitz, 1968, 1977; Pollard, 1973).

When insects which breed continuously (e.g. aphids) are considered the situation is far more complicated and difficult. Information concerning the population dynamics of species with overlapping generations is lacking or, at the most, very scant, and also a satisfactory technique for analysing stage-structured populations is still to be developed.

During the last two decades a number of detailed simulation models describing stage-structured populations have been developed, e.g., Aphis fabae Scop. (Crawley, 1973), A. craccivora Koch (Gutierrez et al., 1974), Acyrtosiphon pisum (Harris) (Gutierrez, Baumgaertner, and Summers, 1984), Brevicoryne brassicae (Hughes and Gilbert, 1968; Gilbert and Hughes, 1971; Chua, 1975; Raworth et al., 1984), Eucallipterus tiliae L. (Barlow and Dixon, 1980), Microlophium evansi Theob. (Perrin, 1974), Rhopalosiphum maidis and R. prunifolia (Shiyomi, 1974), and Sitobion

avenae (Carter, Dixon, and Rabbinge, 1982). Almost all these models are deterministic (dependent on proportions) and the authors have assumed that the relationships between rates and functions incorporated in the models are linear (Hughes, 1963; Gilbert et al. 1976; Barlow and Dixon, 1980; Carter, Dixon, and Rabbinge, 1982). The only exceptional cases are those by Gilbert and Hughes (1971) and Shiyomi (1974), which predict values dependent on probability distributions. A stochastic approach is avoided because of the lack of biological information and the exorbitant amount of computer time required by realistic stochastic models of complex population processes and, instead, a deterministic approach with a discrete time step has been used.

The object of this chapter is to develop a model describing population processes in the cabbage aphid. The model used is basically deterministic but is modified to include different stage-classes for individuals (c.f. Rabbinge and Sabelis, 1980). The chapter can be divided into three parts. The first part describes the development of the model, a partial differential equation system including stage-specific demographic parameters, from which a series of compartment models are constructed.

In the second section, the demographic functions dependent on time and density, developed in previous chapters, are incorporated into the model system and a simulation computer programme presented. Finally, the model is used to simulate the behaviour of populations of the aphids and the results of these simulations are discussed.

5.2 Development of the Model

5.2.1 Formulation of the Continuous-Time Model

The simplest population model is that for exponential growth

$$\frac{dN}{dt} = rN, \quad (5.1)$$

where N is the total population at time t , and r is the growth rate. Clearly, this is not suitable for populations within which competition takes place. In these situations r should be dependent on population size, the larger the population, the smaller the r value. This model has since been modified independently by Verhulst (1838), and Pearl and Reed (1920) to

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \quad (5.2)$$

where K is a stable upper limit known as the carrying capacity, for populations with $N(t) < K$ growth monotonically to K as t tends to infinity. This model is now known as the logistic or Verhulst-Pearl equation. If the model is examined and the ideas expressed in word form, it is evident that it is the product of three factors: (1) a rate constant, r , (2) a measure of population density, N , (3) a measure of the proportion of available limiting resource not yet utilized by the population. Using Taylor's Theorem and a characteristic equation, Lotka (1925) determined the solution of equation (5.2) to be,

$$N(t) = \frac{K}{1 + \left(\frac{K}{N(0)} - 1\right) e^{-r \cdot t}} \quad (5.3)$$

where $N(t)$ is the total population size at time t , and $N(0)$, the initial population size. The model has proved very successful when applied to the growth curves of populations, for example, Drosophila, a bacterial culture (Lotka, 1925), Paramecium caudatum (Gause, 1934),

and the growth of yeast in culture (Odum, 1971). Although the model provided an average fit to the population of the United States between 1790 and 1910 (Pearl and Reed, 1920), the predictive errors have increased dramatically, either as a result of a poor model or an unexpected change in environmental conditions (Varley, Gradwell, and Hassell 1973). The limitations of this model are widely appreciated and is generally regarded as appropriate for describing the growth of populations with binary fission but much less so age-structured populations.

The major problem, therefore, in constructing a model system to describe such populations is incorporating the effects of age structure. Let the size of populations of ages between a and $a + \Delta a$ at time t be $\Delta N(a,t)$. If their number is sufficiently large, it is necessary to introduce the idealization that differential quotients have to be defined for a population. It has been assumed, therefore, that the limit, $\lim_{\Delta a \rightarrow 0} \Delta N(a,t)/\Delta a$, exists and is equal to a quantity $n(a,t)$, the age density function. The total population $N(t)$ can be given by

$$N(t) = \int_{n=0}^{\infty} n(a,t) da. \quad (5.4)$$

More specifically, the subpopulation contains $\int_{a=a_1}^{a_2} n(a,t) da$ individuals with ages between a_1 and a_2 . The number of individuals which are in the age category $(a, \dots, a + \Delta a)$ at time t , is equal to $n(a,t) \cdot \Delta a$. The age of each individual is thus increased by Δa in a small time unit dt . Consequently, if the age group had been isolated during the interval dt (i.e., no immigration or emigration) and no deaths had occurred, it would be held that

$$n(a + dt, t + dt) \cdot \Delta a = n(a,t) \cdot \Delta a. \quad (5.5)$$

Here the units of age and time have been measured in the same dimension. In fact, the net loss of individuals are represented by the difference between the two sides of equation (5.5). Assuming that the loss, $\underline{L}$, is proportional to the number of individuals in the age group, $\underline{n(a,t)\Delta a}$, and to $\underline{dt}$, the loss function is given by

$$L = -D \cdot n(a,t) \Delta a \cdot dt, \quad (5.6)$$

where $\underline{D}$, the mortality function, depends on $\underline{a}$, $\underline{t}$, and $\underline{n}$ or on other factors specifying the system. Thus, the balance equation, using equations (5.5) and (5.6), is given by

$$n(a + dt, t + dt) \Delta a - n(a,t) \Delta a = L,$$

which gives,

$$n(a + dt, t + dt) - n(a,t) = - D \cdot n(a,t) dt. \quad (5.7)$$

By expanding the first term on the left side to the power of $\underline{dt}$ (Dunning-Davies, 1982), $\underline{n(a + dt, t + dt)}$ becomes

$$n(a + dt, t + dt) = n(a,t) + \frac{\partial n}{\partial t} \cdot dt + \frac{\partial n}{\partial a} \cdot dt + \dots + 0 \cdot (dt^2).$$

The result is replaced in equation 5.7, so that the term $n(a,t)$ can be eliminated. By dividing by $\underline{dt}$ and letting $\underline{dt}$ tend to 0, the partial differential equation will hold

$$\frac{\partial n(a,t)}{\partial a} + \frac{\partial n(a,t)}{\partial t} = - D(a,n,t,\dots) \cdot n(a,t). \quad (5.8)$$

Scherbaum and Rasch (1957) and von Foerster (1959) independently derived this equation, but Scherbaum and Rasch's equation is only suitable for the special case of a vanishing loss term. Any solution, $\underline{n(a,t)}$, must be such that the integral equation (5.4) converges, thus implying that

$$\lim_{a \rightarrow \infty} n(a,t) = 0.$$

Thus, integrating equation (5.8) over $\underline{a}$, from $a = 0$ to $a = \infty$, gives:

$$\frac{dN(t)}{dt} = n(0,t) - \int_{a=0}^{\infty} D(a,n,t,\dots) \cdot n(a,t) da. \quad (5.9)$$

Here, the quantity $\underline{n(0,t)}$ is the generalized recruitment rate; that is, the number of individuals that are recruited into the population per unit time, either by birth or by the maturation of individuals from other age subpopulations. Lotka (1925) suggested that the birth process can be described by the "renewal equation"

$$n(0,t) = \int_0^{\infty} b(a) \cdot n(a,t) da, \quad (5.10)$$

where $\underline{b(a)}$, the fecundity function, is the average number of offspring produced by an individual of age $\underline{a}$ per unit time. Let the initial age distribution be

$$n(a,0) = N_0(a). \quad (5.11)$$

Thus, the system (5.6), (5.8) and (5.10) with the initial condition (5.11) constitute the Lotka - von Foerster model. A number of similar objections to the logistic equation, i.e., birth and death processes independent of the population $\underline{n}$, can be applied to the Lotka - von Foerster model. To rectify this, Gurtin and MacCamy (1974) allowed $\underline{b}$ and $\underline{D}$ to be dependent on age $\underline{a}$ and population size $\underline{N}$. The theory is based on the following system

$$\begin{aligned} \frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} &= - D(a,n) \cdot n(a,t), \\ N(t) &= \int_0^{\infty} n(a,t) da, \\ n(0,t) &= \int_0^{\infty} b(a,N) \cdot n(a,t) da, \end{aligned} \quad (5.12)$$

and the initial condition (5.11). Assuming that the mortality function,

$\underline{D}$, the fecundity function, $\underline{b}$, and the initial population, $\underline{N}_0$, are non-negative and sufficiently smooth (in a certain precise sense), Gurtin and MacCamy (1974) established the existence of a unique solution on a sufficiently small time-interval, and proved that if (in addition to the above assumption) $\underline{b}$ is uniformly bounded, then existence and uniqueness hold for all time. All of these results were based on the reduction of the problem (5.11) and (5.12) to a pair of non-linear functional equations for the total population $\underline{N(t)}$ and the birth rate $\underline{B(t)} = \underline{n(o,t)}$. These equations are natural extensions of the linear Volterra integral equation for $\underline{B(t)}$ which occurs in the Lotka - von Foerster theory (Keyfitz, 1968, page 99).

In more general situations, such as in this study, a variable linked in some way to the population's stage of development has been considered instead of the age $\underline{a}$, and the development rate of stage $\underline{I}$ is denoted as $\underline{P_i} = dI/dt$. The partial differential equation which describes the continuous process of the subpopulation of stage $\underline{I}$ becomes (Sinko and Streifer, 1967, 1969):

$$\frac{\partial n(I,t)}{\partial t} + \frac{\partial P_i \cdot n(I,t)}{\partial t} = - D(I,t) \cdot n(I,t). \quad (5.13)$$

In the study of natural populations of B. brassicae, it is difficult to obtain a precise subpopulation of stage $\underline{I}$, $\underline{n(I,t)}$, within a stage structured population. Often while examining the experiment one finds that the subpopulation of stage $\underline{I}$ has been observed in subintervals of the developmental stage $\underline{I}$. Let these subintervals be defined by:

$$S = [I_k, I_{k+1}], \quad (5.14)$$

where $k = 1, 2, 3 \dots$, denotes the developmental stage. Subinterval

measurement has involved the use of the same unit of time, i.e. day, as in the equation system. The equation 5.13 can then be integrated at each subinterval (Argentesi, de Bernardi, and di Cola, 1974) and written as:

$$\begin{aligned} & \frac{d \int_{I_k}^{I_{k+1}} n(I,t) dI}{dt} - P(I_k,t) \cdot n(I_k,t) + P(I_{k+1},t) \cdot n(I_{k+1},t) \\ &= \int_{I_k}^{I_{k+1}} D(I,t) \cdot n(I,t) dI. \end{aligned} \quad (5.14)$$

Let $\underline{N_I}$ denote the subpopulation which include all individuals in stage

$\underline{I}$, i.e. $\int_{I_k}^{I_{k+1}} n(I,t) dI$ or $n(I,t)$,

in equation 5.14. Thus the equation becomes:

$$\frac{dN_I}{dt} = P_{I-1} N_{I-1} - P_I \cdot N_I - D_I \cdot N_I. \quad (5.15)$$

The recruitment to the first instar stage is given by the reproduction of the adult cohort which depends on the fecundity rate, $\underline{F}$, and adult population size, $\underline{N_a}$. The changing rate of the subpopulation for the first instar can thus be written in:

$$\frac{dN_1}{dt} = F \cdot N_a - P_1 \cdot N_1 - D_1 \cdot N_1, \quad (5.16)$$

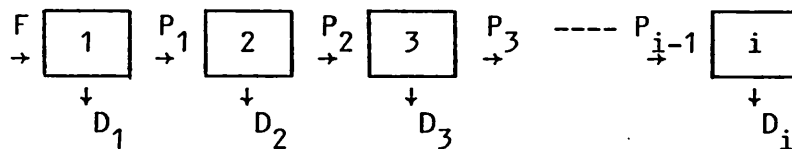
where $\underline{N_1}$ denotes the subpopulations for the first instar. These demographic parameters, fecundity, $\underline{F}$, development, $\underline{P}$, and mortality, $\underline{D}$, discussed in previous chapters are density dependent and age-specific functions.

The mathematical approach applied here has some advantages, in that

it is precise and abstract, it transfers information in a logical way, and acts as an unambiguous medium of communication. The apparent complexity of the symbolic logic, however, at least to non-mathematicians, results in difficulties. A relatively easier approach, compartmental analysis, is, therefore, introduced in a subsequent subsection.

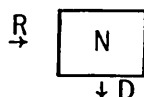
5.2.2 Development of the Compartment Model

The dynamics of stage-structured populations can conveniently be interpreted as a compartmental approach (Atkins, 1969). In this representation the i stages are identified by stage homogeneous and mixed compartments, and the processes of birth ($\underline{F}$), development ($\underline{P}$), and death ($\underline{D}$) in the population are represented by fluxes of input, output, and connections between various compartments, or stages. In general, a population with continuous recruitment, subdivided into i stages of development, can be described by the graph:



This model system will be used as a background model for examining the dynamic effects of population demographic parameters.

In the first case, the population is assumed to be composed only of stage homogeneous individuals, $\underline{N}$, in which the functional difference among the various stages of development are ignored. The juveniles are not considered to be a stage of development, but only as new recruits to the population. This can be expressed by the graph:

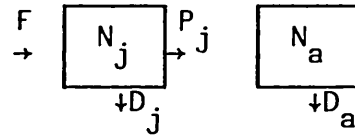


and the process is described by the differential equation:

$$\frac{dN}{dt} = (R - D) \cdot N, \quad (5.17)$$

where R denotes recruitment rate, including birth and development, and D denotes mortality rate.

Secondly the juveniles are considered as an autonomous stage of development, with its own dynamics. Thus the development process of the population can be expanded from one stage to two stages, and is expressed by the graph:



Its dynamic process can be written by a system of differential equations:

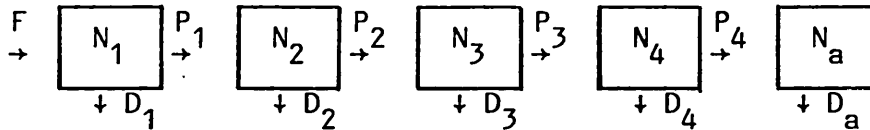
$$\begin{aligned} \frac{dN_j}{dt} &= F \cdot N_a - (P_j + D_j) \cdot N_j, \\ \frac{dN_a}{dt} &= P_j \cdot N_j - D_a \cdot N_a, \end{aligned} \quad (5.18)$$

where a and j denote adult and juvenile stages respectively. Here the subscripts have been used to identify the developmental stages.

The difference between the instantaneous recruitment rate and the mortality rate, R - D, in the one compartment model can be compared with population growth rate in Eqn. 5.1, γ, which is the theoretical innate capacity for increase (Andrewartha and Birch, 1954). The model can be used for the study of those populations in which the development time of the immature stage is very short while living in an unlimited environment.

For populations with a more complex structure and a slower development, such as cabbage aphids, one must subdivide the total population

of aphids into five subpopulations, i.e. first instars (N_1), second instars (N_2), third instars (N_3), fourth instars (N_4), and adult (N_a). To construct a five compartment model, a similar approach to that used for the two compartment model is employed. In this case the scheme of the model becomes:



and is described by the system of differential equations:

$$\begin{aligned}
 \frac{dN_1}{dt} &= F \cdot N_a - (P_1 + D_1) \cdot N_1, \\
 \frac{dN_2}{dt} &= P_1 \cdot N_1 - (P_2 + D_2) \cdot N_2, \\
 \frac{dN_3}{dt} &= P_2 \cdot N_2 - (P_3 + D_3) \cdot N_3, \\
 \frac{dN_4}{dt} &= P_3 \cdot N_3 - (P_4 + D_4) \cdot N_4, \\
 \frac{dN_a}{dt} &= P_4 \cdot N_4 - D_a \cdot N_a.
 \end{aligned} \tag{5.19}$$

Generally, in studies of populations with more complicated stage structures, this model can easily be extended to fit the situation by introducing a new compartment for each additional stage, and describing its dynamics with a suitable differential equation.

The system discussed is one in which the population present is considered to be distributed between a number of separate compartments. The rate of transfer of individuals from a given compartment is proportional to the subpopulation of the aphids within that compartment. The system can thus be simply described by a set of linear differential equations and this constitutes the model for the system. Consequently,

the analysis of this type of biological system, leading to a multi-compartment model for its description allows one to obtain quantitative information about the dynamics of the aphid population within that system.

Basically, the population model is developed from von Foerster's equation (1959). The partial differential equation (5.8) is a kind of first-order quasi-linear equation in which the right term is, in general, a function of age a , time t and population density n , but not of $\partial n/\partial a$ or $\partial n/\partial t$ (i.e., the first order derivatives occur only to the first degree although the equation need not be linear in n).

5.3 A Computer Simulation Model

Demographic processes of the cabbage aphid, Brevicoryne brassicae, on Brussels sprouts, dependent on population density and age of the aphid, were discussed in two previous chapters. In the preceding section, identical models developed from two different approaches for the age-structured aphid population with continuous recruitment have been constructed. This section will consolidate information from the previous studies in the form of a computer model. The computer model was written in BASIC to describe the population dynamics of the aphid. It is a deterministic model predicting age and stage structures of the aphid population in summer. No attempt has been made to simulate population growth on alternative hosts or to model the processes between years. Although the model system developed in the preceding section is in continuous time, the computer model uses discrete time steps which is a constraint imposed when BASIC is used.

Applying a physiological time scale, i.e., degree-day, could simplify a temperature-dependent model (e.g., Campbell, Frazer, Gilbert, Gutierrez,

and MacKauer, 1974). Barlow and Dixon (1980) mentioned three reasons which could cause the physiological time scale to be not generally applicable: (1) some rates of population fluctuation are related non-linearly to temperature so that day-degree totals above a threshold are not applicable, (2) different processes are related to temperature in different ways, and (3) some are related by various factors other than temperature. Furthermore, in this study temperatures were either held constant (in C.T. room) or were relatively uniform (in the field c.f. Chapter 2). It is, therefore, convenient and reasonable to apply a chronological time scale of a day, instead of degree-days.

Generally the differential equations in the model can be re-written in discrete form as:

$$\frac{\Delta N_i}{\Delta T} = P_{i-1} \cdot N_{i-1}(T, A_{i-1}) - P_i \cdot N_i(T, A_i) - D_i \cdot N_i(T, A_i),$$

namely,

$$\frac{N_i(T+\Delta T, A_i+\Delta T) - N_i(T, A_i)}{(T+\Delta T) - T} = P_{i-1} \cdot N_{i-1}(T, A_{i-1}) - P_i \cdot N_i(T, A_i) - D_i \cdot N_i(T, A_i).$$

As the system is operating over a step-length of one day, the equation can be rearranged such that

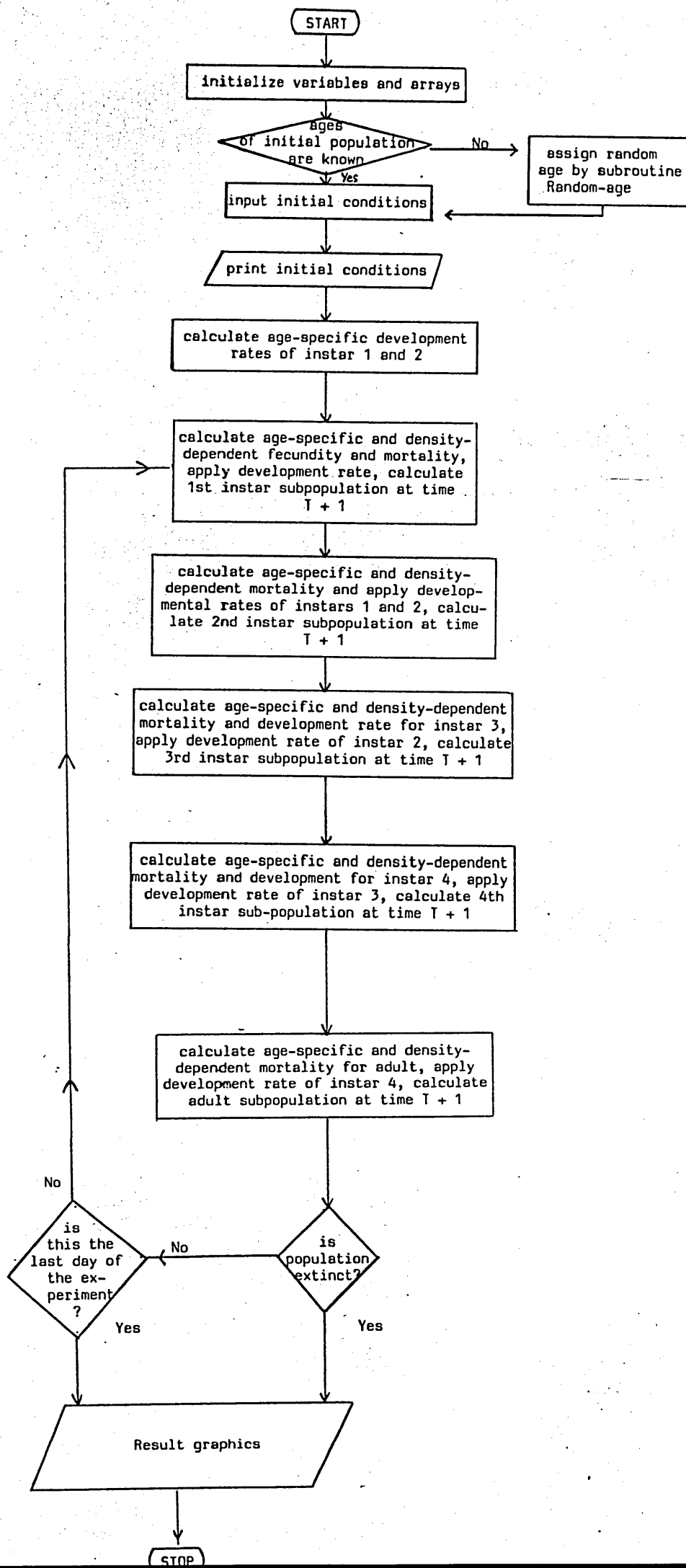
$$N_i(T+1, A_i+1) = N_i(T, A_i) + P_{i-1} \cdot N_{i-1}(T, A_{i-1}) - P_i \cdot N_i(T, A_i) - D_i \cdot N_i(T, A_i). \quad (5.20)$$

This equation is the basis for calculating subpopulations of stage i of age A_i+1 at time T + 1 in the model system.

A flowchart describing the structure of the simulation model is presented in Figure 5.1. During the computation of each stage subpopulation at time T, a series of subroutines for calculating the age-specific and density-dependent mortality, D, fecundity, F, and development

Figure 5.1

Flowchart for the simulation model of a B. brassicae population with continuous recruitment on Brussels sprouts.



P_i , have been executed. These demographic processes were firstly assumed to be functions of the initial total population, $N(1)$, and the age of the cohort, A_i . During population growth it is assumed that the density dependence operates instantaneously. However, in natural situations, it is much more likely that the density dependent effects of fecundity, development, and mortality could operate with some inherent time lags, which will vary from stage to stage. Thus, for simplicity, an average time delay has been assumed for the demographic processes in this model. A delayed density dependent factor, T_d , has, therefore, been introduced into the system. These demographic functions are thus dependent on the variable total population at time $T-T_d$, $N(T-T_d)$, instead of the constant initial population, $N(1)$. The equation (5.20) can be replaced in the form:

$$N_i(T+1, A_i+1) = N_i(T, A_i) + P_{i-1}(N(T-T_d), A_{i-1}) \cdot N_{i-1}(T, A_{i-1}) - P_i(N(T-T_d), A_i) \cdot N_i(T, A_i) - D_i(N(T-T_d), A_i) \cdot N_i(T, A_i). \quad (5.21)$$

The census results collected in Chapter two, experiments I and II, from C.T. room and caged field populations are used in a subjective comparison with the simulated results of the model. The details of the two experiments have been described in Section 2.2.1. Simulations were run with initial conditions similar to those from the experiments. The initial population was 10 first-instar nymphs of less than 24 hours old. An age parameter was set at day one for the initial cohort. For the case of an initial population whose age is unknown the programme provides a subroutine to assign the assumed age to each corresponding stage cohort. The age range of the first instar is from day one to eight; second instar, from day two to nine; third instar, from day four to ten; fourth instar, from day six to eleven; and adult stage,

from day seven to thirty-eight (see Chapter 2). A detailed instruction and full listing of the computer programme are given in Appendix two.

5.4 Validation of the Model

The objective of this section is to determine whether the above model predicts a sensible range of population dynamics (conceptual validation) and the extent to what it can describe specific and independent aphid population data (empirical validation).

5.4.1 Conceptual Validation of the Model

There are two reasons for an initial conceptual approach to validation:

- (1) Conceptual validation which can examine individual parameters, variables, and components in a model, is often difficult and costly in empirical validation; and
- (2) Empirical approaches often provide only limited validation of the overall behaviour of a model.

Conceptual approaches are thus crucial in the validation of models.

To carry out a detailed investigation of model properties requires a systematic analysis of the model, such as:

- (1) Form analysis, which studies the basic structure and implicit assumptions of the model;
- (2) Behaviour analysis, which studies the expected, asymptotic, and probabilistic behaviour of the model.
- (3) Sensitivity analysis, which studies the influences of changes in the model components (e.g. Barlow and Dixon, 1980; Carter, Dixon, and Rabbinge, 1982); and
- (4) Misspecification analysis which is relatively rarely used, studies the effects of using an incorrect model in place of an assumed

correct model (Gilchrist, 1984).

The form analysis of the model system can be checked in Section 5.2 during the development of the model by two different approaches. As model misspecification analysis is seldom applied no attempt has been made to use this method in this study. For a relatively simple model, a feasible method of investigating model behaviour is mathematical analysis which can obtain exact formulae describing the behaviour, (e.g. May, 1972, 1973a; 1973b; 1974a; 1974b; 1980; Hassell and May, 1973; Beddington, Free and Lawton, 1975; May and Oster, 1976; Hassell, Lawton, and May, 1976; Wang and Gutierrez, 1980). Numerical analysis or computer simulation will be applied to approximate the model equations or to simulate a normal model behaviour as the model system becomes increasingly complex.

Since the demographic functions in the model system are dependent on the age and population density simultaneously, it is seldom possible to examine these complex inter-relationships by sensitivity analysis. Two initial conditions, i.e. the initial population density and the time delay of density regulation, are feasible however, and merit further study to investigate their effects on model behaviour. In the present case; therefore, a sensitivity analysis concerns testing selected ranges of specific alternative hypotheses. This method of investigating model behaviour is to compare the simulation results from the model's output of constant proportional changes in each initial condition. The stable, unstable or oscillatory behaviour of the model system as time passes will be investigated qualitatively.

The population trajectories through time corresponding to various time delays with a constant initial population density of ten, have been

shown in Figure 5.1. It is widely known that the magnitude of the time delay, $\underline{Id}$, in a population model governs the fluctuation trajectories of the population (e.g. May 1973a; 1974b; Maynard Smith, 1974; Brauer and Sanchez, 1975; Beddington and May, 1975; Gurney, Blythe, and Nisbet, 1980; Cushing, 1980). Generally, the behaviour of the population model can be qualitatively subdivided into three categories, i.e., approaching a non-zero steady state, oscillating between certain levels, and approaching zero (Figure 5.2).

In this case, the initial population is ten, and when $1 \leq \underline{Id} \leq 13$, there is a singly stable steady state, $N = 235$. Following the increase of the time delay, the amplitude of the population oscillations increase. It is natural to conjecture that here all populations ultimately approach this state. Such oscillatory character of population models caused by a time delay effect has been widely appreciated since Hutchinson (1948) introduced the effect into ecology.

When $14 \leq \underline{Id} \leq 17$, there is no steady state. The population trajectory does not approach a finite steady state, but oscillates continuously while remaining bounded between certain population levels. The decrease for populations that are higher than the steady state is so powerful that they are thrown below the steady state, and as a result the oscillations vary continuously in time. When $18 \leq \underline{Id}$, the effect is so strong that the populations will decrease not only to below the steady state, but to zero at which the population becomes extinct.

Figure 5.3 illustrates the role of $\underline{Id}$ in this population model. As the initial population is changed, the interval of the oscillatory mode is also shifted. When the initial population is higher than 4000,

Figure 5.2

Results of the simulation model for the aphid B. brassicae showing the effects of time delays in the density dependence on the stability of the insect population. Arrow denotes the extinction date of the population.

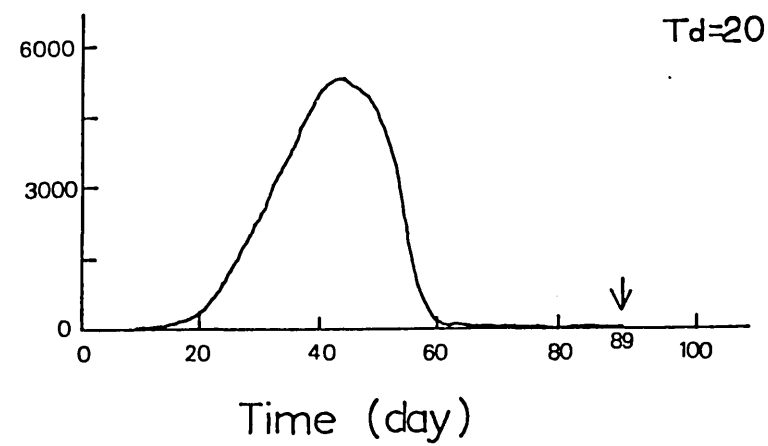
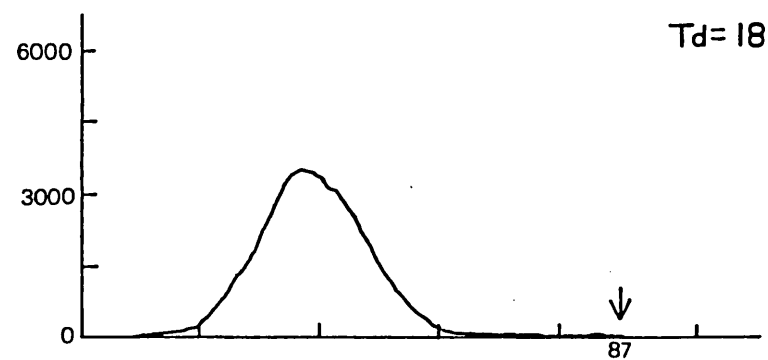
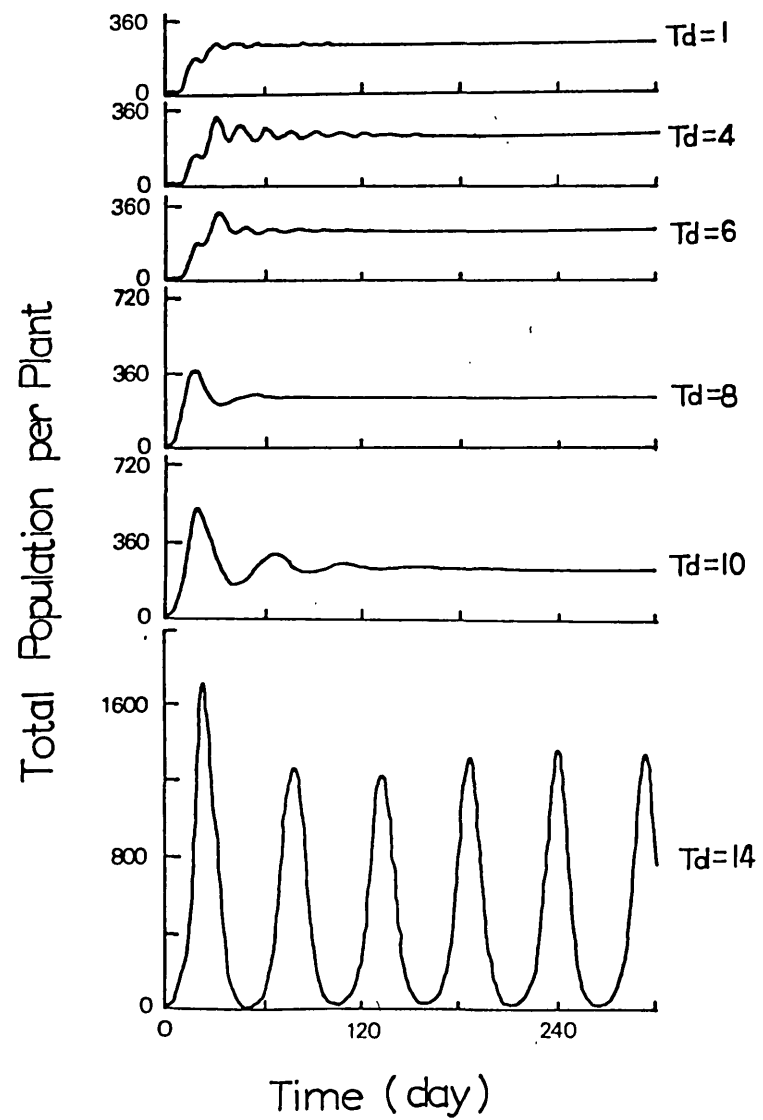
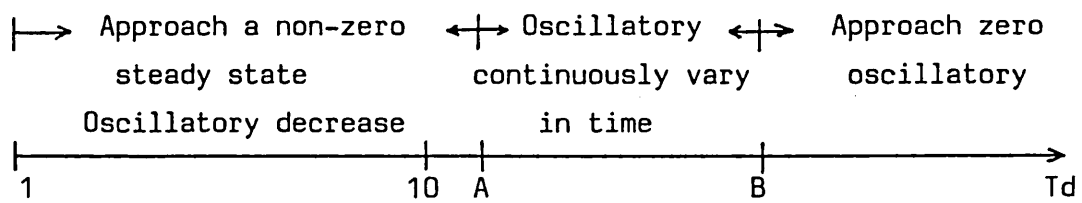


Figure 5.3

Qualitative behaviour of the population model governed by the time delay τ_d . A and B denote the interval of the oscillatory mode.



extinction occurs on day 25 if T_d is 14. If the initial population is 5000 and T_d is 13, extinction will also occur on day 25. Generally, there is little interest in the model system when time delays and initial population densities, are extremely high. Since the demographic functions in the model are developed from experiments with initial populations from one to 200 (Chapter 3 and 4). It, therefore, becomes increasingly unreliable to apply the model to initial conditions with higher values than these.

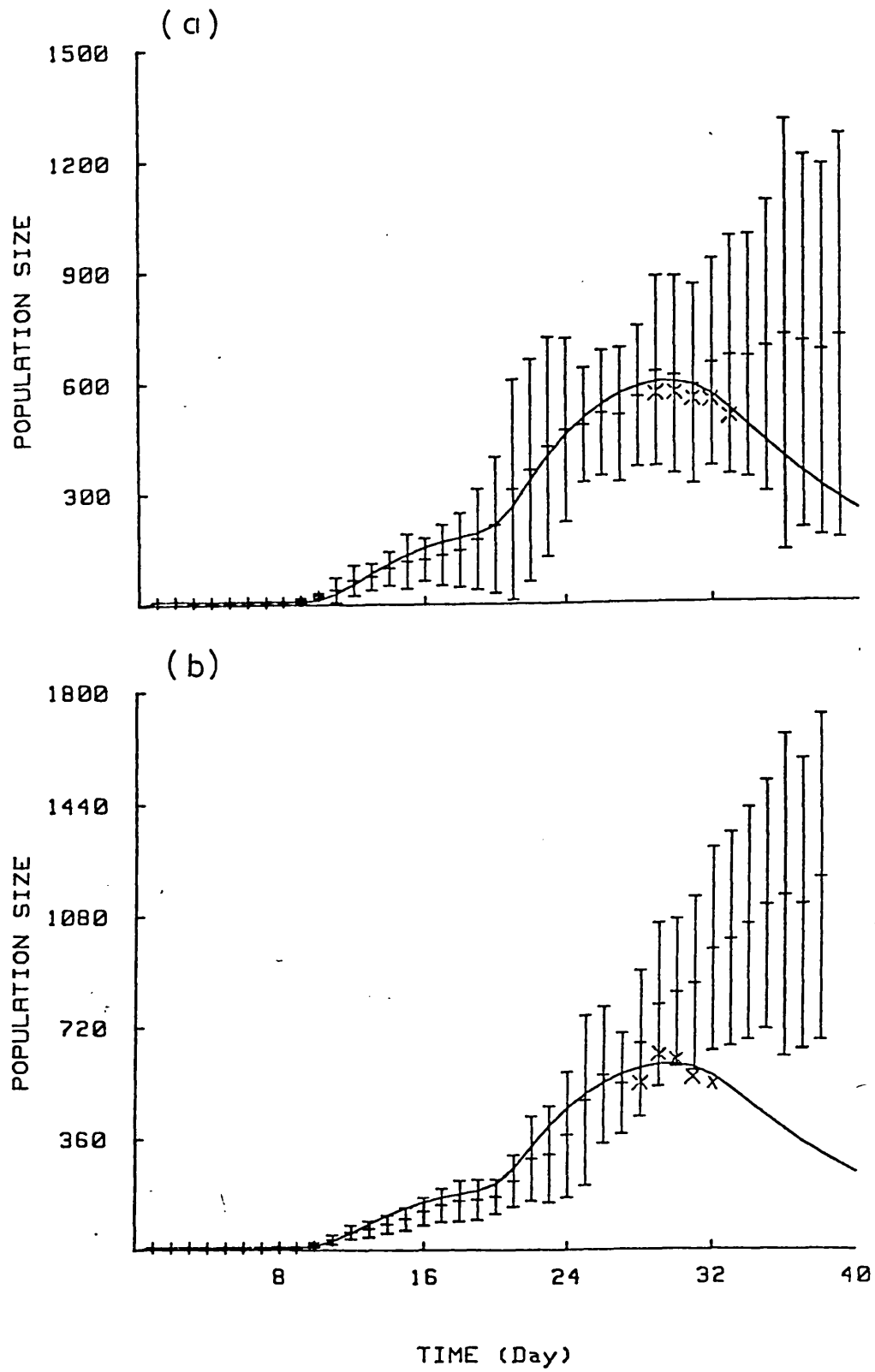
In brief, the behaviour of the model system is determined by the values of the time delays and initial populations. Increasing time delays lead first to a regime of stable states approached by decreasing oscillations, and then to steady states oscillating continuously within limits, and finally to a regime of extinction approached by oscillations. In the absence of time delays numerical calculation shows the model to approach a stable state monotonically. If the initial population is increasing, the extinction date will be shifted forward for longer time delay.

5.4.2. Empirical Validation of the Model

When the validating data (referred to in the experiments I and II with an initial population of ten in Chapter two) are considered and compared with the simulation results a time delay of ten is found to give the most suitable fit to the model (Figure 5.4). For each demographic function in the model, various factors, such as nutrient stress, crowding, and maternal control, etc., could play roles with different weighting in terms of the time delay. For instance some time delays could be longer than the generation time (i.e. the time interval from birth to develop

Figure 5.4

Population changes of the cabbage aphid cultured in (a) Experiment I and (b) Experiment II. The fitted curves refer to the population model with initial population ten and time delay of ten days. Data given as mean $\pm$ S.E. "—+—" includes alate adults. "X" denotes the data excluding alate adults when different.



to an adult), such as nutrient stress or host quality, are considerably crucial to influence demographic rates. Some could be shorter than the generation time, such as the short term effects of crowding and maternal control, and these are more important in influencing rates. For this situation the time delay is an average value of that in the demographic functions and is near the generation time of the cabbage aphid.

In the validating data, the total populations include alate and apterous adults. Since the populations in both experiments are closed alate adults could not fly away from cages. During the first 33 and 32 days, respectively, the records of alate and apterous adults are separated in experiments I and II. Subsequently there is no separate record for the two morphs in either experiments.

The discrepancies between the simulation results and the experimental populations increased after the 31st and 28th day in experiments I and II. It thus seems likely that the discrepancy is due to the production of alate adults which in the model is considered to be a component of adult mortality. The total populations excluding alate adults, show population trajectories for the two sets of experimental data which are consistent with the simulation results (see Figure 5.4), although the data supporting this are limiting.

In Chapters three and four, the Kolmogorov-Smirnov test was used to validate the demographic components of the simulation model. An alternative test for the overall population model uses the residuals, as they contain all the information that is not explicit in the model. If and only if the simulation model fits well to the experimental data, will the residuals between the independent validating data and the

simulation results come from a normal distribution. Thus, each of four standard regression assumptions, i.e., independence, zero expectation, variance, and normality, can be tested. Also, this method does not require the model to be linear (Gilchrist, 1984). It is possible, therefore, to use any functional form that will give simulation data in terms of the known independent variables and parameters.

In this chapter simulation results are compared with the validating data by the differences between them,

$$N_i - \hat{N}_i = e_i,$$

where N_i denotes the population size at time i for the validating data, $\hat{N}_i$, the population size at time i for simulation data, and e_i , the error. Where the fitted model provides an estimate variance S^2 based on known degrees of freedom m , then given n errors e_i a test statistic with an F-distribution with n , m degrees of freedom can be held (Lindgren, 1968),

$$F = \frac{\sum e_i^2 / n}{S^2 / m}.$$

If either the hypothesis that the expectation of errors equals zero, $E(e) = 0$, or, the variance of errors, $V(e)$, equals the variance of the fitted model, σ^2 , are invalid the test will reject the model. The test statistics for the validation of the model system with the population data from experiments I and II are presented in Table 5.1. In this test, the observed data are the population excluding alate adults as for the assumption implied in the model. Thus, only 33 and 32 data points are available for the validation test for experiments I and II, respectively.

Table 5.1 Statistics of the test for the validation of the model system with the data from two independent experiments

Validating Data Source	n	Σe^2	m	S^2	F
Experiment I	33	26124	1	53528.39	0.0148
Experiment II	32	38962	1	52615.18	0.0231

As the calculated values of F are well below the tabulated values, $F_{0.05} = 250.3$ for $n = 33$ and $m = 1$, or 250.2 for $n = 32$ and $m = 1$, the hypotheses of the error expectation and variance, i.e., $E(e) = 0$ and $V(e) = \sigma^2$, are thus accepted ($P > 0.05$). It implies that the residuals between the simulation results and the experimental data are normally distributed. These results thus lead to acceptance of the aphid population model.

Apparently if the production of alate adults, which emigrate from the population, is omitted this would cause a dramatic change in the development of the aphid population. This is a general feature of cereal aphids when natural enemies are not very numerous (Watt and Dixon, 1981; Carter, Dixon, and Rabbinge, 1982).

The predicted and observed data on the stage distributions for each stage are shown for both experiments in Figure 5.5 and 5.6. It should be recalled that age-specific mortality is of considerable importance in determining the total population. The predictions for both experiments, however, were in reasonable agreement with the observed data. A few points require discussion; the predicted distribution curves of the adult stage for both experiments are grossly overestimated due largely to an exaggeration of juvenile mortality at high densities. The juvenile stage distributions, therefore, decreased while the adult stage distribution increases.

For the population model of a species with discrete generations it is useful and convenient to consider the growth of the population in terms of generations (e.g. Nicholson, 1954; May, Conway, Hassell, and Southwood, 1974; Maynard Smith, 1974; Hassell, 1975; Hassell and Comins, 1976; Bellows, 1982a, 1982b). The situation for aphids which

Figure 5.5

The observed and predicted stage-distribution curves for B. brassicae in each stage, (a) - (e). The curves give the predictions from the population model system. Data given as mean $\pm$ S.E. are obtained from Experiment I including alate adults.

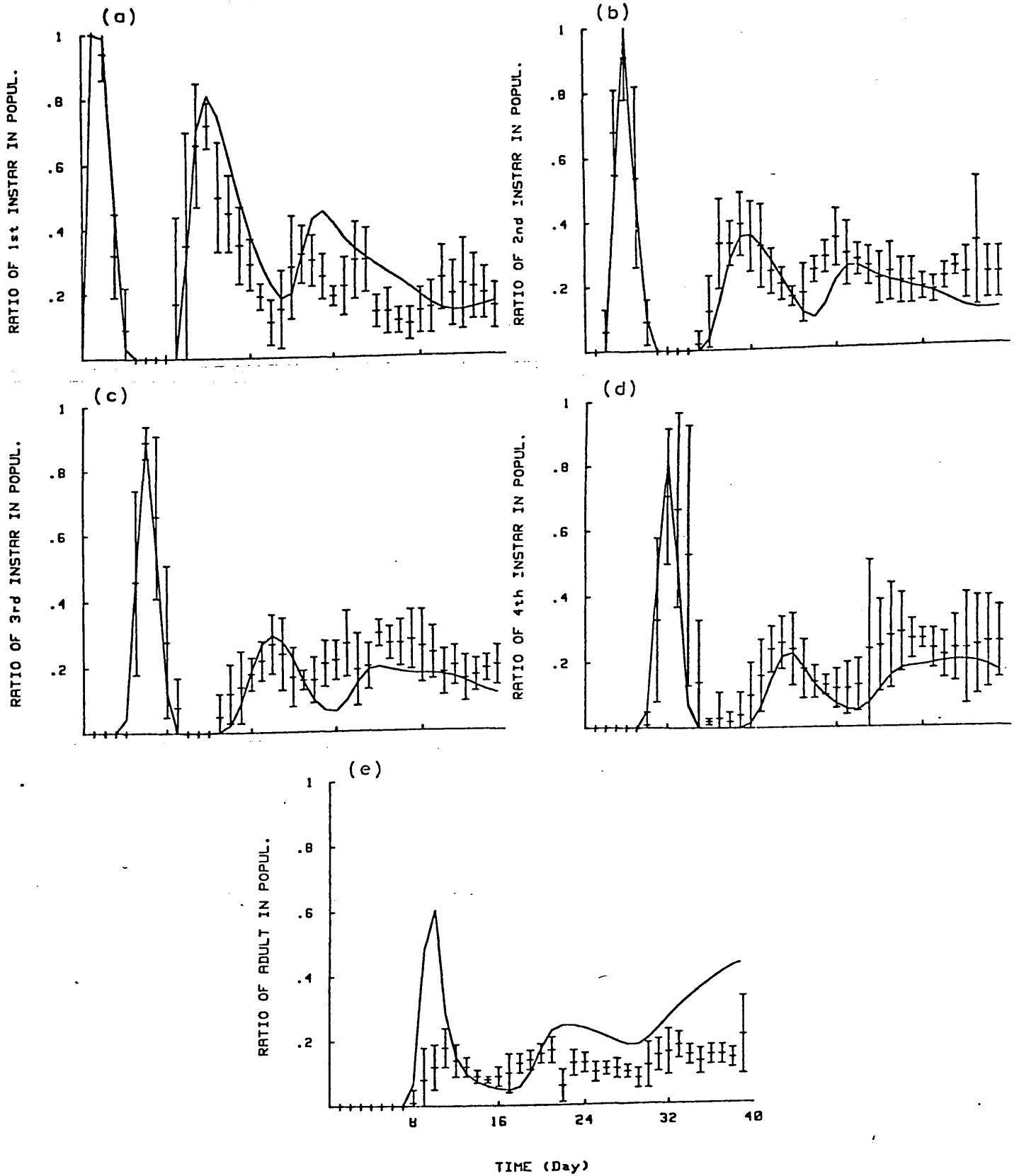
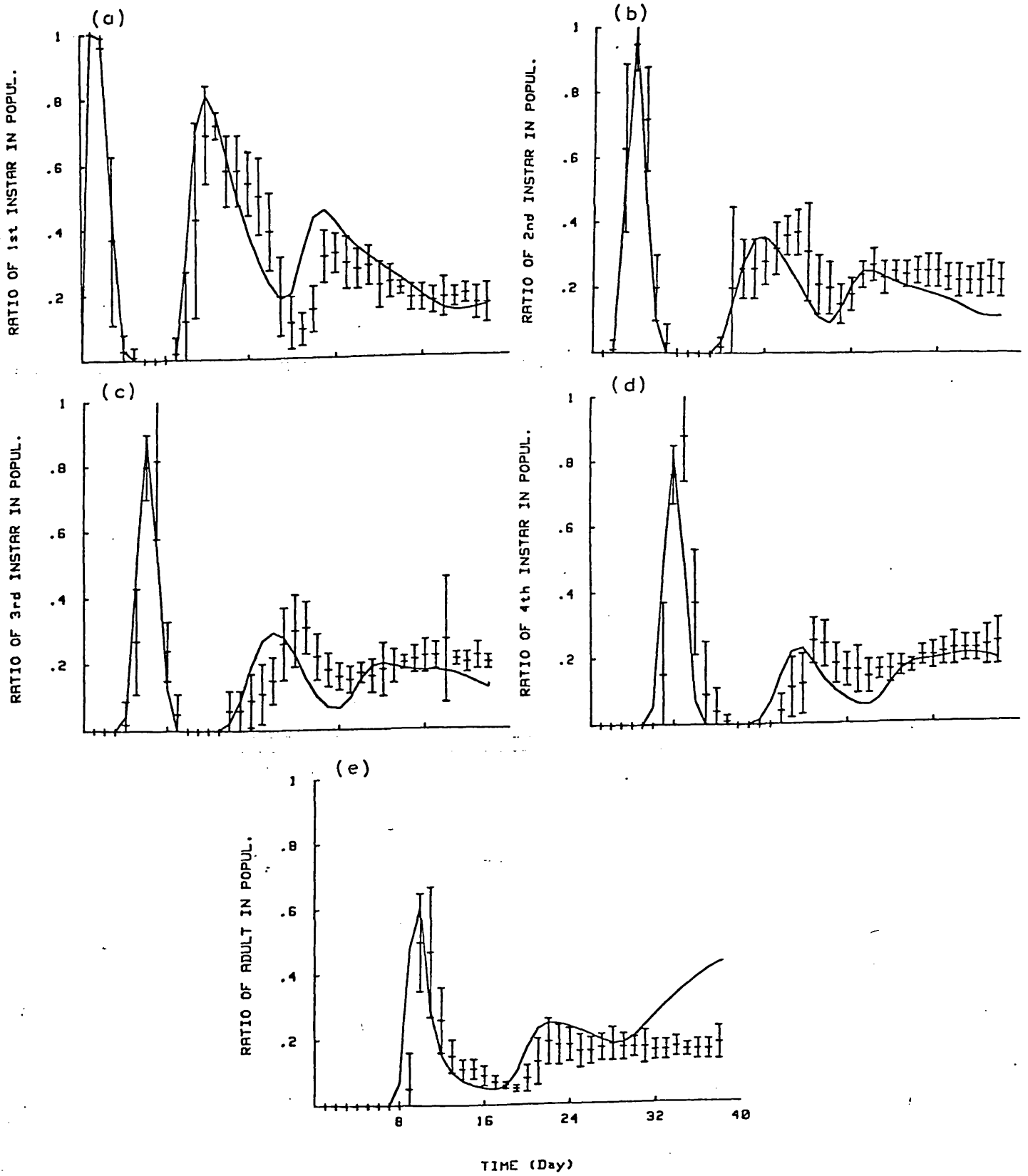


Figure 5.6

The observed and predicted stage-distribution curves for B. brassicae in each stage, (a) - (e). The curves give the predictions from the population model system. Data given as mean $\pm$ S.E. are obtained from Experiment II including alate adults.



breed continuously causing overlapping generations, is different. It is reasonable to consider the growth of the population in terms of time as it is impossible to distinguish generations for each individual when several generations overlap completely (e.g. Gurtin and MacCamy, 1974, 1979; Rorres 1976, 1979; Coleman, 1978; Coffman and Coleman, 1978, 1979; Gurney and Nisbet, 1980; Barlow and Dixon, 1980; Carter, Dixon and Rabbinge, 1982).

It is well known that the most useful validation of the prediction equilibrium or extinction results is by comparison with results of long term studies. Unfortunately, the nature of the aphid and the host plant make such an experiment impossible. Such equilibrium and extinction results, however, would be only pure guesswork and hence are not discussed here.

5.5 Conclusion

The model for B. brassicae based on von Foerster's first-order quasi-linear equation is an age-specific and density-dependent model. The whole system is based on the application of the non-linear demographic functions to a set of differential equations for each stage cohort. It enables us to determine the population growth in terms of an initial age distribution. In the theoretical framework the processes determining population stage-class structure and dynamic behaviour may be closely examined, and thus lead to a better representation of the population and the factors affecting it.

Mathematical and compartmental approaches both serve as valuable tools in the development of the model. Generally mathematical approaches

are relatively abstract in model development and precise in information transfer. This property is particularly useful when the factors concerning the population fluctuation are interacting in a complex manner. Compartmental approaches require extra work in theoretical framework in terms of a series of compartments to describe the behaviour of a biological system. Although the complexity of mathematics required in compartmental approaches is about the same as that in mathematical approaches, the theoretical model of compartmentalisation illustrated by a graph may be accepted more easily.

The term validation used here is in a very wide sense to cover all those processes that take place when considering the practical value of the model in a given situation. In either conceptual or empirical validation it can be found that the model behaves the way in which we could conceive it to behaving and matches the observed data obtained from independent experiments.

The most important contribution made in this chapter to the modelling of insect populations is the development of a five stage-class one-species model. The model has two features:

- (1) It is an age-specific and density-dependent model and can provide detailed information of stage structured populations.
- (2) It may be used to analyse populations with continuous recruitment and overlapping generations.

Furthermore, the model system can be easily extended to include other interacting species, i.e. parasitoid or predator, and it is intended to pursue this problem in the next chapter by incorporating a parasitoid, Diaeretiella rapae (McIntosh).

Chapter Six

Parasitism

6.1 Introduction

In previous chapters populations were treated as isolated or closed. There was no consideration of the possibility that some external factors, such as natural resources (e.g. food, habitat, etc.) and natural enemies (e.g. predators, parasitoids, etc.) might also affect the population dynamics. All of these factors are closely and dynamically related to the population fluctuations. As we can see, the population model for Brevicoryne brassicae developed in previous chapters is far from completely in detail, and attempts to incorporate realism in all factors would lead to fearsomely intractable mathematics. It is feasible, however, to include one or two additional factors in the model.

In this study, the quantity of foliage is not limiting for the cabbage aphids living on Brussels sprouts in the field, but the aphids have a considerable number of natural enemies, i.e. aphid-specific predators, polyphagous predators, parasitoids and fungal pathogens. Diaeretiella rapae (McIntosh) is usually recorded as the most important primary parasitoid of the aphid in the field (George, 1957; Sedlag, 1958, 1964; Hafez, 1961; Hagen and van den Bosch, 1968; Alkinlosotu, 1973; Chua, 1975; and Jusoh, 1984). The parasitoid, D. rapae, is, therefore, chosen to investigate the effect of parasitism on B. brassicae populations.

A detailed review of the relationships between a host and its parasitoid has shown the general importance of these relationships in developing population models (Hassell, 1978). Population models of aphids with parasitoids, which have been constructed for a particular system, however, such as those for the winter moth (e.g. Varley and

Gradwell, 1968; Hassell, 1977) or for some other species in laboratory systems (e.g. Hassell and Huffaker, 1969; Benson, 1974; Podoler, 1974; and Bellow, 1980), are relatively few (e.g. Crawley, 1973; Chua, 1975; Barlow and Dixon, 1980; Carter *et al.*, 1982).

In this chapter a simulation model for B. brassicae with the parasitoid, D. rapae, will be developed. Firstly, a brief review of the biology of D. rapae will be presented. Special attention will be given to the effects of host age and stage parasitized on the host survival and fecundity. Secondly, the functional responses of D. rapae to four developmental stages of B. brassicae (i.e., first, third, and fourth instar, and adult stage) have been examined in order to quantify the dynamic relationship between the aphid and the parasitoid. Finally, this information will be incorporated into the model of B. brassicae developed in previous chapters and the simulation results will be discussed.

6.2 The Biology of Diaeretiella rapae (McIntosh)

D. rapae is an aphidiid parasitoid and has frequently been recorded as being the only parasitoid of the cabbage aphid (c.f. Hafez, 1961). This does not imply that the wasp's host range is limited to a single host species (i.e., monophagous). Starý (1964) suggests its host specificity is restricted to two or more genera of the same group of more or less closely related hosts and other hosts are rarely parasitized (i.e., between oligophagous and polyphagous). Following the world-wide spread of its main host, B. brassicae, the parasitoid, D. rapae, is almost cosmopolitan in its geographical distribution (e.g., Starý and Schlinger, 1967; Starý, 1970). Since 1960, there has apparently been little confusion over its taxonomic position and nomenclature;

its early synonyms are reviewed by Starý (1961).

D. rapae is an internal parasitoid which attacks aphids and deposits its eggs into the body of its host. There are five larval instars. First instar larvae are caudate, the cauda and dorsal regions having spines. They are mandibulate and have a number of oral sense organs. Second and third instar larvae are hymenopteriform and amandibulate, also lacking spines and oral sense organs. Larvae of the fourth instar are hymenopteriform, and have mandibles and sense organs. The presence of mandibles and sense organs in the first and fourth instar larvae is related to their diet and behaviour. Both these instars feed on localised solid tissues and are quite active within the host; but during the second and third instar are quiescent, feeding on surrounding liquid or semi-liquid nutrients in the haemocoel (Couchman and King, 1977). The mandibulate larvae thus have a disruptive effect on the tissues of the host (Mackauer, 1959) and hormone balance (Johnson, 1959, 1965), these physiological effects also causing external morphological alternations in parasitized aphids (Bonnemaison, 1970). It is probable that the secretions of the larva, together with its feeding activity, affect the host and its feeding intake. The amandibulate larvae, however, do not affect the host in a similar manner, and host feeding intake in the early stages of the parasitism resembles the non-parasitized aphids. During the third instar stage, the parasitoid larva fills the abdomen of its host which becomes very sluggish, reluctant to respond to physical stimuli, and which dies in 24 hours. Finally, the mandibulate fourth and fifth instar larvae consume the digestive organs and other remaining tissues of the host (Couchman and King, 1977). By this time all the internal contents of the aphid are

consumed and the thin integument remaining turns into a hardened, brownish mummy. The final instar larva of the parasitoid cuts a slit in the ventral surface of the mummy and fixes it onto the plant with the threads of the cocoon which is spun to line the inside of the host integument (Hafez, 1961). Couchman and King (1979) investigated the effects of parasitism on the aphid food intake. Aphids that were parasitized during the first, second, or third instar died, generally in the fourth instar, without reproducing. Some old third instar aphids (i.e., older than five-day old) if parasitized can survive to the adult stage. Most of the aphids that were parasitized when they were six days old or older produced some offspring, although reproduction depended more on the aphid's developmental stage than on its precise chronological age at the time of parasitism (Mackauer and Kambhampati, 1984). Only aphids parasitized during the fourth instar or the adult stage can, thus, produce offspring. The fecundity of the parasitized aphids varies with aphid age at the beginning of parasitism, which determines gonadal development (Soldan and Starý, 1981) and the number of embryos present that potentially could be consumed by the larva of D. rapae (Couchman and King, 1977).

The developmental periods of the parasitoid reared at various temperatures are different. It takes 20.2 days from egg deposition to adult emergence at 15°C, 14.7 days at 20°C, and 10.4 days at 25°C (Sedlag, 1958). The developmental rate of D. rapae increased with an increase in temperature within the range 6.5°C to 25°C. A further decrease or increase in temperature beyond this interval could terminate the development and kill the larvae of the parasitoid. Hafez (1961)

has a similar approximation as Sedlag's result for the developmental time at average temperature 25°C, i.e. ten days. Generally the host will be killed two or three days before the adult parasitoid emerges. The parasitoid emerges through a small circular hole cut dorsally on the mummy's abdomen, and mating and ovipositing may take place immediately. This species is arrhenotokous so a virgin female will have all-male offspring. The total number of eggs deposited by a D. rapae during its life is about 83 and the average longevity of a female adult is approximately one week in mid-summer (Hafez, 1961). The female parasitoid deposits more than 50% of its total egg complement uniformly during the first four days after emergence (Hafez, 1961). It deposits indiscriminately in parasitized or un-parasitized cabbage aphids but prefers old nymphs (i.e., third and fourth instars) and young adults to old adults which are covered with thick milky wax. Although two or more eggs may be deposited in a host, only one adult parasitoid can emerge. Adult parasitoids fed honeydew from B. brassicae lived as long or longer than those fed honey only (Hagen and van den Bosch, 1968).

The female parasitoid is initially attracted to the plants by a component of the mustard oil glucosides (isothiocyanates) (Read et al., 1970). Once on the plant, the parasitoids tend to search for longer periods on leaves of high host density than on those with few hosts, implying that a non-random search might occur (Akinlosotu, 1973). This is probably due to the response of the parasitoid to the aggregation behaviour of the aphid.

In some places, such as England (George, 1957; van Emden, 1963), Germany (Sedlag, 1958), the Netherlands (Hafez, 1961), Australia (Hughes, 1963), and Taiwan (Tao and Chiu, 1971), D. rapae has only minor

importance as a natural enemy of B. brassicae. Sedlag suggests that insufficient aphids to sustain the vigorous reproductive momentum of the parasitoid early in the season, superparasitism, hyperparasitism, and the long developmental time of the parasitoid compared to that of the aphid are the main factors which reduce the impact of D. rapae. If the rate of increase of the aphid falls below a certain level, however, the parasitoid becomes effective (Sedlag, 1964). Hafez (1961) reports that the limited fecundity of the parasitoid and hyperparasitism are probably responsible for the poor ability of the parasitoid at high host densities. Comparing the potential rate of increase, the overall mortality rate, and the reproductive rate of the aphid populations in the field with those parameters of the parasitoid, Hughes (1962, 1963) concluded that the parasitoid could not increase in numbers comparable to those of its host in the field in Australia. Using a test of synchronisation in the laboratory, Chua (1975) suggests that there is a critical B. brassicae density which is ideal for the immediate establishment of D. rapae, a situation in which the wasp can lay the full complement of eggs, and yet not leave so many aphids that the population increases to a level which is uncontrollable by successive generations of parasitoids. The experiment indicated that to eliminate a B. brassicae population in the shortest time, D. rapae must be introduced to the aphid population in the parasitoid to aphid ratio of 1:80 and in the second or third instar populations of the aphids (Chua, 1975).

Generally the aphids live in colonies and all the stages are exposed simultaneously to the parasitoid in the field throughout the growth period of the aphid population. An experiment was therefore conducted to examine the preference of the parasitoid in attacking

the stage-structured population of the aphids. The total population was 50, in which each stage had 10 individuals obtained from the standard cohort cultures (c.f. Chapter two). Before the 50 aphids were placed onto the leaf of the potted Brussels sprouts seedling (c.f. Chapter two), the stage-structured population was kept in an empty petri dish for half an hour. After being transferred onto the plant and covered with a leaf cage, the aphids settled down and formed a colony in approximately half an hour. The leaf cage was removed from the plant before it was placed in a cylindrical insect cage (c.f. Chapter two). A two-day old female parasitoid obtained from cultures (c.f. Section 6.3) was introduced to the insect cage and the aphid colony was exposed to the parasitoid for 24 hours. After a further 24 hours the aphids were dissected and the number of the aphids in each stage which had been parasitized was recorded. The parasitism for each stage was calculated. The experiment has ten replicates. The age for each stage of the aphid in this experiment was one, two, four, six and eight days old, for the first, second, third, fourth instar, and adult respectively.

The results are shown in Table 6.1. The first point to be considered is the difference between the means for the aphids parasitized at various stages, showing the adults and the fourth instar nymphs to be preferable to the others. Furthermore, in the presence of these older stages, parasitism of any younger stage present will be lower. The most pronounced difference was observed between that of the third and fourth instars. Hafez (1961) suggests that the difference of the parasitism between stages is due to the variation of body size for the aphid host.

Secondly, the results of this experiment are different from a pre-

Table 6.1 Preference of the parasitoid, *Diaeretiella rapae*, for different stages of *B. brassicae* *

No. of Colony	No. of Aphid Parasitized at Various Stages				
	I	II	III	IV	Adult
1	2	2	4	8	9
2	0	2	5	7	8
3	1	1	4	7	7
4	0	1	3	8	8
5	1	0	2	7	8
6	0	1	4	6	7
7	0	0	3	6	6
8	0	0	2	7	8
9	1	3	6	6	7
10	0	3	5	5	6
Total	5	13	38	67	74
Mean	0.5a	1.3a	3.8b	6.7c	7.4c
S.D.	0.71	1.16	1.32	0.95	0.97
Average Parasitism (%)	1.0	2.6	7.6	13.4	14.8
Preference Index (Q)	0.13	0.34	1.00	1.76	1.95

*: The means of the number of aphid parasitized at various stages were compared by Tukey's w - procedure (Steel and Torrie, 1960). The same letter indicates no significant difference between stages ($P < 0.05$).

vious one (Hafez, 1961) in which D. rapae prefers the "half-grown nymphs" to the "adults" of B. brassicae. As the age of the aphids used by Hafez has not been specified a comparison with the results of this experiment is difficult.. The preference is probably due to the fact that an old adult is covered by a thick wax secretion which might protect the aphid and reduce the chance of the parasitoid depositing its egg into the aphid successfully. Since the oviposition attempts of D. rapae to the adult aphids are apparently higher than that of the nymphs and the number of parasitized adults are lower than that of parasitized nymphs (Hafez, 1961), it might be that full size adults are preferred by the parasitoid but the chance of successful parasitism is reduced by the wax. By comparing the average parasitism of the third instar aphids with the others in Table 6.1, it is easy to calculate the index of the comparative number of hosts parasitized in each of the five aphid stages. The index denotes the preference of the parasitoid attacking the aphids and is, therefore, called the preference index, $\underline{Q}$, as shown in Table 6.1.

6.3 The Functional Responses of D. rapae to B. brassicae

Although a considerable amount of work has been done on the population ecology of B. brassicae, relatively little of this has looked at the effect of parasitism on the population growth of the aphid (e.g. Hafez, 1961; Akinlosotu, 1973; Chua, 1975). Previous work has also failed to look at the full age-structure of the aphid population, and is thus unsuitable for the interpretation of the dynamic relationship of the parasitoid in a stage-structured population of B. brassicae. In this section the searching time of the parasitoid at different densities of B. brassicae per cabbage leaf will be re-analysed to investigate the

searching strategy of the parasitoid, i.e., random or non-random search. This is followed by experiments dealing with the functional responses of D. rapae to various stages of B. brassicae. The experimental results will be quantified and described by some suitable models.

Cabbage aphids have a strong tendency to form compact colonies (Hayamizu, 1982), making it likely that the aphid populations under natural condition will exhibit a clumped distribution among units of their habitat. Akinlosotu (1973) has conducted an experiment to investigate the relationship between aphid density and searching time of the parasitoid. Although the results showed that the time spent may increase exponentially with increasing host density, the variances in treatments are relatively high as four out of the six treatments had coefficients of variation greater than 100 (Table 6.2). It is, therefore, necessary to re-analyse the data statistically. As confirmed in his conclusion, the analysis of variance of the regression shows that the slope of the graph of time (Min.) against density (as $\log_{10}$) has a slope which is significantly greater than zero ($P < 0.05$) (Figure 6.1). It implies that the parasitoid will tend to spend more of its searching time where the aphids are abundant rather than scarce, though the experimental error is relatively high in this experiment. Additionally, the analysis shows that the relationship does not depart significantly from the linear relationship ($P < 0.05$).

$$T = -19.7886 + 46.5355 \cdot \log_{10} N,$$

$$(\gamma = 0.4202)$$

where T is the searching time in minutes and N is the aphid density

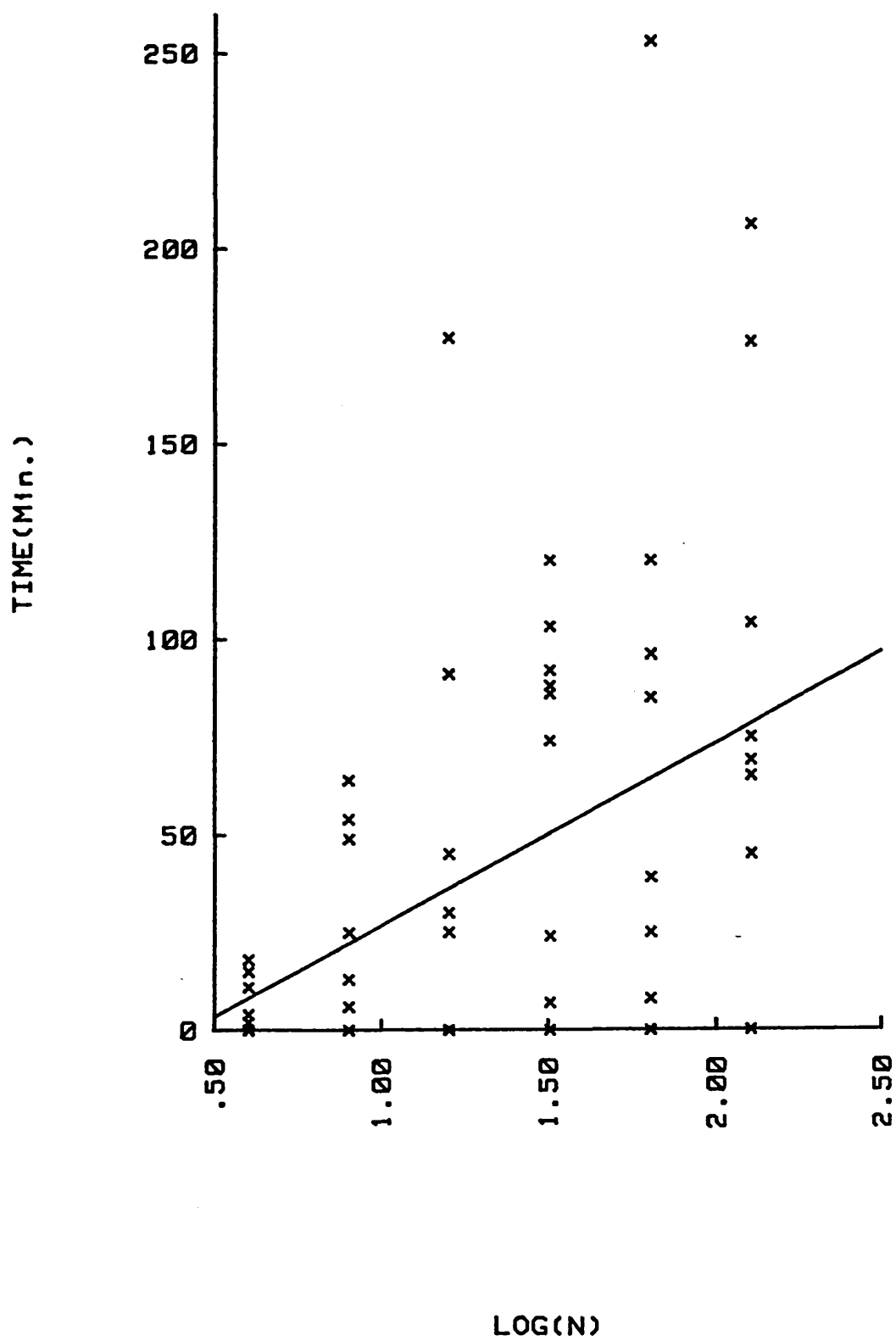
Table 6.2 Searching time of D. rapae at various densities of B. brassicae per cabbage leaf (data from Akinlosotu (1973)).

Host density level	No. of replicate	Mean	Standard deviation	Coefficient of variation
4	10	5.0	6.99	139.84
8	10	21.7	24.88	114.64
16	10	36.8	57.37	155.89
32	10	59.4	46.46	78.22
64	10	62.6	80.19	128.10
128	10	74.0	71.57	96.72

Figure 6.1

Searching time (in minutes) of D. rapae at various densities of its aphid host, B. brassicae, per cabbage leaf ($\log(N)$) (analysed from data in Akinlosotu, 1973).

TIME SPENT FOR SEARCHING & HOST DENSITY



per leaf. However, to retain simplicity in the aphid population model, random search will be assumed in this experiment.

The cabbage aphid normally occurs in stage-structured populations which vary considerably in their stage structure and size from plant to plant in the field. In some previous studies the functional responses of D. rapae to the aphid population, which is treated as a cohort, have been considered. However, the functional responses of D. rapae to various stages of B. brassicae are still lacking. Experiments were, therefore, performed to investigate these responses.

Laboratory colonies of D. rapae were established from specimens that had been collected on Brussels sprouts in the field, Silwood Bottom, in June 1982. To obtain aphids of known age, the aphids were transferred from the standard cohort cultures (c.f. Chapter two). The aphids were transferred onto a leaf of Brussels sprouts grown to the 5-7 leaf stage in 10-cm diameter pots in a constant temperature room at $25 \pm 1^\circ\text{C}$ with a 16-hour photoperiod and 60-70% R.H. As D. rapae prefers old nymphs and young adults of B. brassicae, a total of four treatments, the first, third, fourth instar, and adult, were exposed to a one-to-two day old mated female of D. rapae for 24 hours. Various numbers of aphids (1, 5, 10, 20, 50, and 100) were placed on the experimental plants which were covered in the polythene cylindrical insect cages used in the previous experiments (c.f. Chapter two), each density being replicated ten times. After the experiment the parasitoid was removed from the insect cage. All the aphids exposed to the parasitoid were reared under the same conditions for three days, and then dissected under the microscope to investigate the number of aphids parasitized. In this experiment, it has been assumed that the functional responses

for the parasitoid to the first and second instar nymphs of the aphid are similar. For convenience, the results of the experiment of the first instar nymphs will be applied to the second instar nymph of the aphid. The results of these functional response experiments are shown in Figures 6.3(a) to (d).

In order to quantify these results it was necessary to specify a formula for the proportion of hosts parasitized or attacked. Since the forms of the results indicated type II functional responses for the fourth instar and adult hosts, the formula given by Rogers (1972) could be used, namely:

$$N_a = N \cdot [1 - \text{Exp} \left(- \frac{a' \cdot T \cdot P}{1 + a' \cdot T_h \cdot N} \right)] \quad (6.1)$$

where N is the number of hosts, N_a is the number of host attacked by P parasitoids, T is the total time of the interaction, T_h is the handling time per host attacked, and a' is the instantaneous measure of searching efficiency. Each set of data in the experiments has been described by the model, and the estimates of a' and T_h have come from a standard non-linear least squares technique applied directly to the untransformed data (Table 6.3a).

For the sigmoid functional responses of the first and third instars, a specific assumption in the model is that the instantaneous search rate a' depends upon the host population density:

$$a' = b \cdot N, \quad (6.2)$$

where b is a constant (c.f. Hassell, Lawton, and Beddington (1977) who assumed $a' = b \cdot N / (1 + c \cdot N)$, i.e., search rate a' increases rapidly at

Figure 6.2

Functional responses for D. rapae to various development stages of B. brassicae in laboratory. The mean and 95% confidence intervals are shown. Curves are fitted by the modified type III ((a) and (b)) and type II ((c) and (d)) models. See text for discussion.

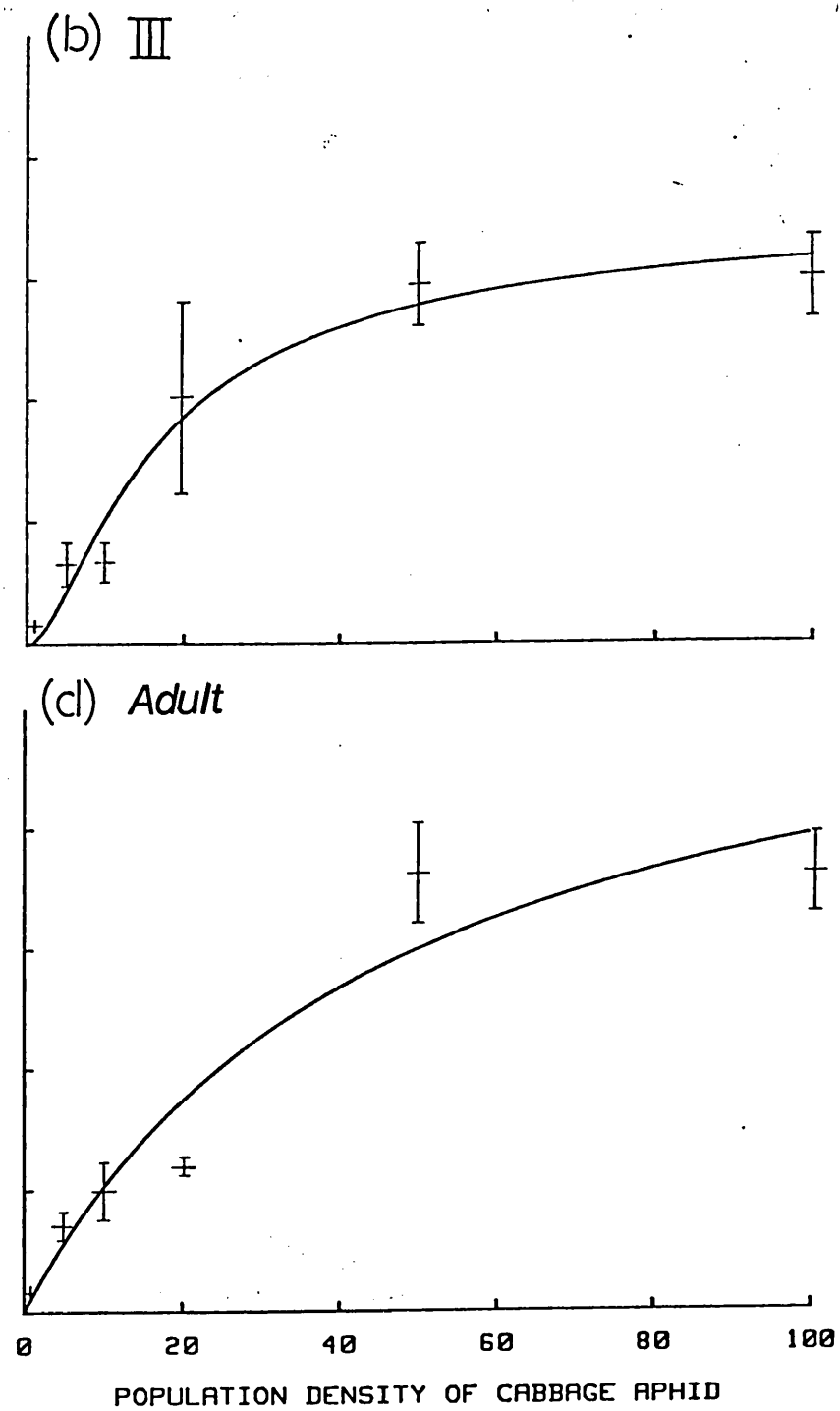
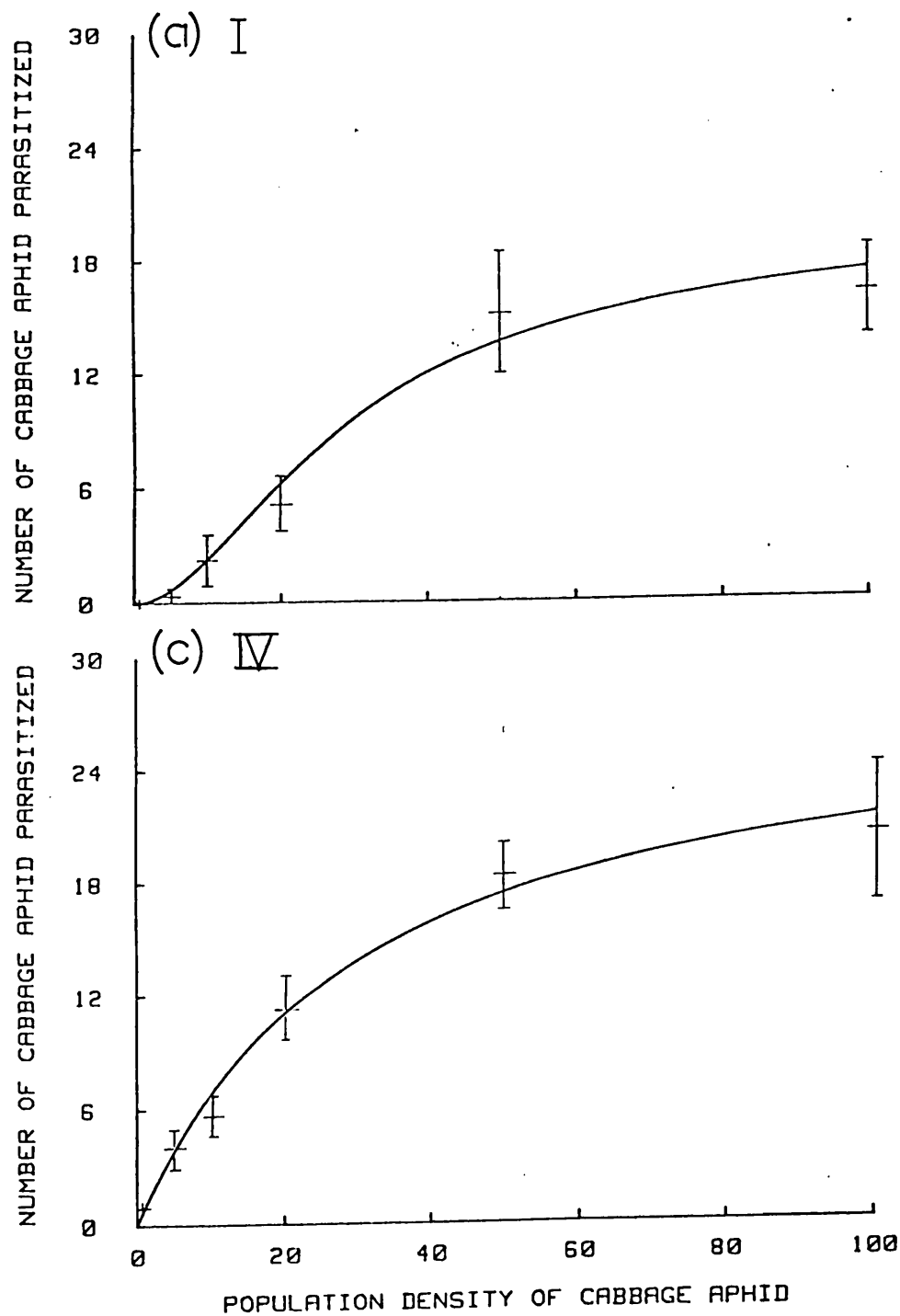


Table 6.3 Estimated parameters ($\pm 95\%$ confidence limits) obtained by fitting the models of type II and modified type III to the functional responses in Figure 6.2 using a non-linear least squares procedure, and their sums of squared residuals (SSR).

(a) Type II Model

Aphid developmental stage	Parameter		SSR
	Th	a'	
First Instar	0.0324 $\pm$ 0.0088	0.5243 $\pm$ 0.1791	328.06
Third Instar	0.0419 $\pm$ 0.0058	2.2239 $\pm$ 1.3673	429.51
Fourth Instar	0.0363 $\pm$ 0.0030	1.9170 $\pm$ 0.5803	148.21
Adult	0.0292 $\pm$ 0.0045	1.2916 $\pm$ 0.4719	395.17

(b) Modified Type III Model

Aphid developmental stage	Parameter		SSR
	Th	b	
First Instar	0.0492 $\pm$ 0.0042	0.0297 $\pm$ 0.0094	213.89
Third Instar	0.0466 $\pm$ 0.0038	0.1740 $\pm$ 0.0992	392.88
Fourth Instar	0.0422 $\pm$ 0.0020	0.1714 $\pm$ 0.0576	155.76
Adult	0.0363 $\pm$ 0.0028	0.0803 $\pm$ 0.0317	404.01

the lowest host density towards a maximum as host density increases). Applying Eq. 6.2 to Eq. 6.1, now gives us a modified type III equation which is a special case of the Hassell et al. model (1977):

$$N_a = N \cdot [1 - \text{Exp} \left(- \frac{b \cdot T \cdot N \cdot P}{1 + b \cdot T_h \cdot N^2} \right)] \quad (6.3)$$

The modified type III model has been adopted to avoid the problem of negative search rate which occur in the Hassell et al. model. The same assumption was made by analysing the functional responses of Trybliographa rapae (Westw.) parasitizing the cabbage root fly, Delia radicum (L.) (T.H. Jones, personal communication). The modified type III equation has been fitted to each set of data shown in Table 6.3b, which also gives the estimated parameter values obtained from the non-linear least squares procedure.

By comparing the fitted results of the two models listed in Table 6.3, the modified type III model was chosen to describe the functional responses of the parasitoid to the first and third instar aphids and the type II model to those of the fourth instar and adult aphids as their sums of squared residuals are less than the others. Hassell (1978) suggests that by providing a preferred host species, by making the conditions somewhat more favourable, or by providing larger hosts or prey the sigmoid functional responses for some species of predator or parasitoid might be converted to the typical type II responses. This is probably due to the predator or parasitoid maintaining a constant search rate under those favourable conditions which result in a type II response. From this we have further evidence that D. rapae prefers to attack the older stages (i.e., the fourth instar and adult aphids) rather than the younger stages of B. brassicae.

6.4 A Simulation Model of Brevicoryne brassicae with its Parasitoid, D. rapae

The general framework for the aphid-parasitoid simulation model is similar to that used previously for the aphid population alone (Chapter five). Here, it is assumed that the introduction of D. rapae to a population will affect the survival and fecundity of the aphids. In other words, the two demographic processes are influenced by parasitism, and this parasitism will be incorporated into the two demographic functions. The influence of the parasitism on the development of the aphid is not included, though it might be important.

In the previous section, the functional responses for the parasitoid to various stages of the aphid have provided a mortality function for each stage of the aphid caused by the parasitoid, depending upon the aphid population density. As the preference of the parasitoid for various stages of B. brassicae in a colony is known (see Table 6.1), in terms of the preference index for the stage i, Q_i, it is reasonable to assume that the parasitism of the stage-structured aphid population depends on the number of aphids available and the parasitoid's preference for them. The relationship of the aphid colony and the parasitoid can be represented by:

$$D_{pai}(N) = Q_i \cdot D_{si} \cdot FR_i(N), \quad (6.5)$$

where D_{pai}(N) is the number of the aphids parasitized at stage i, FR_i(N) is the functional response for the parasitoid to the aphids at stage i with total population N and D_{si}, the proportion of the stage i cohort in the total population. It is assumed, for simplicity, that a female parasitoid remains on the colony for only 24 hours and discriminates between parasitized and unparasitized hosts, since a

re-analysis of Hafez's work (Rogers, 1975) suggests that some discrimination does occur. As the parasitoid takes 7.8 days to develop from egg to pupae and kill its host (Hafez, 1961; Mackauer and Kambhampati, 1984), it is reasonable to assume that there is a time lag existing between parasitism and the death of the host. Equation 6.5 can therefore be rewritten as:

$$D_{pai}(N, T + 8) = Q_i \cdot D_{si}(T + 8) \cdot FR_i(N, T), \quad (6.6)$$

where T is the time in days at which parasitism occurs.

As mentioned earlier, the number of aphid offspring produced by parasitized aphids before death (or mummification) depends on the stage at which the aphids are parasitized rather than their age (Mackauer and Kambhampati, 1984). It has been found that parasitized adults and about 70% of parasitized fourth instar eventually produced some offspring, whereas the identically aged third instars did not (Mackauer and Kambhampati, 1984). The evaluation of parasitoid impact on cabbage aphid fecundity was complicated by the observed variability in the aphid's rate of development. A detailed analysis of the relationships between plants, aphids and parasitoids, although possible, would be laborious to conduct due to their complexity and the variability in the developmental rate of the parasitoids. Such an analysis might not be justified in most cases in which this host-related variability is suspected. Therefore, some simple and convenient alternatives have been used previously, for example, a fixed fecundity of a two nymphs per aphid parasitized in the third instar (Akinlosotu, 1973; Chua, 1975), and a linear regression model dependent on the aphid's age at the beginning of parasitism and the length of the aphid's pre-reproductive period (Mackauer and Kambhampati, 1984). According to this previous information, we assume

that the age-specific fecundity of the parasitized aphid is reduced completely for aphids younger than (and including) the third instar at the time of parasitism, and is reduced 50% and 30% for the fourth instars and adults, respectively.

The model employs a discrete time step of one day and consists of a set of recursive relationships defining the size and stage-structure of the aphid population at time t as a function of that at time $t-1$. Thus the time lag between parasitism and the death of the host is set at eight days. The input information is similar to the programme used in the previous chapter (see Appendix II), the only addition being the time and the number of the parasitoid attacking the aphid population. A full listing of the computer programme is given in Appendix III.

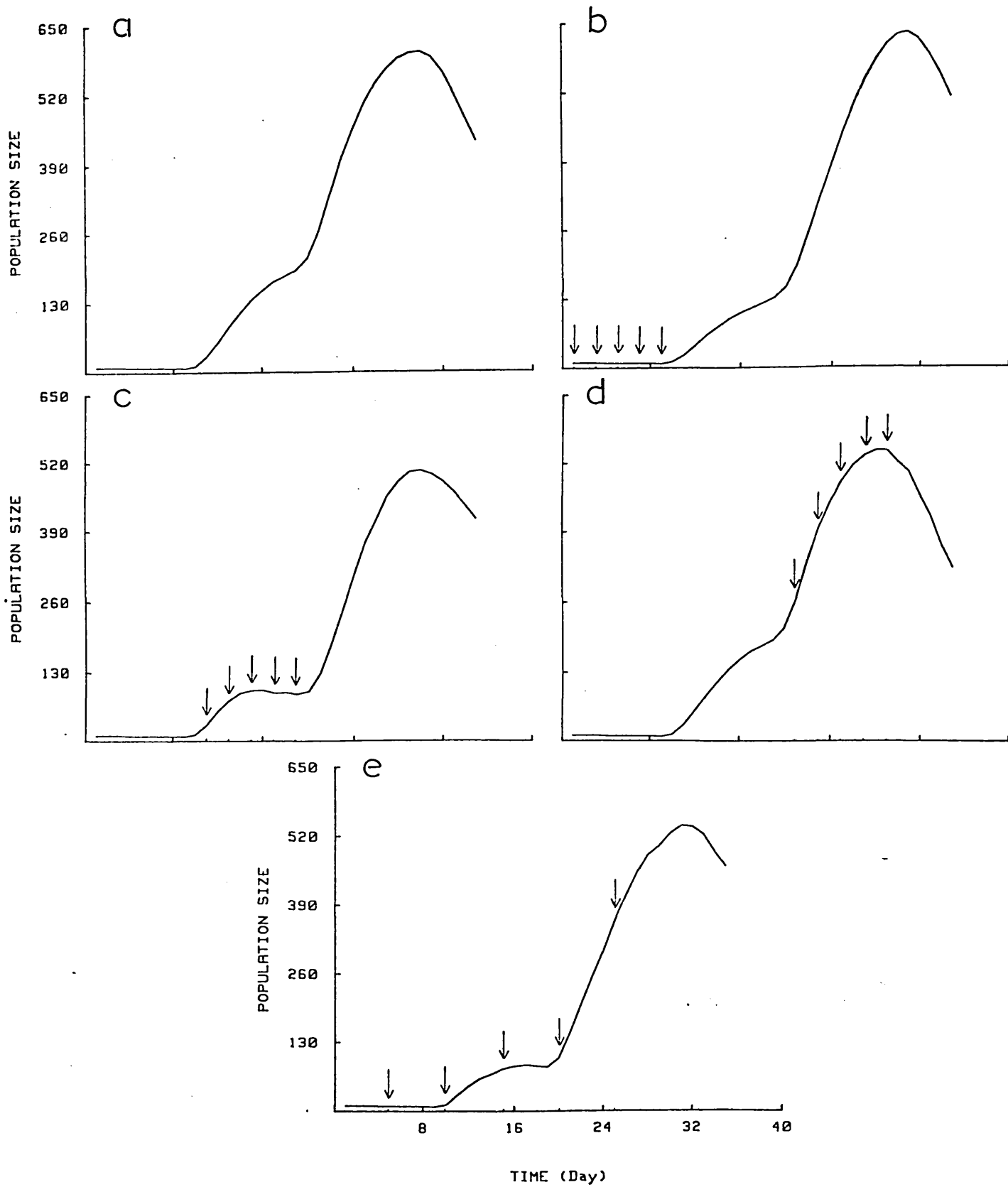
6.5 Simulation Results

The initial population and the time lag of the density dependence applied in the simulation were set as 10 first instar nymphs and 10 days, respectively, to be consistent with the previous simulations in Chapter five. Also in keeping with Chapter five, the model simulations run from day 1 to 35. According to the shape of the curve, the duration of the simulation can be divided into three periods, i.e. day 1 to 10, day 11 to 20, and day 21 to 35. In addition, the timing of parasitism can be considered under two headings: concentrated or uniform. Firstly, considering a series of the parasitoid attacks concentrated in a certain period, it is clear that there are different responses for various periods attacked, although the basic pattern of the population trajectory is similar (Figure 6.3b, c, and d). If the parasitoid attacks in the first period the population size will be reduced in the second period, compared with the control (Figure 6.3a), but population growth increases

Figure 6.3

The predicted populations of B. brassicae attacked by D. rapae on various dates (indicated by arrows), with a starting aphid density of 10 nymphs of instar one.

- (a) Control;
- (b) D. rapae attacked on day 1, 3, 5, 7 and 9;
- (c) on day 11, 13, 15, 17 and 19;
- (d) on day 21, 23, 25, 27 and 29;
- (e) on day 5, 10, 15, 20 and 25.



rapidly over the next period, reaching an even higher level than the control in the third period. The concentrated parasitism occurring in the second period suppressed population growth to around 90 aphids per plant during this period and reduced the population in the third period. Parasitism occurred in the third period reduces the population size substantially, compared with the control, only during the final period.

Secondly, if the attacks occurred uniformly in all periods (Figure 6.3e), the population in each period is lower than the control but with a similar pattern of population growth. The similar pattern of the population trajectories and the limited difference between the aphid populations attacked at various times and the control implies that the parasitoid can not regulate the aphid population efficiently in this simulation model.

This model is a single-species population model, not a parasitoid-host model, and the parasitism is only considered as one mortality factor in the aphid population. Basic biological assumptions, such as a parasitoid attacking an aphid population for only 24 hours, the new-born parasitoid dispersing without parasitism, only one parasitoid attacking aphids at any one time, a uniform reduction of fecundity of parasitized aphids before mummification, and uniform developmental time of parasitoids, all might influence the ability of the parasitoid to control the aphid population. Other factors, such as hyperparasitism and mutual interference of the parasitoids, have also not been included and would affect the accuracy of the model. It is clearly important that the dynamics of the D. rapae population is also considered together with that of the stage-structured population of B. brassicae. This has

not been attempted in the present study and must await further work.

6.6 Conclusions

The primary object of this chapter was to extend the simulation model of Chapter five to include parasitism caused by the parasitoid D. rapae. The structure of the aphid population model permitted the simple inclusion of the functions specifying the proportion of aphids parasitized on the basis of instar. There are no attempts to simulate the dynamic behaviour of the parasitoid population in this model (see Chapter seven).

The evaluation of the parasitoid impact on a stage-structured population of B. brassicae is complicated. In this experiment a set of preference indices of the parasitoid to various stages of the aphid has been calculated, which are comparable to these indices given by Hafez (1961). The functional responses of the parasitoid to various stages of the aphid have been quantified and modelled. Since the effect of different host stages on the parasitoid and the effect of the age of the adult female parasitoid on parasitism have not been clarified quantitatively (c.f. Hafez, 1961), a detailed host-parasitoid population model for B. brassicae and D. rapae needs further work. However, the aphid population model with the parasitoid developed in this chapter provides a basic framework which can be easily extended to include these additional components when they are available.

Chapter Seven

General Discussion

Although experimental evidence of density-dependent demographic processes in age-structured populations is widespread in the study of aphids, the study of simulation models for such populations is as yet limited. The aims of this work have been, therefore, to construct a simulation model for an age-structured population with density dependence and to explain the population development of B. brassicae on Brussels sprouts. To achieve this, comprehensive models are developed to describe the age-specific and density-dependent demographic processes for various instars and these are incorporated to describe the overall population growth. All experimentation in this work was conducted under controlled conditions, and thus the effects of changes in each variable could be examined. From such an approach, the model is expected to permit some generalizations on the population dynamics of any age-structured species. The general framework could, therefore, be a useful tool for the improvement of integrated pest management in tropical and subtropical areas where pest populations such as, Tetranychus spp., Nephotettix, spp., Plutella xylostella, and Nilaparvata lugens, are age-structured and breed continuously.

The concept of a stable age distribution, developed primarily by A.J. Lotka (1922), has been a basic assumption in ecology and genetics for many years. In ecology some of the recent interest has been directed towards the more practical aspects of applying this theory (e.g. Carey, 1982a, 1982b, 1983, 1984), though more interest has concentrated on the theoretical aspects (e.g. May, 1981). In all of these discussions little attention has been given to analysing the process of convergence from arbitrary initial circumstances to the stable form (Taylor, 1979) or to investigating the stage stability of field populations (Hughes,

1963; Carter et al., 1978). Obviously the process of convergence is an important aspect of the theory of stable populations. If the stable forms are closely approached only after an unpractical length of time, the stable population would indeed be an abstract concept. In Chapter Two, by applying the method of analysis of Carter et al. (1978), it was found that the assumption of a stable stage distribution for populations of B. brassicae could not be confirmed statistically in the laboratory or in the field as the stage distribution varies with time. The results of this investigation agree with the findings of Carter et al. (1978) in that the stage distribution of the aphid population fails to become stable primarily due to the short time available for the aphid population to develop on a rather ephemeral host plant.

Laboratory experiments showed that the variation of temperature expected in summer does not affect the pattern of the stage distribution. This is probably due to the change in the demographic processes affected by temperature having a similar effect on each developmental stage. That is at higher temperatures the mean chronological age of a population may be younger than at lower temperature, but the stage distribution will remain approximately the same (Carey, 1983). A slight tendency of the stage distribution to approach a certain level, is revealed when the population density is higher than 40 aphids per plant, though a stable form is not achieved. This implies that population density might be a crucial factor affecting the stage distribution of the aphid population.

The effect of intraspecific competition can always be measured as some forms of density dependent process. Thus, competition for an essential resource may result in density dependent mortality, reduction

in fecundity or delay in developmental time. The experiments described in Chapter Three showed that a density dependent process acts on the aphid population, though the form of competition (i.e. contest or scramble competition (Nicholson, 1954)) could not be recognized from this particular experiment, probably because the experimental population densities were too low.

Models to describe the experimental data on the density-related demographic processes (i.e. development of each instar, fecundity of adults and survivorship) have been developed. These models are then used as the basic component in the construction of an overall model. Using a more mathematical approach, an age-specific population model, involving density dependence, based on von Foerster's first-order quasi-linear equation was developed. An alternative compartmental approach gave broadly the same results. In this case the aphids are assumed to be distributed between a number of separate compartments (i.e. a stage cohort). The rate of "transfer" of an aphid out of a given compartment is proportional to the number of aphids within the system. The system can thus be simply described by a set of quasi-linear equations which then constitutes the model. This model can provide detailed information on stage structured populations and may be used to analyse populations with continuous recruitment and overlapping generations.

To complete a model simulating population dynamics, it is necessary to consider the role of natural enemies. For this an explicative approach was adopted. The relationships of the number of hosts parasitized to the host density are modelled as the non-linear Holling Type-II and the modified Type-III functional response equations for various

stage cohorts of the aphid. The parasitoid, D. rapae shows a preference for the fourth instar and adult stages of the aphid, though the thick wax secreted by the old adults may reduce the chance of successful parasitization. The detailed investigation of the functional responses of the parasitoid to various stages of the aphid provides crucial information for the mortality and fecundity functions and for completing the population dynamics model of the aphid. However, there are some other aspects, such as migration, aphid-plant relationship, polymorphism of aphid, and weather etc., which have not been considered. More important, validation of the predictions must await further study.

In this work, three tests were applied to validate or compare the models developed: the Kolmogorov-Smirnov statistic, the two-sample Kolmogorov-Smirnov test and a residual analysis test. Firstly, in comparing an assumed distribution function with data, the Kolmogorov-Smirnov statistic (or the K-S statistic) is applied to test the difference between the prediction and the observed data. The difference between the assumed distribution functions and the validating data should be a useful statistic in determining whether the former is correct. The statistic has a distribution which is independent of the distribution function (i.e. distribution-free (Lindgren, 1968)). Secondly, the two-sample Kolmogorov-Smirnov test (or the Smirnov test) was applied to compare different distribution functions which have been developed in this work and which described the same demographic process. The test is tested on the statistic which is defined as the differences between the corresponding predictions of the two functions. The K-S statistic and the Smirnov Test share the same fundamental principle. In the K-S statistic, the sample sizes of an assumed distribution function and its validating data must be equal, but this is

not necessary in the Smirnov test. Finally considering the validity of the aphid population model, a simple residual analysis has been applied to test the quasi-linear model and its validating data. As the simulation model and the validation data are independent, the residuals between the simulation results and the data are the true model errors if the model is correct. Thus the residuals actually equal the errors which are an independent normal distribution under the simulation model. The sequence of residuals have the property of zero mean and independence and consequently can be conveniently used to test model validity.

Modelling the cabbage aphid has shown that further experimentation is needed in several areas three of which are discussed below, and also that there is considerable scope for further development of the model.

(1) The effect of polymorphism on population growth.

The significance of polymorphism is highlighted, firstly, by the discrepancies between observed population trends including alatae and the simulation results of the model which assume that all alatae emigrate as soon as they mature, and secondly, by the simulation results of the model agreeing with the observed population trends excluding alatae. Furthermore, in considering natural aphid populations, it is clear that winged and wingless morphs are playing rather different roles in the population dynamics of the aphid in terms of demographic processes and migration.

Future work could commence with the study of morph determination of the aphid. Proportions of alatae and apterae would be assessed in the field from monitoring experiments. Although experiments already conducted suggest that population density (Bonnemaison, 1951; Clark

et al., 1967) and food quality (Bonnemaison, 1951) of the aphid are two important factors affecting the production rate of alatae, it seems that other factors might be involved, such as temperature, day-length, age of host plant, etc. By responding to a number of stimuli rather than just one, aphids might achieve a closer and more reliable tracking of environmental conditions (Dixon, 1985). However, during the summer the variations of temperature and day-length are relatively limited, and thus, for convenience, they could be ignored. By investigating the effects of these stimuli on morph determination in the laboratory and recording the intensity of these stimuli in the field, it is feasible to construct a function that predicts the formation rates of the aphid morphs.

The demographic processes of alatae and apterae could then be quantified and modelled in the laboratory in a manner similar to the experiments described in Chapters three and four. Migration of the aphid should also be considered in the field by monitoring the numbers of emigrating and immigrating aphids. The effects of population density, age of the host plant, time of day, light intensity, wind speed and rainfall on the aphid migration should also be examined. This task is large, but without it population growth models of the aphid cannot be tested properly, nor can the alate production responses be confirmed. Growth models have limited ability for self-improvement without these properties. Especially, the termination of growth cycles depends on the production and behaviour of alatae. With this information predictive equations relating daily morph formation and migration to the aphid population, the age of host plant, and the environmental conditions can be derived so that the extended model simulates the dynamic behaviour of the aphid population in summer more accurately.

(2) The effect of different host instars on the demographic processes of the parasitoid and the effect of the age of adult female parasitoids on parasitism.

Brief laboratory experiments have confirmed the existence of such effects on the parasitoid and parasitism (Hafez, 1961). But, unfortunately, the results of Hafez's experiments have not provided enough information to quantify these effects. The next step is, therefore, to investigate these effects comprehensively in the laboratory by examining the demographic rates of the parasitoid affected by host instars when hosts are parasitized and the age-specific fecundity rate of the parasitoid. The results could be quantified and modelled in terms of the developmental stages of the host and the age of the parasitoid, accordingly. As mentioned previously, demographic processes which include the rates of development, mortality and reproduction are the three basic components of a population model. The aim of this work would be to construct a population model for the parasitoids on the basis of age specificity, similar to the procedure described in chapter five.

(3) The effects of mutual interference and spatial heterogeneity on parasitism.

Mutual interference among searching parasitoids is widespread and complicated, but some aspects of this phenomenon (e.g. variations in available searching time and emigration rates and shifts in sex ratio) may affect host-parasitoid population dynamics and should be investigated. Within the confines of laboratory cages, parasitoids have been observed to react markedly to the presence of other searching individuals nearby and show an increasing tendency to fly-off the host food-plant (Akinlosotu, 1973). These effects need to be investigated quantitatively. As

described earlier, the cabbage aphid has a strong tendency to aggregate in patches (Hayamizu, 1982) and D. rapae to spend more time in patches of high aphid density (see Section 6.3). Thus the spatial heterogeneity in the host's distribution might be crucial to the overall level of parasitism. Experiments should thus be carried out both in the laboratory and field to determine the spatial patterns of parasitoid in relation to host distribution and these evaluated within an extended model framework.

These represent the main areas of uncertainty in the model. With this information the single species model could be extended towards a host-parasitoid model that provides a more realistic description of the population dynamics of the two interacting species.

SUMMARY

1. The stage distributions and structures of cabbage aphid populations are investigated in the laboratory, field cages and the field, and several methods are applied to test the stability of the stage distribution. Although the stable stage distribution has not been statistically confirmed in the study, there is a strong suggestion of a relationship between the latter and the aphid population density. When the population density of the aphid increases to above 40 aphids per plant, its stage distributions tend to approach a steady state. This convergent process is very sensitive to population density.

2. A series of experiments is described to determine the effect of age dependence on the demographic processes of the aphid population, and a simple investigation is conducted to detect the severity of density dependence. By applying Maynard Smith and Slatkin's model (1973), it is shown that a density dependent process acts on the aphid population, though the form of competition could not be recognized. Several types of survivorship curves considered by Pearl and Miner (1935), Deevey (1947) and Slobodkin (1962) have been found in the aphid populations, merely by changing density. Models of age-specific survival, development and fecundity are developed in several non-linear equations. The importance of these demographic rates in relation to the aphid population density is considered, and an "Allee type" density effect which might influence these demographic rates is suggested.

3. Age-specific demographic models with density dependence are considered, models being constructed to describe the relationships between parameters values and population density. As the effect of stage structures of the aphid population on the demographic rates is not

significant in this particular experiment, stage classes are thus not incorporated into the demographic functions.

4. A model of the growth of the cabbage aphid population can be developed by a mathematical or compartment approach. The model based on von Foerster's first-order quasi-linear equation and consisting of the non-linear demographic functions, is an age-specific and density-dependent model. The model can provide detailed information of stage structured populations and may be used to analyse populations with continuous recruitment and overlapping generations.

5. Experiments to determine the preference of D. rapae attacking various stages of B. brassicae and the corresponding functional responses of D. rapae are described, and a brief review of the biology of D. rapae is presented. The dynamic relationships between the aphid and D. rapae are quantified and then incorporated into the population model of the aphid, and a single species model of the cabbage aphid population with the parasitoid is constructed.

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Appendix I

The Equivalence of Survivorship, Age-Specific Survival and Age-Specific Mortality Functions.

Appendix I

The general form of a survivorship function can be written

$$S(t) = P_Y(t \leq T), \quad (\text{AI.1})$$

where T is the maximum life span of the organism, $S(t)$ is the probability at birth of an individual surviving to age t . The age-specific survival function of the continuous distribution is

$$f(t) = \lim_{\Delta t \rightarrow 0+} \frac{P_Y(t \leq T < t + \Delta t)}{\Delta t}, \quad (\text{AI.2})$$

so that

$$S(t) = \int_t^{\infty} f(u) du. \quad (\text{AI.3})$$

The functions f and S provide two mathematically equivalent ways of specifying the distribution of a continuous non-negative random variable, and there are of course many other equivalent functions. The age-specific mortality function, is one of them, defined by:

$$H(t) = \lim_{\Delta t \rightarrow 0+} \frac{P_Y(t \leq T < t + \Delta t \mid t \leq T)}{\Delta t}, \quad (\text{AI.4})$$

namely,

$$H(t) = f(t) / S(t). \quad (\text{AI.5})$$

From (AI.2) and (AI.5)

$$\begin{aligned} H(t) &= - \frac{d(S(t))}{dt} / S(t) \\ &= - \frac{d(\ln S(t))}{dt}. \end{aligned} \quad (\text{AI.6})$$

Since $S(0) = 1$, by (AI.6),

$$\begin{aligned} S(t) &= \text{Exp} \left(- \int_0^t H(u) du \right) \\ &= \text{Exp} \left(- H_c(t) \right), \end{aligned} \quad (\text{AI.7})$$

where H_c is called the cumulative mortality rate. From (AI.5),

$$f(t) = H(t) \cdot \text{Exp} (-H_c(t)). \quad (\text{AI.8})$$

Appendix II

A Simulation Model of the Cabbage Aphid without Parasitoid.

Appendix II

The programme is written in BASIC. It includes a main programme and several subroutines. The main programme controls the programme flow, requiring initial condition, calling subroutines in a specified order, calculating population size for each stage, and plotting graphics. The subroutines Fecundity, Mortality, Development 1, Development 2, Development 3, and Development 4 are concerned with the demographic processes of the aphid population, while Simpson 1 and Simpson 2 are concerned with the calculation of development rates. The result of the programme can be plotted by the subroutine Graphics.

This programme requires an initial condition, including:

- (a) initial population density for each stage, $S1(A1)$, $S2(A2)$, $S3(A3)$, $S4(A4)$, and $Sa(Aa)$;
- (b) the age of the initial population for each stage, $A1$, $A2$, $A3$, $A4$, and Aa ;
- (c) duration of the experiment, T_{max} ; and
- (d) a time delay of density dependent regulatory effect, T_d .

If the ages of the initial population are unknown or uncertain, a subroutine Random-age will be executed and certain random ages between the age intervals of various stages (see Chapter 3) will be assigned to the initial populations for various stages.

```

10  ! THE FILE NAME IS THES6
20  OPTION BASE 1
30  PRINTER IS 16
40  PRINT "*****"
****"
50  PRINT "*"
  "*"
60  PRINT "          POPULATION DYNAMICS OF CABBAGE APHID,"
  "*"
70  PRINT "          Brevicoryne brassicae (L.)"
  "*"
80  PRINT "*"
  "*"
90  PRINT "*****"
****"
100  DIM S1(100),S2(100),S3(100),S4(100),Sa(100),S(100),A#[30],B#[30],Age(5,40)
110  DIM N1(100,40),N2(100,40),N3(100,40),N4(100,40),Na(100,40),D1(100),D2(100)
,D3(100),D4(100),Da(100)
120  INPUT "Do you know the ages of the initial stage groups ?(Press: Y/N)",T#
130  IF T#="N" THEN GOTO 200
140  INPUT "INITIAL AGES OF THE INITIAL STAGE GROUPS,(seperated by comma)",A1,A
2,A3,A4,Aa
150  GOTO 550
160  !
170  !
180  !
190  !
200  Random_age: ! *****
210  FOR I=1 TO 100 !
220  I1=INT(RND*10) MOD 9 !
230  RANDOMIZE !
240  NEXT I !
250  IF I1<1 THEN GOTO 200 !          THIS SUBROUTINE ASSIGNS RANDOM AGE
260  A1=I1 !          TO THE INITIAL STAGE POPULATION WHOSE
270  FOR I=1 TO 100 !          AGES ARE UNKNOWN OR UNCERTAIN.
280  I2=INT(RND*10) MOD 10 !
290  RANDOMIZE !
300  NEXT I !
310  IF I2<2 THEN GOTO 270 !
320  A2=I2 !
330  FOR I=1 TO 100 !
340  I3=INT(RND*100) MOD 11 !
350  RANDOMIZE !
360  NEXT I !
370  IF I3<4 THEN GOTO 330 !
380  A3=I3 !
390  FOR I=1 TO 100 !
400  I4=INT(RND*100) MOD 13 !
410  RANDOMIZE !
420  NEXT I !
430  IF I4<6 THEN GOTO 390 !
440  A4=I4 !
450  FOR I=1 TO 100 !
460  Ia=INT(RND*1000) MOD 40 !
470  RANDOMIZE !
480  NEXT I !
490  IF I4<7 THEN GOTO 450 !
500  Aa=Ia !*****
510  !
520  !

```

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530 !
540 !
550 INPUT "INITIAL POPULATION DENSITY FOR EACH STAGE ?",S1(1),S2(1),S3(1),S4(1),Sa(1)
560 !
570 !
580 !
590 !
600 INPUT "HARD-COPY OPTIONS (CRT or PRINTER, Press C/P)",A$
610 IF A$="P" THEN PRINTER IS 0
620 T=1
630 S(T)=S1(T)+S2(T)+S3(T)+S4(T)+Sa(T) ! TOTAL POPULATION
640 W=S(T)
650 PRINT "INITIAL TOTAL POPULATION =";W
660 PRINT
670 PRINT
680 Amax=39 ! MAXIMUM LIFE-SPAN
690 INPUT "How long does the experiment last ? (day)",Tmax
700 REDIM N1(Tmax+1,Amax+1),N2(Tmax+1,Amax+1),N3(Tmax+1,Amax+1),N4(Tmax+1,Amax+1),Na(Tmax+1,Amax+1)
710 REDIM D1(Tmax+1),D2(Tmax+1),D3(Tmax+1),D4(Tmax+1),Da(Tmax+1),S1(Tmax+1),S2(Tmax+1),S3(Tmax+1),S4(Tmax+1),Sa(Tmax+1)
720 !
730 !
740 N1(1,A1)=S1(1) !*****
750 N2(1,A2)=S2(1) !*
760 N3(1,A3)=S3(1) ! ASSIGN INITIAL STAGE POPULATIONS *
770 N4(1,A4)=S4(1) ! TO THEIR AGE GROUPS. *
780 Na(1,Aa)=Sa(1) !*****
790 !
800 INPUT "TIME DELAY, Td= ?",Td
810 PRINT "TIME DELAY = ";Td
820 !
830 ! ***** STAGE DEVELOPMENT FUNCTIONS **
840 DEF FNP1(Age)=A*EXP(-B*EXP(C*Age)) !*
850 DEF FNP(Age)=EXP(-((1/Age-C)/B)^2/2)/(A*B*SQR(2*PI)) !*
860 !*
870 ! *****
880 !
890 !
900 !
910 !
920 !
930 !
940 !
950 GOSUB Development1
960 GOSUB Development2
970 IMAGE 3D,1X,8D,1X,8D,1X,8D,1X,8D,1X,8D,3X,8D
980 PRINT " TIME 1st 2nd 3rd 4th Adult Total"
990 PRINT "-----"
1000 PRINT
1010 !
1020 FOR T=1 TO Tmax
1030 S(T)=INT(S1(T)+.5)+INT(S2(T)+.5)+INT(S3(T)+.5)+INT(S4(T)+.5)+INT(Sa(T)+.5)
! TOTAL POPULATION
1040 PRINT USING 970;T,INT(S1(T)+.5),INT(S2(T)+.5),INT(S3(T)+.5),INT(S4(T)+.5),INT(Sa(T)+.5),S(T)
1050 !
1060 IF S(T)=0 THEN GOTO 2070
1070 IF T<Td THEN GOTO 1100
1080 W=S(T-Td)
1090 GOTO 1110
1100 W=S(1)
1110 !

```

```

1120  !
1130 First:!! ***** FIRST INSTAR SUBPOPULATION *****
1140  Dv1=Dv2=0
1150  FOR Aa=7 TO 39
1160  Age=Aa
1170  GOSUB Fecundity
1180  N1(T+1,1)=N1(T+1,1)+Na(T,Aa)*F
1190  NEXT Aa
1200  Dv1=N1(T+1,1)
1210  FOR A1=1 TO 8
1220  Age=A1
1230  P1=P1(A1)
1240  GOSUB Mortality
1250  D1(T+1)=D1(T+1)+N1(T,A1)*D
1260  N1(T,A1)=N1(T,A1)*(1-D)
1270  N1(T+1,A1+1)=N1(T,A1)*(1-P1)
1280  N2(T+1,A1+1)=N1(T,A1)*P1
1290  Dv2=Dv2+N2(T+1,A1+1)
1300  NEXT A1
1310  S1(T+1)=S1(T)+Dv1-Dv2-D1(T+1)
1320  !
1330  IF S1(T+1)<=.1 THEN S1(T+1)=0 !*****
1340  !
1350  !
1360 Second:!! ***** SECOND INSTAR SUBPOPULATION *****
1370  Dv3=0
1380  FOR A2=2 TO 9
1390  Age=A2
1400  P2=P2(A2)
1410  GOSUB Mortality
1420  D2(T+1)=D2(T+1)+N2(T,A2)*D
1430  N2(T,A2)=N2(T,A2)*(1-D)
1440  N2(T+1,A2+1)=N2(T,A2)*(1-P2)+N2(T+1,A2+1)
1450  N3(T+1,A2+1)=N2(T,A2)*P2
1460  Dv3=Dv3+N3(T+1,A2+1)
1470  NEXT A2
1480  S2(T+1)=S2(T)+Dv2-Dv3-D2(T+1)
1490  IF S2(T+1)<=.1 THEN S2(T+1)=0 !*****
1500  !
1510  !
1520  !
1530  !
1540  !
1550  !
1560 Third: ! ***** THIRD INSTAR SUBPOPULATION *****
1570  Dv4=0
1580  FOR A3=4 TO 10
1590  Age=A3
1600  GOSUB Development3
1610  GOSUB Mortality
1620  D3(T+1)=D3(T+1)+N3(T,A3)*D
1630  N3(T,A3)=N3(T,A3)*(1-D)
1640  N3(T+1,A3+1)=N3(T,A3)*(1-P3)+N3(T+1,A3+1)
1650  N4(T+1,A3+1)=N3(T,A3)*P3
1660  Dv4=Dv4+N4(T+1,A3+1)
1670  NEXT A3
1680  S3(T+1)=S3(T)+Dv3-Dv4-D3(T+1)
1690  !
1700  IF S3(T+1)<=.1 THEN S3(T+1)=0 !*****
1710  !
1720  !

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1730 !
1740 !
1750 Fourth: ! ***** FOURTH INSTAR SUBPOPULATION *****
1760 Dva=0 !*
1770 FOR A4=6 TO 12 !*
1780 Age=A4 !*
1790 GOSUB Development4 !*
1800 GOSUB Mortality !*
1810 D4(T+1)=D4(T)+N4(T,A4)*D !*
1820 N4(T,A4)=N4(T,A4)*(1-D) !*
1830 N4(T+1,A4+1)=N4(T,A4)*(1-P4)+N4(T+1,A4+1) !*
1840 Na(T+1,A4+1)=N4(T,A4)*P4 !*
1850 Dva=Dva+Na(T+1,A4+1) !*
1860 NEXT A4 !*
1870 S4(T+1)=S4(T)+Dv4-Dva-D4(T+1) !*
1880 ! !*
1890 IF S4(T+1)<=.1 THEN S4(T+1)=0 !*****
1900 !
1910 !
1920 Adult: ! ***** ADULT SUBPOPULATION *****
1930 FOR Aa=7 TO 39 !*
1940 Age=Aa !*
1950 GOSUB Mortality !*
1960 Da(T+1)=Da(T)+Na(T,Aa)*D !*
1970 IF Aa=39 THEN 1990 !*
1980 Na(T+1,Aa+1)=Na(T,Aa)*(1-D)+Na(T+1,Aa+1) !*
1990 NEXT Aa !*
2000 Sa(T+1)=Sa(T)+Dva-Da(T+1) !*
2010 ! !*
2020 IF Sa(T+1)<=.1 THEN Sa(T+1)=0 !*****
2030 !
2040 !
2050 NEXT T
2060 GOTO 3210
2070 PRINT "THE POPULATION EXTINGUISHED ON DAY";T;"!!!!!!"
2080 FOR I=T TO Tmax
2090 S(I)=0
2100 NEXT I
2110 !
2120 GOTO 3210
2130 Fecundity: ! ***** AGE-SPECIFIC FECUNDITY *****
2140 A=19.6788+4.2255*LGT(W) !*
2150 B=5.8097-2.1420*LGT(W)+1.7336*LGT(W)^2 !*
2160 C=11.7247-.7473*LGT(W)+1.6430*LGT(W)^2 !*
2170 K=7 !*
2180 IF Aa>=K THEN GOTO 2210 !*
2190 F=0 !*
2200 GOTO 2220 !*
2210 F=EXP(A)*(Aa-K)^B*Aa^(-C) !*
2220 RETURN !*****
2230 !
2240 Mortality: ! ***** AGE-SPECIFIC MORTALITY *****
2250 Amax=38.51 !*
2260 B=.9068-1.4795*LGT(W)+1.0294*LGT(W)^2 !*
2270 IF Amax>=Age THEN GOTO 2300 !*
2280 D=1 !*
2290 GOTO 2310 !*
2300 D=B/(Amax-Age) !*
2310 RETURN !*****

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2320  !
2330 Development1: A=100.64 !*****
2340 B=.0012
2350 C=2.2059
2360 T1=1
2370 FOR T2=8 TO 2 STEP -1
2380 GOSUB Simpson1
2390 P1(T2)=Ps
2400 NEXT T2
2410 FOR T2=2 TO 8
2420 P1(T2)=P1(T2)/P1(8)
2430 IF P1(T2)>1 THEN P1(T2)=1
2440 NEXT T2
2450 RETURN !*****
2460  !
2470 Development2: A=.0773 !*****
2480 B=.0573
2490 C=.2751
2500 T1=2
2510 FOR T2=9 TO 3 STEP -1
2520 GOSUB Simpson2
2530 P2(T2)=Ps
2540 NEXT T2
2550 FOR T2=3 TO 9
2560 P2(T2)=P2(T2)/P2(9)
2570 IF P2(T2)>1 THEN P2(T2)=1
2580 NEXT T2
2590 RETURN !*****
2600  !
2610 Development3: A=.2320-.0429*LGT(W)+.0125*LGT(W)^2 !*****
2620 B=.0274
2630 C=.1613+.0183*LGT(W)-.0060*LGT(W)^2
2640 T1=4
2650 T2=Age
2660 IF T2<=T1 THEN GOTO 2730
2670 GOSUB Simpson2
2680 Pt=Ps
2690 T2=10
2700 GOSUB Simpson2
2710 P3=Pt/Ps
2720 GOTO 2740
2730 P3=0
2740 RETURN !*****
2750  !
2760  !
2770 Development4: A=.4001-.1145*LGT(W)+.0664*LGT(W)^2 !*****
2780 B=.0199-.0048*LGT(W)+.0016*LGT(W)^2
2790 C=.1192+.0200*LGT(W)-.0091*LGT(W)^2
2800 T1=6
2810 T2=Age
2820 IF T2<=T1 THEN GOTO 2890
2830 GOSUB Simpson2
2840 Pt=Ps
2850 T2=12
2860 GOSUB Simpson2
2870 P4=Pt/Ps
2880 GOTO 2900
2890 P4=0
2900 RETURN !*****
2910  !

```

```

2920 !
2930 Simpson1:! ***** INTEGRATION BY SIMPSON'S RULE *****
*
2940 Ps=0
2950 Pa=0
2960 N=10
2970 H=(T2-T1)/N
2980 Pa=FNP1(T2)+FNP1(T1)
2990 Z=4
3000 FOR R=1 TO N-1
3010 Pa=Pa+Z*FNP1(T1+R*H)
3020 Z=6-Z
3030 NEXT R
3040 Ps=H*Pa/3
3050 RETURN !*****
3060 Simpson2:! ***** INTEGRATION BY SIMPSON'S RULE *****
3070 Ps=0
3080 Pa=0
3090 N=10
3100 H=(T2-T1)/N
3110 Pa=FNP(T2)+FNP(T1)
3120 Z=4
3130 FOR R=1 TO N-1
3140 Pa=Pa+Z*FNP(T1+R*H)
3150 Z=6-Z
3160 NEXT R
3170 Ps=H*Pa/3
3180 RETURN !*****
3190 !
3200 !
3210 INPUT "Do you want GRAPHICS ? Press(Y/N)",A$
3220 IF A$="N" THEN STOP
3230 Graphics: ! *****
3240 GCLEAR ! THIS SUBROUTINE PLOTS RESULT IN GRAPHICS.
3250 GRAPHICS
3260 ! ----- Scaling the frame -----
3270 LOCATE 20,110,20,90
3280 Xmin=0
3290 INPUT "Xmax = ?",Xmax
3300 Ymin=0
3310 INPUT "Ymax = ?",Ymax
3320 SCALE Xmin,Xmax,Ymin,Ymax
3330 Ytick=INT(Ymax/5)
3340 Xtick=INT(Xmax/5)
3350 AXES Xtick,Ytick
3360 !
3370 ! ----- Plotting data points -----
3380 MOVE 0,0
3390 FOR T=1 TO Tmax
3400 MOVE T,S1(T)
3410 IF S1(T)<=.1 THEN GOTO 3430
3420 LABEL "."
3430 MOVE T,S2(T)
3440 IF S2(T)<=.1 THEN GOTO 3460
3450 LABEL "*"
3460 MOVE T,S3(T)
3470 IF S3(T)<=.1 THEN GOTO 3490
3480 LABEL "o"
3490 MOVE T,S4(T)
3500 IF S4(T)<=.1 THEN GOTO 3520
3510 LABEL "+"
3520 MOVE T,Sa(T)
3530 IF Sa(T)<=.1 THEN GOTO 3550
3540 LABEL "e"
3550 NEXT T !-----

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```

3560 !
3570 ! ----- Label the X-axis and the Y-axis -----
3580 LDIR 0
3590 FOR X=Xtick TO Xmax STEP Xtick
3600     LORG 6
3610     MOVE X,Ymin-.034*Ymax
3620     LABEL X
3630 NEXT X
3640 A$="Time (Day)"
3650 LORG 4
3660 MOVE Xmax/2,Ymin-.2*Ymax
3670 LABEL A$
3680 FOR Y=Ytick TO Ymax STEP Ytick
3690     LORG 8
3700     MOVE Xmin-.0200*Xmax,Y
3710     LABEL Y
3720 NEXT Y
3730 DEG
3740 B$="Number in each stage"
3750 LORG 4
3760 MOVE Xmin-.15*Xmax,Ymax/2
3770 LDIR 90
3780 LABEL B$ !-----
3790 !
3800 ! ----- Drawing lines to connect data points -----
3810 LINE TYPE 1
3820 MOVE 1,S1(1)
3830 FOR T=1 TO Tmax
3840     DRAW T,S1(T)
3850 NEXT T
3860 PENUP
3870 MOVE 1,S2(1)
3880 FOR T=1 TO Tmax
3890     DRAW T,S2(T)
3900 NEXT T
3910 PENUP
3920 MOVE 1,S3(1)
3930 FOR T=1 TO Tmax
3940     DRAW T,S3(T)
3950 NEXT T
3960 PENUP
3970 MOVE 1,S4(1)
3980 FOR T=1 TO Tmax
3990     DRAW T,S4(T)
4000 NEXT T
4010 PENUP
4020 MOVE 1,Sa(1)
4030 FOR T=1 TO Tmax
4040     DRAW T,Sa(T)
4050 NEXT T
4060 PENUP
4070 MOVE 1,S(1)
4080 FOR T=1 TO Tmax
4090     DRAW T,S(T)
4100 NEXT T
4110 PENUP ! -----
4120 PAUSE
4130 !
4140 !
4150 !
4160 INPUT "Do you want to DUMPGRAPHICS ? Press (Y/N)",Dump$
4170 IF Dump$="N" THEN GOTO 4210
4180 DUMP GRAPHICS
4190 EXIT GRAPHICS
4200 !
4210 STOP !*****
4220 !
4230 !
4240 !
4250 !
4260 END

```

Appendix III

Simulation Model of the Cabbage Aphid with Parasitoid, D. rapae.

Appendix III

This programme is used in simulation of the population dynamics of the cabbage aphid with the parasitoid, D. rapae. The programme is written in BASIC. Generally it has the same structure as the programme in Appendix II. The only modified parts are subroutines Fecundity and Mortality. In the initial condition, it needs the extra information for the time (T_p) and the number (N_p) of the parasitoid attacking the aphid population in addition to the information needed in the previous programme in Appendix II.

```

10  ! THE FILE NAME IS THES7
20  OPTION BASE 1
30  PRINTER IS 16
40  PRINT "*****"
****"
50  PRINT "*"
  "*"
60  PRINT "          POPULATION DYNAMICS OF CABBAGE APHID,"
  "*"
70  PRINT "          Brevicoryne brassicae (L.), WITH THE PARASITOID,"
  "*"
80  PRINT "          Diaeretiella rapae (M'Intosh)"
  "*"
90  PRINT "*"
  "*"
100 PRINT "*****"
****"
110 DIM S1(50),S2(50),S3(50),S4(50),Sa(50),S(50),A#(30),B#(30),Age(5,40)
120 DIM N1(50,40),N2(50,40),N3(50,40),N4(50,40),Na(50,40),D1(50),D2(50),D3(50),
  D4(50),Da(50)
130 DIM Dpa1(60),Dpa2(60),Dpa3(60),Dpa4(60),Dpa5(60),Np(60,40),Nq(60,40),Tp(20),
  Pn(20)
140 INPUT "Do you know the ages of the initial stage groups of the aphid ?(Pre
ss: Y/N)",T$
150 IF T$="N" THEN GOTO 220
160 INPUT "INITIAL AGES OF THE INITIAL STAGE GROUPS,(seperated by comma)",A1,A
2,A3,A4,As
170 GOTO 570
180 !
190 !
200 !
210 !
220 Random_age: ! *****
230 FOR I=1 TO 100 !
240   I1=INT(RND*10) MOD 9 !
250   RANDOMIZE !
260 NEXT I !
270 IF I1<1 THEN GOTO 220 !          THIS SUBROUTINE ASSIGNS RANDOM AGE
280 A1=I1 !          TO THE INITIAL STAGE POPULATION WHOSE
290 FOR I=1 TO 100 !          AGES ARE UNKNOWN OR UNCERTAIN.
300   I2=INT(RND*10) MOD 10 !
310   RANDOMIZE !
320 NEXT I !
330 IF I2<2 THEN GOTO 290 !
340 A2=I2 !
350 FOR I=1 TO 100 !
360   I3=INT(RND*100) MOD 11 !
370   RANDOMIZE !
380 NEXT I !
390 IF I3<4 THEN GOTO 350 !
400 A3=I3 !
410 FOR I=1 TO 100 !
420   I4=INT(RND*100) MOD 13 !
430   RANDOMIZE !
440 NEXT I !
450 IF I4<6 THEN GOTO 410 !
460 A4=I4 !
470 FOR I=1 TO 100 !
480   Ia=INT(RND*1000) MOD 40 !
490   RANDOMIZE !
500 NEXT I !
510 IF I4<7 THEN GOTO 470 !
520 As=Ia !*****
530 !
540 !
550 !

```

```

560 !
570 INPUT "INITIAL POPULATION DENSITY FOR EACH STAGE OF THE APHID ?",S1(1),S2(
1),S3(1),S4(1),Sa(1)
580 !
590 INPUT "IS THERE ANY PARASITOID ? (Y/N)",P$
600 IF P$="N" THEN GOTO 670
610 Para=1
620 INPUT "HOW MANY TIMES HAS THE PARASITOID ATTACKED THE APHID POPULATION ?",
An
630 FOR I=1 TO An
640 INPUT "TIME & NO. OF THE PARASITOID OBSERVED (separated by comma)",Tp(I),
Pn(I)
650 NEXT I
660 GOTO 680
670 Para=0
680 !
690 !
700 INPUT "HARD-COPY OPTIONS (CRT or PRINTER, Press C/P)",A$
710 IF A$="P" THEN PRINTER IS 0
720 T=1
730 S(T)=S1(T)+S2(T)+S3(T)+S4(T)+Sa(T) ! TOTAL POPULATION
740 W=S(T)
750 PRINT "INITIAL TOTAL POPULATION =";W
760 PRINT
770 PRINT
780 Amax=39 ! MAXIMUM LIFE-SPAN
790 INPUT "How long does the experiment last ? (day)",Tmax
800 REDIM N1(Tmax+1,Amax+1),N2(Tmax+1,Amax+1),N3(Tmax+1,Amax+1),N4(Tmax+1,Amax
+1),Na(Tmax+1,Amax+1)
810 REDIM D1(Tmax+1),D2(Tmax+1),D3(Tmax+1),D4(Tmax+1),Da(Tmax+1),S1(Tmax+1),S2
(Tmax+1),S3(Tmax+1),S4(Tmax+1),Sa(Tmax+1)
820 !
830 !
840 N1(1,A1)=S1(1) !*****
850 N2(1,A2)=S2(1) !
860 N3(1,A3)=S3(1) ! ASSIGN INITIAL STAGE POPULATIONS *
870 N4(1,A4)=S4(1) ! TO THEIR AGE GROUPS. *
880 Na(1,Aa)=Sa(1) !*****
890 !
900 Td=10 ! THE TIME DELAY OF DENSITY DEPENDENCE
910 !
920 ! ***** STAGE DEVELOPMENT FUNCTIONS **
930 DEF FNP1(Age)=A*EXP(-B*EXP(C*Age)) !
940 DEF FNP(Age)=EXP(-(1/Age-C)/B)^2/2)/(A*B*SQR(2*PI)) !
950 !
960 ! *****
970 !
980 ! ***** FUNCTIONAL RESPONSE EQUATIONS *****
990 DEF FNFr1(N)=N*(1-EXP(-.0297*N/(1+.0297*.0492*N^2))) !
1000 DEF FNFr3(N)=N*(1-EXP(-.174*N/(1+.174*.0466*N^2))) !
1010 DEF FNFr4(N)=N*(1-EXP(-1.917/(1+1.917*.0363*N))) !
1020 DEF FNFr5(N)=N*(1-EXP(-1.2916/(1+1.2916*.0292*N))) !
1030 ! *****
1040 !
1050 !
1060 !
1070 ! ***** PREFERENCE INDEX *****
1080 Q1=.13 ! OF THE PARASITOID TO ATTACK
1090 Q2=.34 ! VARIOUS STAGES OF THE APHID
1100 Q3=1 !
1110 Q4=1.76 !
1120 Q5=1.95 !
1130 ! *****
1140 !
1150 !

```

```

1160 !
1170 !
1180 !
1190 !
1200 !
1210 !
1220 GOSUB Development1
1230 GOSUB Development2
1240 IMAGE 3D,1X,8D,1X,8D,1X,8D,1X,8D,1X,8D,3X,8D
1250 PRINT " TIME      1st      2nd      3rd      4th      Adult      Total"
1260 PRINT "-----"
1270 PRINT
1280 !
1290 FOR T=1 TO Tmax
1300 S(T)=INT(S1(T)+.5)+INT(S2(T)+.5)+INT(S3(T)+.5)+INT(S4(T)+.5)+INT(Sa(T)+.5)
    ! TOTAL POPULATION
1310 PRINT USING 1240;T,INT(S1(T)+.5),INT(S2(T)+.5),INT(S3(T)+.5),INT(S4(T)+.5)
    ,INT(Sa(T)+.5),S(T)
1320 !
1330 IF S(T)=0 THEN GOTO 2480
1340 IF T<=Td THEN GOTO 1370
1350 W=S(T-Td)
1360 GOTO 1380
1370 W=S(1)
1380 !
1390 !
1400 First:Stage=1 !***** FIRST INSTAR SUBPOPULATION *****
1410 R1=S1(T)/S(T)
1420 Dv1=Dv2=0 !*
1430 FOR A1=1 TO 8 !*
1440 Age=A1 !*
1450 P1=P1(A1) !*
1460 GOSUB Mortality !*
1470 D1(T+1)=D1(T+1)+N1(T,A1)*D !*
1480 N1(T,A1)=N1(T,A1)*(1-D) !*
1490 N1(T+1,A1+1)=N1(T,A1)*(1-P1) !*
1500 N2(T+1,A1+1)=N1(T,A1)*P1 !*
1510 Dv2=Dv2+N2(T+1,A1+1) !*
1520 NEXT A1 !*
1530 ! *****
1540 !
1550 !
1560 Second:Stage=2 !***** SECOND INSTAR SUBPOPULATION *****
1570 R2=S2(T)/S(T) !*
1580 Dv3=0 !*
1590 FOR A2=2 TO 9 !*
1600 Age=A2 !*
1610 P2=P2(A2) !*
1620 GOSUB Mortality !*
1630 D2(T+1)=D2(T+1)+N2(T,A2)*D !*
1640 N2(T,A2)=N2(T,A2)*(1-D) !*
1650 N2(T+1,A2+1)=N2(T,A2)*(1-P2)+N2(T+1,A2+1) !*
1660 N3(T+1,A2+1)=N2(T,A2)*P2 !*
1670 Dv3=Dv3+N3(T+1,A2+1) !*
1680 NEXT A2 !*
1690 S2(T+1)=S2(T)+Dv2-Dv3-D2(T+1) !*
1700 IF S2(T+1)<=.49 THEN S2(T+1)=0 !*****
1710 !
1720 !
1730 !
1740 !
1750 !

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1760 !
1770 Third:Stage=3 !***** THIRD INSTAR SUBPOPULATION *****
1780 R3=S3(T)/S(T) !*
1790 Dv4=0 !*
1800 FOR A3=4 TO 10 !*
1810 Age=A3 !*
1820 GOSUB Development3 !*
1830 GOSUB Mortality !*
1840 D3(T+1)=D3(T+1)+N3(T,A3)*D !*
1850 N3(T,A3)=N3(T,A3)*(1-D) !*
1860 N3(T+1,A3+1)=N3(T,A3)*(1-P3)+N3(T+1,A3+1) !*
1870 N4(T+1,A3+1)=N3(T,A3)*P3 !*
1880 Dv4=Dv4+N4(T+1,A3+1) !*
1890 NEXT A3 !*
1900 S3(T+1)=S3(T)+Dv3-Dv4-D3(T+1) !*
1910 ! !*
1920 IF S3(T+1)<=.49 THEN S3(T+1)=0 !*****
1930 !
1940 !
1950 !
1960 !
1970 Fourth:Stage=4 !***** FOURTH INSTAR SUBPOPULATION *****
1980 Dva=0 !*
1990 FOR A4=6 TO 12 !*
2000 Age=A4 !*
2010 GOSUB Development4 !*
2020 GOSUB Mortality !*
2030 D4(T+1)=D4(T+1)+N4(T,A4)*D !*
2040 N4(T,A4)=N4(T,A4)*(1-D) !*
2050 N4(T+1,A4+1)=N4(T,A4)*(1-P4)+N4(T+1,A4+1) !*
2060 Na(T+1,A4+1)=N4(T,A4)*P4 !*
2070 Dva=Dva+Na(T+1,A4+1) !*
2080 NEXT A4 !*
2090 S4(T+1)=S4(T)+Dv4-Dva-D4(T+1)-Dpa1(T)-Dpa2(T) !*
2100 ! !*
2110 IF S4(T+1)<=.49 THEN S4(T+1)=0 !*****
2120 !
2130 !
2140 Adult:Stage=5 !***** ADULT SUBPOPULATION *****
2150 R5=Sa(T)/S(T) !*
2160 FOR Aa=7 TO 39 !*
2170 Age=Aa !*
2180 GOSUB Mortality !*
2190 Da(T+1)=Da(T+1)+Na(T,Aa)*D !*
2200 IF Aa=39 THEN 2220 !*
2210 Na(T+1,Aa+1)=Na(T,Aa)*(1-D)+Na(T+1,Aa+1) !*
2220 NEXT Aa !*
2230 Sa(T+1)=Sa(T)+Dva-Da(T+1)-Dpa3(T)-Dpa4(T)-Dpa5(T) !*
2240 ! !*
2250 IF Sa<=.49 THEN Sa(T+1)=0 !*****
2260 ! *****
2270 FOR Aa=7 TO 39 !*
2280 Fp=Fq=0 !*
2290 Age=Aa !*
2300 GOSUB Fecundity !*
2310 Fp=Np(T,Aa)*F*.7 !*
2320 Fq=Nq(T,Aa)*F*.5 !*
2330 N1(T+1,1)=N1(T+1,1)+Na(T,Aa)*F-Fp-Fq !*
2340 NEXT Aa !*
2350 Dv1=N1(T+1,1) !*
2360 S1(T+1)=S1(T)+Dv1-Dv2-D1(T+1) !*
2370 IF S1(T+1)<=.49 THEN S1(T+1)=0 !*****
2380 !
2390 !
2400 !

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2410 !
2420 !
2430 !
2440 !
2450 !
2460 NEXT T
2470 GOTO 4020
2480 PRINT "THE POPULATION EXTINCTED ON DAY";T;"!!!!!"
2490 FOR I=T TO Tmax
2500   S(I)=0
2510 NEXT I
2520 !
2530 GOTO 4020
2540 Fecundity: ! ***** AGE-SPECIFIC FECUNDITY *****
2550 A=19.6788+4.2255*LGT(W) !*
2560 B=5.8097-2.1420*LGT(W)+1.7336*LGT(W)^2 !*
2570 C=11.7247-.7473*LGT(W)+1.6430*LGT(W)^2 !*
2580 K=7 !*
2590 IF Aa>=K THEN GOTO 2620 !*
2600 F=0 !*
2610 GOTO 2700 !*
2620 F=EXP(A)*(Aa-K)^B*Aa^(-C) !*
2630 IF Para=0 THEN GOTO 2700 !*
2640 FOR A=1 TO 5 !*
2650   Np(T+2+A,A+9)=Dpa4(T+8) !*
2660 NEXT A !*
2670 FOR A=1 TO 7 !*
2680   Nq(T+A,A+9)=Dpa5(T+8) !*
2690 NEXT A !*
2700 RETURN !*****
2710 !
2720 Mortality: ! ***** AGE-SPECIFIC MORTALITY *****
2730 Amax=38.51 !*
2740 B=.9068-1.4795*LGT(W)+1.0294*LGT(W)^2 !*
2750 IF Amax>=Age THEN GOTO 2780 !*
2760 D=1 !*
2770 GOTO 3120 !*
2780 D=B/(Amax-Age) !*
2790 IF Para=0 THEN GOTO 3120 !*
2800 ON Stage GOSUB Para1,Para2,Para3,Para4,Para5 !*
2810 N=S(T) !*
2820 Para1:FOR J=1 TO An !*
2830   IF T*Para-Tp(J)<>0 THEN GOTO 2850 !*
2840   Dpa1(T+8)=R1*Q1*FNFr1(N) !*
2850 NEXT J !*
2860 RETURN !*
2870 Para2:FOR J=1 TO An !*
2880   IF T*Para-Tp(J)<>0 THEN GOTO 2900 !*
2890   Dpa2(T+8)=R2*Q2*FNFr1(N) !*
2900 NEXT J !*
2910 RETURN !*
2920 Para3:FOR J=1 TO An !*
2930   IF T*Para-Tp(J)<>0 THEN GOTO 2950 !*
2940   Dpa3(T+8)=R3*Q3*FNFr3(N) !*
2950 NEXT J !*
2960 RETURN !*
2970 Para4:FOR J=1 TO An !*
2980   IF T*Para-Tp(J)<>0 THEN GOTO 3000 !*
2990   Dpa4(T+8)=R4*Q4*FNFr4(N) !*
3000 NEXT J !*
3010 RETURN !*
3020 Para5:FOR J=1 TO An !*
3030   IF T*Para-Tp(J)<>0 THEN GOTO 3050 !*
3040   Dpa5(T+8)=R5*Q5*FNFr5(N) !*
3050 NEXT J !*
3060 RETURN !*
3070 !
3080 !
3090 !

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3100 !
3110 !
3120 RETURN !*****
3130 !
3140 Development1: A=100.64 !*****
3150 B=.0012
3160 C=2.2059
3170 T1=1
3180 FOR T2=8 TO 2 STEP -1
3190 GOSUB Simpson1
3200 P1(T2)=Ps
3210 NEXT T2
3220 FOR T2=2 TO 8
3230 P1(T2)=P1(T2)/P1(8)
3240 IF P1(T2)>1 THEN P1(T2)=1
3250 NEXT T2
3260 RETURN !*****
3270 !
3280 Development2: A=.0773 !*****
3290 B=.0573
3300 C=.2751
3310 T1=2
3320 FOR T2=9 TO 3 STEP -1
3330 GOSUB Simpson2
3340 P2(T2)=Ps
3350 NEXT T2
3360 FOR T2=3 TO 9
3370 P2(T2)=P2(T2)/P2(9)
3380 IF P2(T2)>1 THEN P2(T2)=1
3390 NEXT T2
3400 RETURN !*****
3410 !
3420 Development3: A=.2320-.0429*LGT(W)+.0125*LGT(W)^2 !*****
3430 B=.0274
3440 C=.1613+.0183*LGT(W)-.0060*LGT(W)^2
3450 T1=4
3460 T2=Age
3470 IF T2<=T1 THEN GOTO 3540
3480 GOSUB Simpson2
3490 Pt=Ps
3500 T2=10
3510 GOSUB Simpson2
3520 P3=Pt/Ps
3530 GOTO 3550
3540 P3=0
3550 RETURN !*****
3560 !
3570 !
3580 Development4: A=.4001-.1145*LGT(W)+.0664*LGT(W)^2 !*****
3590 B=.0199-.0048*LGT(W)+.0016*LGT(W)^2
3600 C=.1192+.0200*LGT(W)-.0091*LGT(W)^2
3610 T1=6
3620 T2=Age
3630 IF T2<=T1 THEN GOTO 3700
3640 GOSUB Simpson2
3650 Pt=Ps
3660 T2=12
3670 GOSUB Simpson2
3680 P4=Pt/Ps
3690 GOTO 3710
3700 P4=0
3710 RETURN !*****
3720 !

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```

3730  !
3740 Simpson1:! ***** INTEGRATION BY SIMPSON'S RULE *****
*
3750  Ps=0
3760  Pa=0
3770  N=10
3780  H=(T2-T1)/N
3790  Pa=FNPI(T2)+FNPI(T1)
3800  Z=4
3810  FOR R=1 TO N-1
3820  Pa=Pa+Z*FNPI(T1+R*H)
3830  Z=6-Z
3840  NEXT R
3850  Ps=H*Pa/3
3860  RETURN !*****
3870 Simpson2:! ***** INTEGRATION BY SIMPSON'S RULE *****
3880  Ps=0
3890  Pa=0
3900  N=10
3910  H=(T2-T1)/N
3920  Pa=FNPI(T2)+FNPI(T1)
3930  Z=4
3940  FOR R=1 TO N-1
3950  Pa=Pa+Z*FNPI(T1+R*H)
3960  Z=6-Z
3970  NEXT R
3980  Ps=H*Pa/3
3990  RETURN !*****
4000  !
4010  !
4020  INPUT "Do you want GRAPHICS ? Press(Y/N)",A#
4030  IF A#="N" THEN STOP
4040 Graphics: ! *****
4050 GCLEAR ! THIS SUBROUTINE PLOTS RESULT IN GRAPHICS.
4060 GRAPHICS
4070  ! ----- Scaling the frame -----
4080 LOCATE 20,110,20,90
4090  Xmin=0
4100  INPUT "Xmax = ?",Xmax
4110  Ymin=0
4120  INPUT "Ymax = ?",Ymax
4130 SCALE Xmin,Xmax,Ymin,Ymax
4140  Ytick=INT(Ymax/5)
4150  Xtick=INT(Xmax/5)
4160 AXES Xtick,Ytick
4170  !
4180  ! ----- Plotting data points -----
4190 MOVE 0,0
4200 FOR T=1 TO Tmax
4210  MOVE T,S1(T)
4220  IF S1(T)<=.1 THEN GOTO 4240
4230  LABEL "."
4240  MOVE T,S2(T)
4250  IF S2(T)<=.1 THEN GOTO 4270
4260  LABEL "*"
4270  MOVE T,S3(T)
4280  IF S3(T)<=.1 THEN GOTO 4300
4290  LABEL "o"
4300  MOVE T,S4(T)
4310  IF S4(T)<=.1 THEN GOTO 4330
4320  LABEL "+"
4330  MOVE T,Sa(T)
4340  IF Sa(T)<=.1 THEN GOTO 4360
4350  LABEL "e"
4360 NEXT T !-----
4370  !

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4380 ! ----- Label the X-axis and the Y-axis -----
4390 LDIR 0
4400 FOR X=Xtick TO Xmax STEP Xtick
4410     LORG 6
4420     MOVE X,Ymin-.034*Ymax
4430     LABEL X
4440 NEXT X
4450 A$="Time (Day)"
4460 LORG 4
4470 MOVE Xmax/2,Ymin-.2*Ymax
4480 LABEL A$
4490 FOR Y=Ytick TO Ymax STEP Ytick
4500     LORG 8
4510     MOVE Xmin-.0200*Xmax,Y
4520     LABEL Y
4530 NEXT Y
4540 DEG
4550 B$="Number in each stage"
4560 LORG 4
4570 MOVE Xmin-.15*Xmax,Ymax/2
4580 LDIR 90
4590 LABEL B$ !-----
4600 !
4610 ! ----- Drawing lines to connect data points -----
4620 LINE TYPE 1
4630 MOVE 1,S1(1)
4640 FOR T=1 TO Tmax
4650     DRAW T,S1(T)
4660 NEXT T
4670 PENUP
4680 MOVE 1,S2(1)
4690 FOR T=1 TO Tmax
4700     DRAW T,S2(T)
4710 NEXT T
4720 PENUP
4730 MOVE 1,S3(1)
4740 FOR T=1 TO Tmax
4750     DRAW T,S3(T)
4760 NEXT T
4770 PENUP
4780 MOVE 1,S4(1)
4790 FOR T=1 TO Tmax
4800     DRAW T,S4(T)
4810 NEXT T
4820 PENUP
4830 MOVE 1,Sa(1)
4840 FOR T=1 TO Tmax
4850     DRAW T,Sa(T)
4860 NEXT T
4870 PENUP
4880 MOVE 1,S(1)
4890 FOR T=1 TO Tmax
4900     DRAW T,S(T)
4910 NEXT T
4920 PENUP ! -----
4930 PAUSE
4940 !
4950 !
4960 !
4970 INPUT "Do you want to DUMPGRAPHICS ? Press (Y/N)",Dump$
4980 IF Dump$="N" THEN GOTO 5020
4990 DUMP GRAPHICS
5000 EXIT GRAPHICS
5010 !
5020 STOP !*****
5030 !
5040 !
5050 !
5060 !
5070 END

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