# Simulation of lime aphid population dynamics

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# 1 Introduction

## 1.1 The lime aphid

The lime aphid *Eucallipterus tiliae* L. is a tree-dwelling aphid host-specific to most members of the genus *Tilia*. It varies greatly in numbers from year to year, sometimes seeming to be virtually absent, at others occurring in such large numbers that leaves and town pavements beneath the trees become sticky with honeydew while the leaves blacken with sooty mould which grows upon it.

A number of aspects of the aphid's ecology have been studied in the past, in the field and in the laboratory (Dixon, 1971a, 1971b, 1972; Kidd, 1975, 1976, 1977; White, 1970; Brown, 1975), and aphid populations have been monitored for nine years on six trees in Glasgow, Scotland. Considerable information also exists on the two predators (Glen, 1971, 1973, 1975; Wratten, 1971, 1973) and the leafhopper found on lime (Flanagan, 1974).

Llewellyn (1970) studied the lime aphid population as a whole in terms of energetics, then Dixon (1971a) produced the first description of its dynamics, drawing attention to an inverse relationship between numbers of fundatrices and oviparae and suggesting an explanation based on the population processes known at that stage. This work was expanded by Brown (1975) who introduced studies of populations under controlled conditions in an insectary.

## 1.2 Background to the approach

There are four basically different ways of studying a population's dynamics, which can be considered as theoretical, experimental, analytic and synthetic. In the first case a simple theoretical model, based on *a priori* assumptions and usually consisting of a single difference or differential equation, can be fitted to observed data and conclusions drawn about the population's behaviour based on the known properties of the model. Alternatively, a population in the field may be manipulated by using experimental exclusion techniques to ascertain the main factors responsible for numerical change and their relative importance. As a third alternative the observed changes in numbers can be analysed to show the contributions of reproduction and different mortalities. An age-specific life-table is derived by tracing the fate of a cohort from birth to death, or a time-specific life table by comparing numbers of animals present in successive age-classes at any one time. Both yield a series of age-specific survival rates and fecundities; in the second case these are constant, or assumed to be so, while in the first case they may be variable. Key factor analysis (Varley & Gradwell, 1960) is a particularly widely used application of age-specific life tables, in which a study of the variation in age-specific mortalities from generation to generation demonstrates which is the key factor responsible for population change and which, if any, involves density-dependence. Age-specific life tables of this kind can be used when generations are discrete or when individual cohorts can be identified, while time-specific life tables are applicable when there is considerable overlap between generations and the age-distribution is stable with a constant ratio between numbers in the age-classes. The fourth, synthetic approach involves building up a picture of population behaviour comparable with that observed, by assembly of separately studied component processes in a detailed model.

The study of aphid populations presents particular problems since most are characterized by overlapping generations and unstable age-distributions. Way & 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. While the technique is extremely useful and has the great merit of being a direct measure, there is clearly a limit to the extent to which components of population change can be partitioned in this way and there are some obvious problems in applying the method to tree-dwelling aphids. No simple theoretical models appear to have been successfully applied to aphid populations, in which age-structure and time lags are often of crucial importance; nevertheless, one of the aims of building complex models should be to find out how to build meaningful simple ones. Because of the features of their population behaviour already mentioned, aphids do not readily lend themselves to life-table analysis. However, Hughes (1962, 1963) pioneered one method in a study of *Brevicoryne brassicae* L. that is still widely used. Mortality was estimated as the difference between the potential rate of increase and the observed rate, then partitioned among various causes according to indicators 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 sample date. The analysis was confined to occasions when the instar-distribution was thought to be stable and the numbers formed a geometric series (Carter, Aikman & Dixon, 1978). A second method of estimating mortality was adopted by Glen (1971) and Glen & Barlow (in press), in order to determine the role of the black-kneed capsid *Blepharidopterus angulatus* Fall. as a predator of the lime aphid. The potential number of aphids at any time was simply estimated from that on the previous sampling occasion and independent estimates of the reproductive rate and the instar lengths; the mortality was given by the difference between the potential number thus calculated and the number observed. In this case the underlying assumption is of an even age-distribution among nymphs which become adults during the interval, and the mortality estimate includes loss of recruitment through reduction in the maximum reproductive rate.

However, it was in studies of aphids that some of the first population simulation models appeared, notably that of Hughes & Gilbert (1968) for *Brevicoryne brassicae,* developed further with emphasis on a host/parasite relationship by Gilbert & Hughes (1971). Gilbert & Gutierrez (1973) and Gutierrez et al. (1974) produced similar models for *Masonaphis maxima* Mason on thimbleberry and cowpea aphid, *Aphis craccivora* Koch, respectively. All were based on physiological time and tended to yield greatest insight into the relationships between the aphids and their natural enemies, a feature carried furthest in Frazer & Gilbert's (1976) model of predation in the field by coccinellids on the pea aphid *Acyrthosiphon pisum* Harris. Although drawing heavily on observed population data, the models were not validated against long series of such data. Nevertheless this set of aphid models represents an extremely valuable and possibly underrated contribution to the study of population dynamics. The basic approach adopted by these authors, which differs from the present one in certain respects such as validation and use of physiological time, is described by Gilbert et al. (1976). Two aphid models of a slightly different kind include an extremely detailed one of *Aphis fabae* (Crawley, 1973), designed to examine the effects of various predation strategies, and one used by Perrin (1974) as part of a study of the nettle aphid *Microlophium carnosum* Buckt.; the latter is an excellent example of simple modelling used as a tool in research. Both models took account of temperature-dependent development rates but were not based on physiological time, and because of the way they were used were not validated against independent data.

## 1.3 The objective

Why model the lime aphid? There are two main reasons. The first lies in the disadvantages of the available alternatives. However, the second and most important lies in the positive features of the approach, in integrating available knowledge, providing a functional basis for observed events and a stringent test of understanding, showing precisely where future work is required and providing a framework into which it can be incorporated, and increasing understanding of the roles of interacting component processes.

The aim in this book, therefore, is to use a systems approach to test and improve our understanding of the lime aphid's population dynamics and to guide the course of future research. The model is a tool, not an end result, and its scope was determined by the size of the system and the overall objective of obtaining a qualitatively correct and quantitatively reasonable picture of what determines this aphid's abundance.

Following the Introduction, Chapter 2 describes the system and presents the problem, in terms of the observed behaviour of the aphid population which the model is intended to re-create. Chapter 3 describes how the model was chosen, its structure and the submodels representing the various population processes; for each submodel the relationships used are stated first then their biological bases discussed. The model's output is compared with the observed population data in Chapter 4. Then in the final chapter conclusions are drawn about the roles of the different processes and suggestions made as to further work required.

## 1.4 Terminology

In discussing different kinds of aphids the terms fundatrix, vivipara and ovipara are frequently used. Fundatrices are first generation aphids, viviparae are alate females which reproduce parthenogenetically and viviparously, while oviparae are apterous sexual females which mate and lay eggs. Aphid densities on the tree are expressed as numbers per unit area of mature leaf, usually 100 $cm^2$ or 1 $m^2$, and weights are fresh weights unless otherwise stated.

# 2 The system

## 2.1 Components of the system

The system modelled is a lime tree, or close group of trees, and the animals found on it which affect the aphid. These include two predators and their alternative prey (Fig. 1); parasites are not explicitly considered and the tree is dealt with largely as a black box. Immigration of aphids by flight is pooled with emigration as net emigration, which is equivalent to mortality in the model.

Aphid eggs hatch when the buds break at the beginning of May. The nymphs pass through 4 instars to become alate female adults (viviparae), which produce more nymphs parthenogenetically. The process is repeated, changing towards the end of the season when

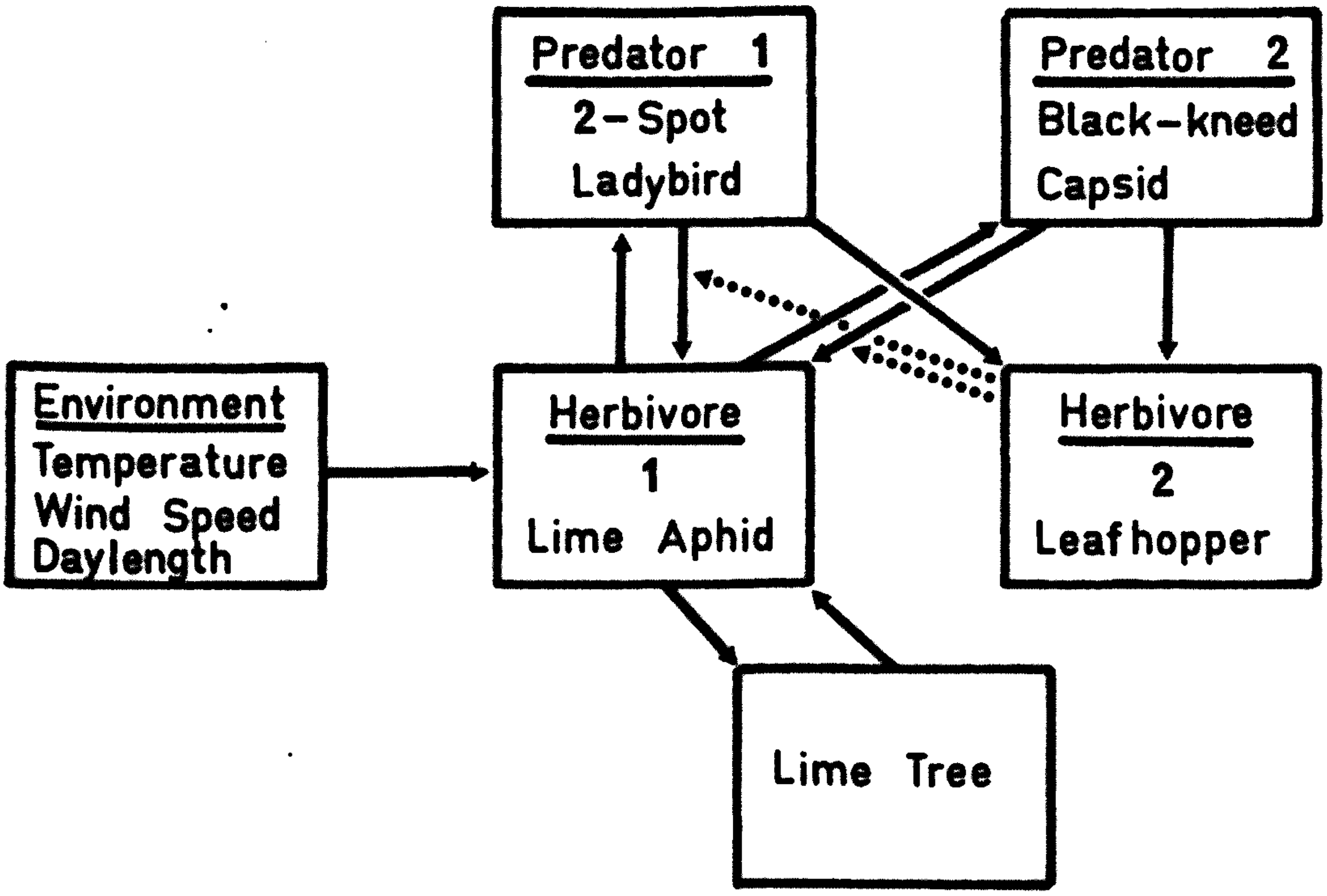


Fig. 1. Simple diagram of the lime aphid population system, showing the main components and interactions.

increasing proportions of sexuals are produced. The males are alate and the sexual females (oviparae) are apterous. The proportion of viviparae therefore declines and population growth in the current season is curtailed, since oviparae lay overwintering eggs on the bark of the tree. Development of each parthenogenetic generation takes about 3 weeks, 5 weeks in early spring, and 4 or 5 generations occur each year, generally with 2 overlapping at any one time. Aphids of the first generation are referred to as fundatrices. Adult aphids weigh between 300 μg and 900 μg in the field and populations can vary nearly a hundredfold in peak abundance from year to year.

The other herbivore which can occur in large numbers on lime trees is the leafhopper *Alnetoidea alneti* Dahlbom. It passes through one generation each year, from overwintering eggs through 5 nymphal instars to a winged, sexually-reproducing adult. Eggs are laid in August and September and hatch around the beginning of May (Flanagan, 1974).

The most important predators are the 2-spot coccinellid *Adalia bipunctata* L. and the black-kneed capsid *Blepharidopterus angulatus* Fall. Syrphid larvae were recorded less often and chrysopid larvae and anthocorid larvae still less frequently. The capsid overwinters in the egg stage on lime and passes through one generation each year. There are 5 nymphal instars and the winged adults lay their eggs in late August (Glen, 1971). The coccinellid overwinters as an adult, feeding on the aphids and laying eggs from the end of May. There are 4 larval instars and a pupal stage and adults appear in largest numbers after the end of July (Wratten, 1971). A second generation seems to occur in some years, such as 1968. The aphids are parasitized by *Praon flavinode* (Hal.) (Brown, 1975) which leaves mummified carcasses.

The tree provides a food source rich in amino-nitrogen for a short period in May while the leaves are growing. Otherwise, the amino-nitrogen level is low and fairly constant (Dixon 1971a). Little is known about the effect on nutritional quality of factors such as water stress, but there is evidence that it is reduced by severe aphid infestation. Using aphid weights as indicators of food quality, although there were short-term fluctuations, the average stayed constant throughout the summers of 1970 and 1972, when densities of aphids were low.

The system is an open one, influenced strongly by weather, and can be divided into 3 subsystems: the tree, the aphid population and the predator and leafhopper populations. The simple diagram of

Fig. 1 is expanded in Fig. 2 to show the time profile of the system throughout the season and the main interactions which occur. The inputs and outputs correspond to those in the model, the 'coccinellid multiplier' being an index of overall abundance of the 2-spot coccinellid in any one year. The aphid subsystem consists, in essence, of a within-season loop, from adults to nymphs, and a between-seasons loop not shown in Fig. 2 from eggs laid at the end of one year to eggs hatching at the beginning of the next. Finally, in Figs 3 to 6 the aphid subsystem and the predator/leafhopper subsystem are shown in sufficient detail to demonstrate the component processes and interactions which are modelled in the next chapter. The only component of the tree subsystem explicitly considered is the amino-nitrogen concentration level in the phloem, aphid-induced tissue deterioration being related directly to cumulative aphid abundance and leaf-fall to the time of year.

## 2.2 Observed behaviour of the aphid population

The population behaviour will be considered in two parts, variations in numbers between years and changes in numbers throughout a year.

Since generations overlap and reproduction occurs continuously throughout the summer, the best measure of changes in numbers between seasons is based on the number of overwintering eggs at the beginning of each. However, since these are difficult to sample, it is more convenient to use as a measure of year-to-year abundance the peak number of fundatrix nymphs in the spring. With one point thus derived for each tree and each year the relationship between numbers one year and those the next is overcompensating, given by (Fig. 7):

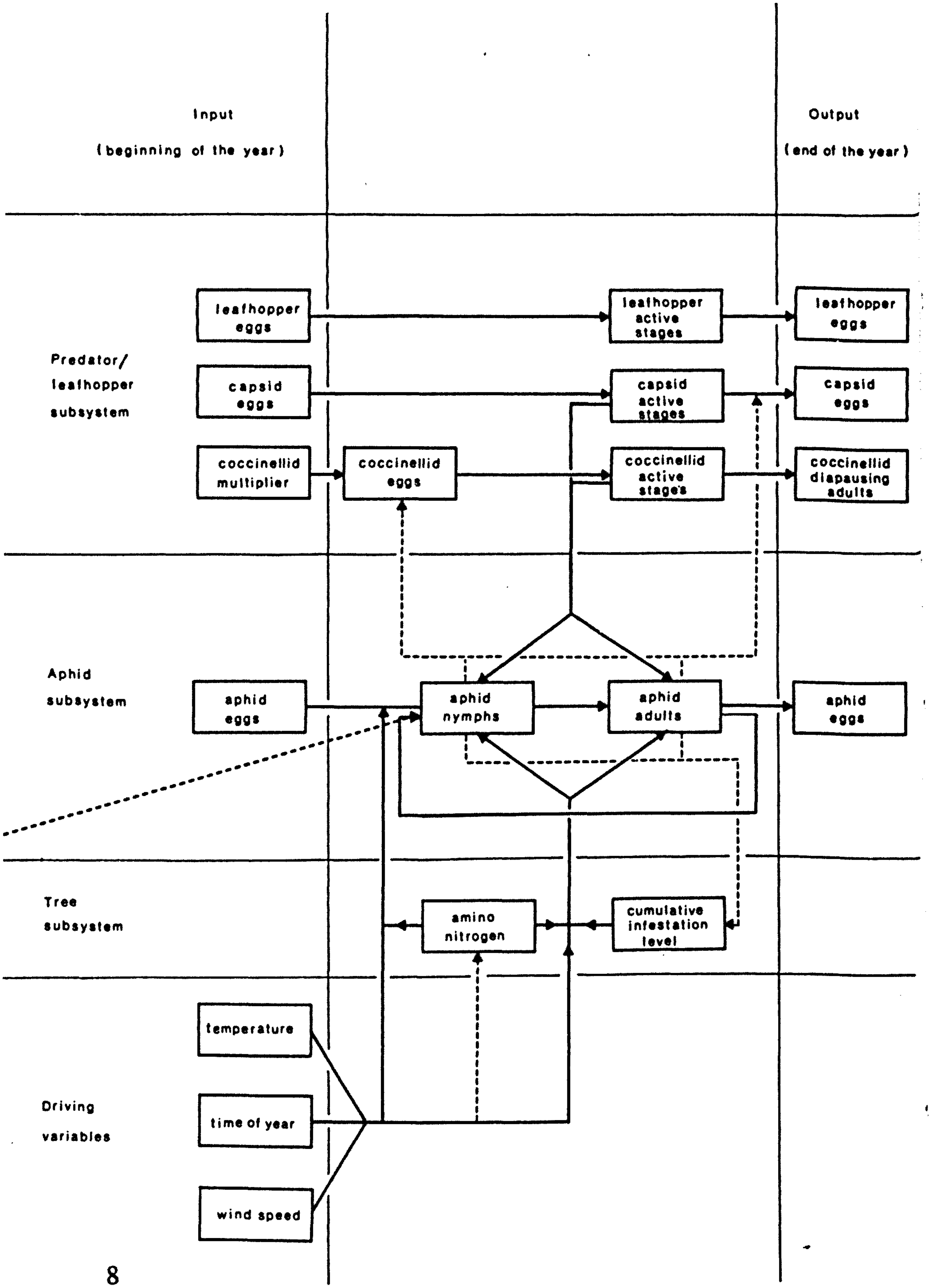
$$\log F_{t+1} = 2.866 - 0.642 \log F_t \qquad r = 0.66,\ \text{d.f. } 36,\ P < 0.01$$

where

$F_{t+1}$ = peak fundatrices/m$^2$, year $t+1$

$F_t$ = peak fundatrices/m$^2$, year $t$

Following Dixon (1971a), this year-to-year relationship can be partitioned into two components, a summer one and a winter one, using peak numbers of oviparae as an index of abundance at the end of a season. The summer component is the relationship between peak numbers of fundatrices at the beginning of a season and peak


Input
(beginning of the year)
Output
(end of the year)
Predator/
leafhopper
subsystem
leafhopper eggs
leafhopper active stages
leafhopper eggs
capsid eggs
capsid active stages
capsid eggs
coccinellid multiplier
coccinellid eggs
coccinellid active stages
coccinellid diapausing adults
Aphid
subsystem
aphid eggs
aphid nymphs
aphid adults
aphid eggs
Tree
subsystem
amino nitrogen
cumulative infestation level
Driving
variables
temperature
time of year
wind speed

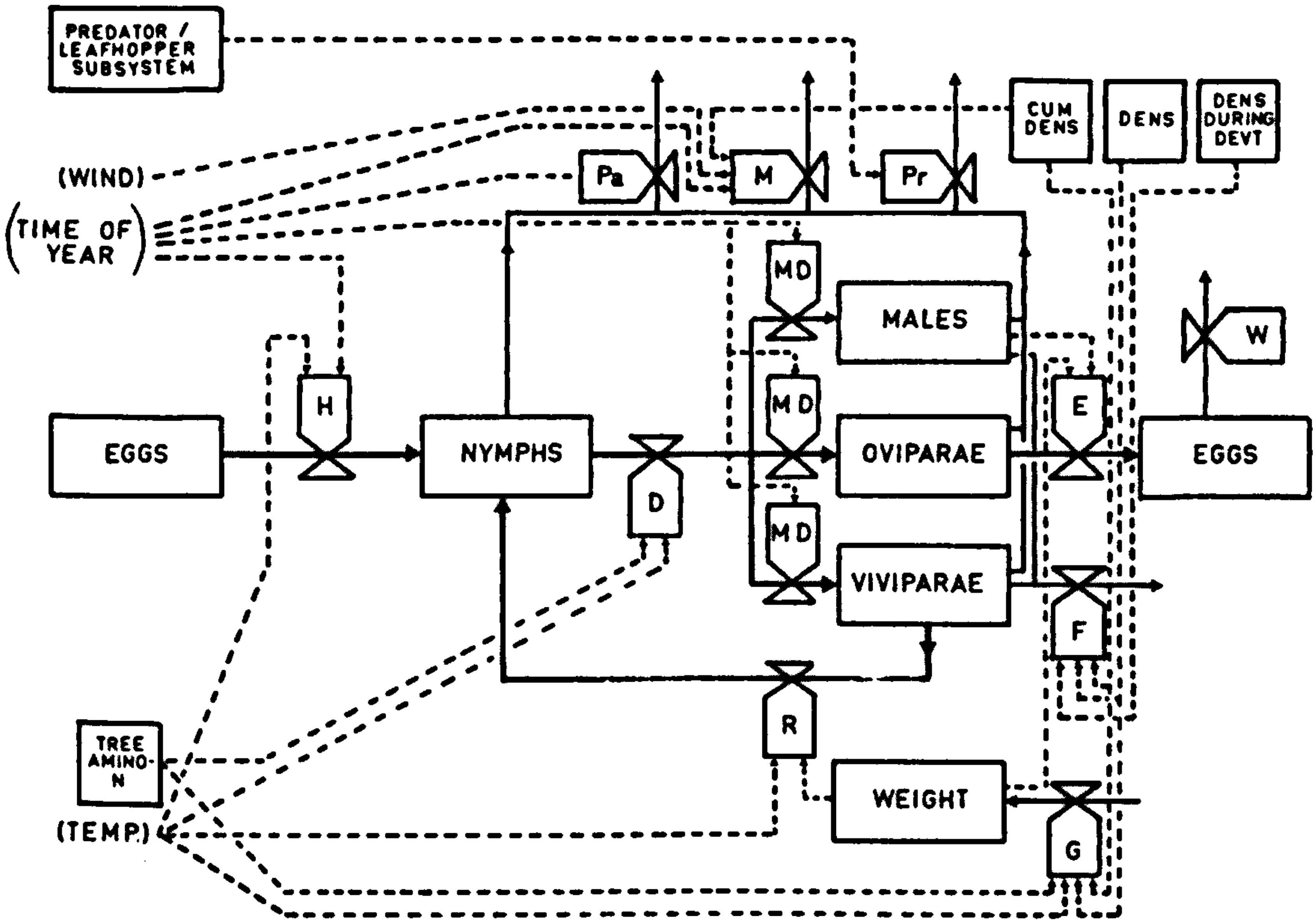


Fig. 3. Detailed relational diagram of the aphid subsystem. Rectangles denote state variables, squares subsidiary variables, brackets driving variables and valve symbols factors affecting rates of flow. → a flow of energy or matter; ⇢ a link denoting an effect of one factor on another; H, egg-hatching rate; D, development rate; MD, morph determination; E, rate of egg-laying; W, winter mortality rate; F, emigration rate of alates; G, growth rate; R, reproductive rate; $P_a$, rate of parasitism; $P_r$, predation rate; M, mortality rate from other causes.

Fig. 2. Time profile of the lime aphid population system summarizing its dynamics. Solid lines indicate flows or interactions and broken ones feedbacks from the aphid to other parts of the system.

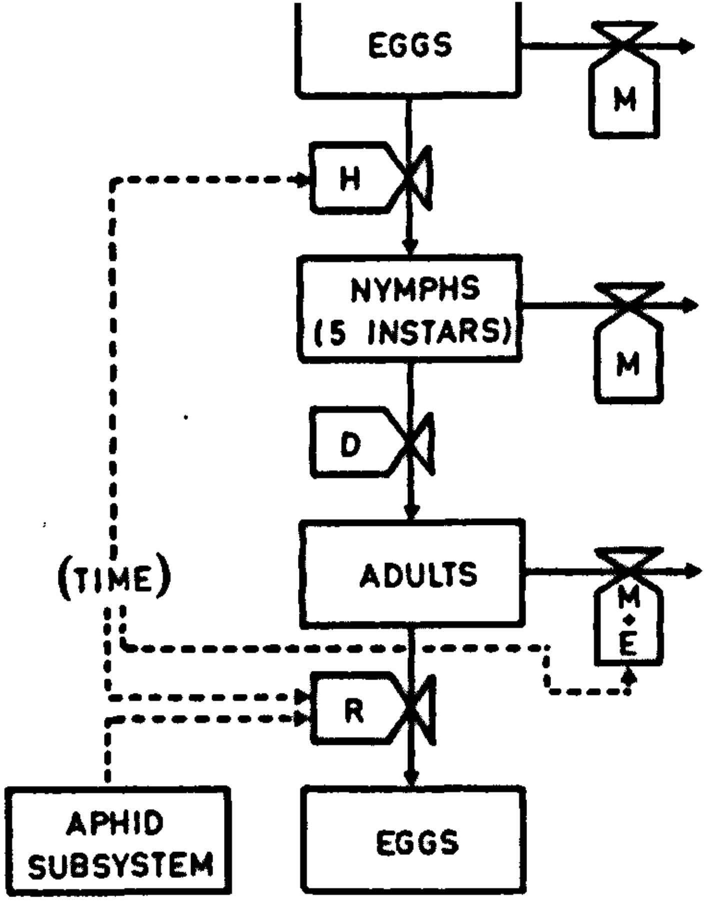


Fig. 4. Relational diagram for the black-kneed capsid population: H, egg-hatching rate; D, development rate; M, mortality rate; E, rate of adult emigration; R, reproductive rate.

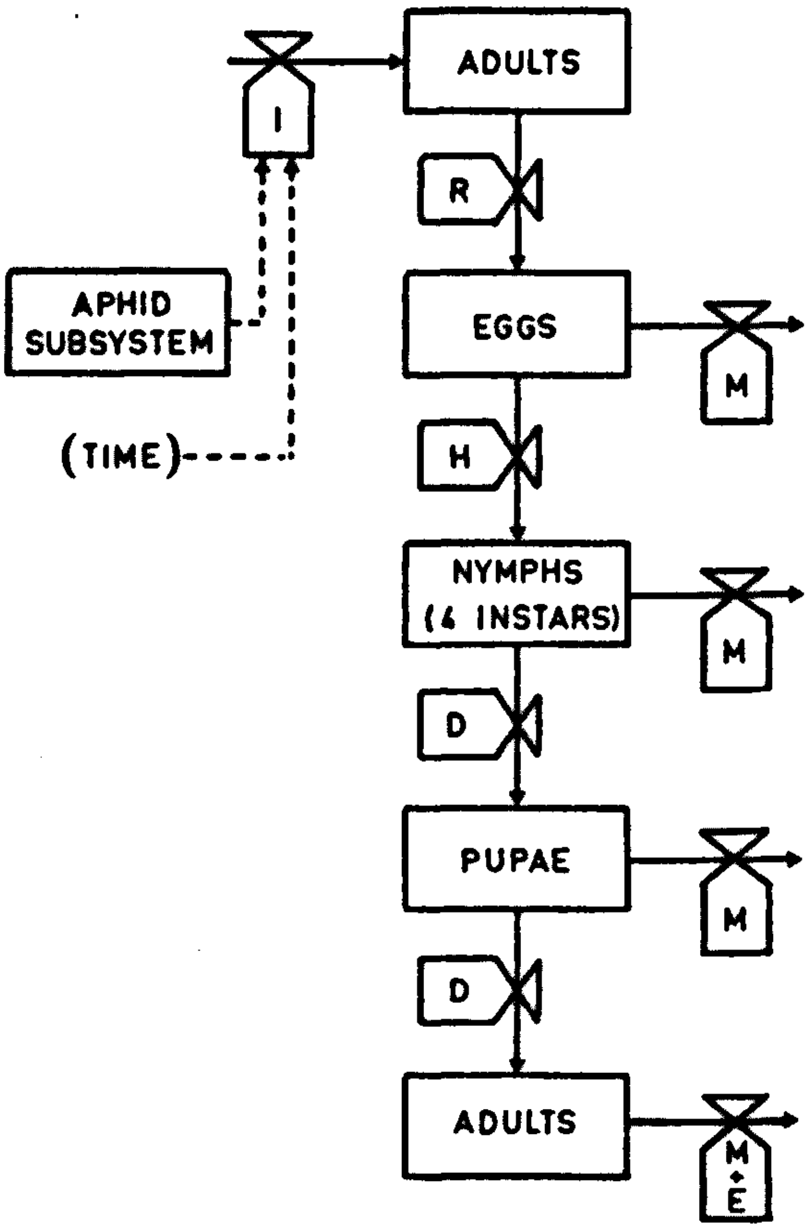


Fig. 5. Relational diagram for the 2-spot coccinellid population: H, egg-hatching rate; D, development rate; M, mortality rate; E, rate of adult emigration; R, reproductive rate; I, rate of adult immigration.

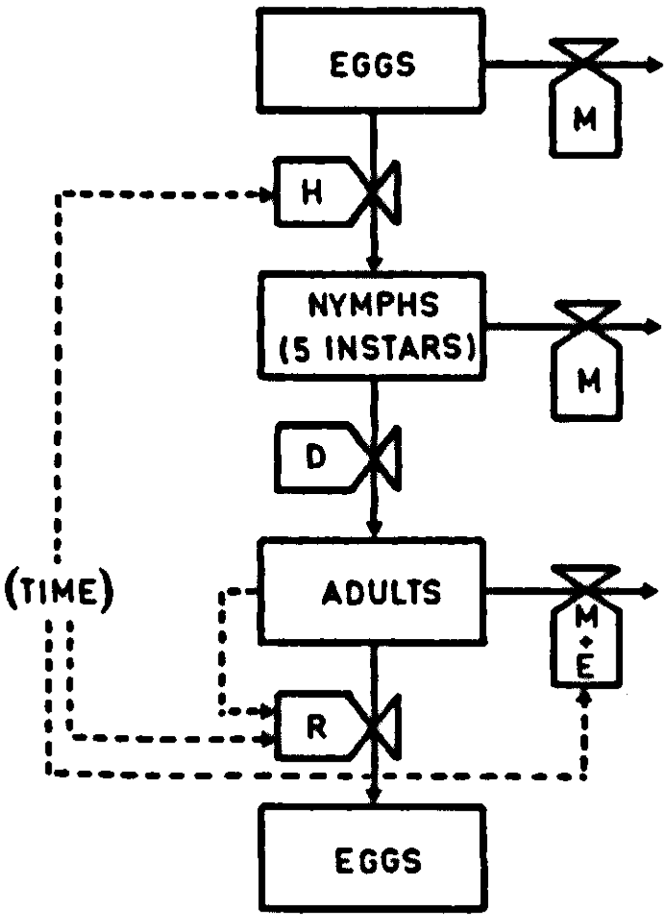


Fig. 6. Relational diagram for the leafhopper population: H, egg-hatching rate; D, development rate; M, mortality rate; E, rate of adult emigration; R, reproductive rate.

numbers of oviparae at the end, and the winter one is the relationship between the peak numbers of oviparae at the end of a season and the peak numbers of fundatrices at the beginning of the next. These relationships do not differ significantly from the ones given by Dixon (1971a) although they include points for another four years. They are shown in Fig. 8 and the equations are:

$$\log O_t = 2.43 - 0.60 \log F_t \qquad r = 0.69, \text{ d.f. } 36, P < 0.01$$

$$\log F_{t+1} = 0.66 + 0.78 \log O_t \qquad r = 0.73, \text{ d.f. } 32, P < 0.01$$

where

$$O_t = \text{peak oviparae/m}^2\text{, year } t$$

Clearly, overcompensation in the year-to-year relationship occurs during summer, the winter component being density-independent with a constant ratio between peak numbers of oviparae and numbers of fundatrices the next spring. However, it is noticeable that in 1971 and on one tree in 1973, when numbers reached very high levels in summer and oviparae were significantly lighter in weight than normal, much of the year-to-year decline is accounted for by the winter component. The peak numbers of oviparae produced are quite high (see Fig. 54b), although these are actually reached earlier in the season than in other years, but the number of eggs, hence the

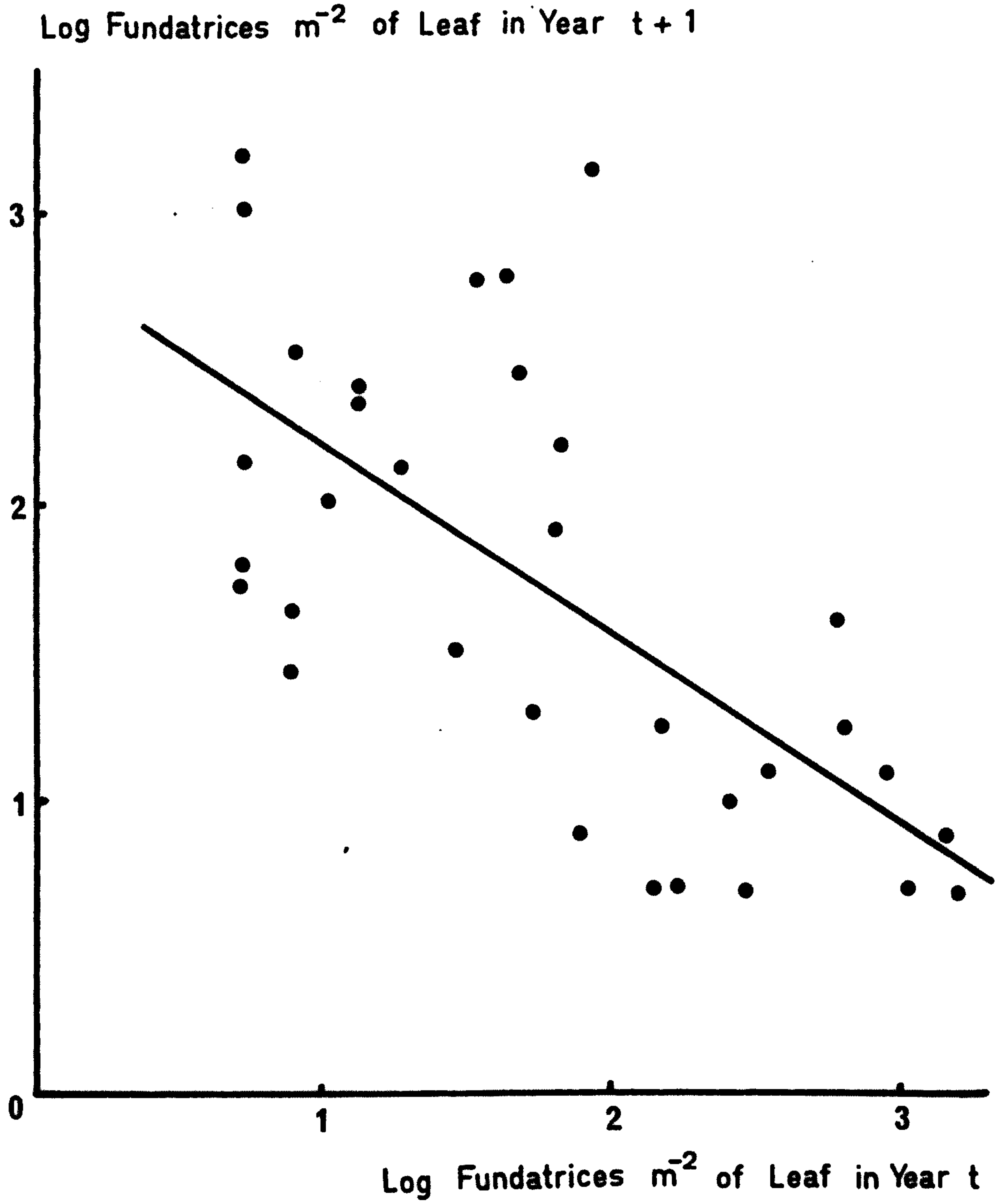


Fig. 7. The observed relationship between peak densities of fundatrices in successive years. Each point represents 1 tree in 1 year.

number of fundatrices, produced by each ovipara is low. There is also a suggestion of non-linearity in the summer component (Barlow, 1977) such that changes in initial fundatrix numbers over the range 0–2 have little effect on the numbers of oviparae at the end of the year. The scatter in the relationships indicates, too, that disturbing factors are important in determining absolute abundance in any one year.

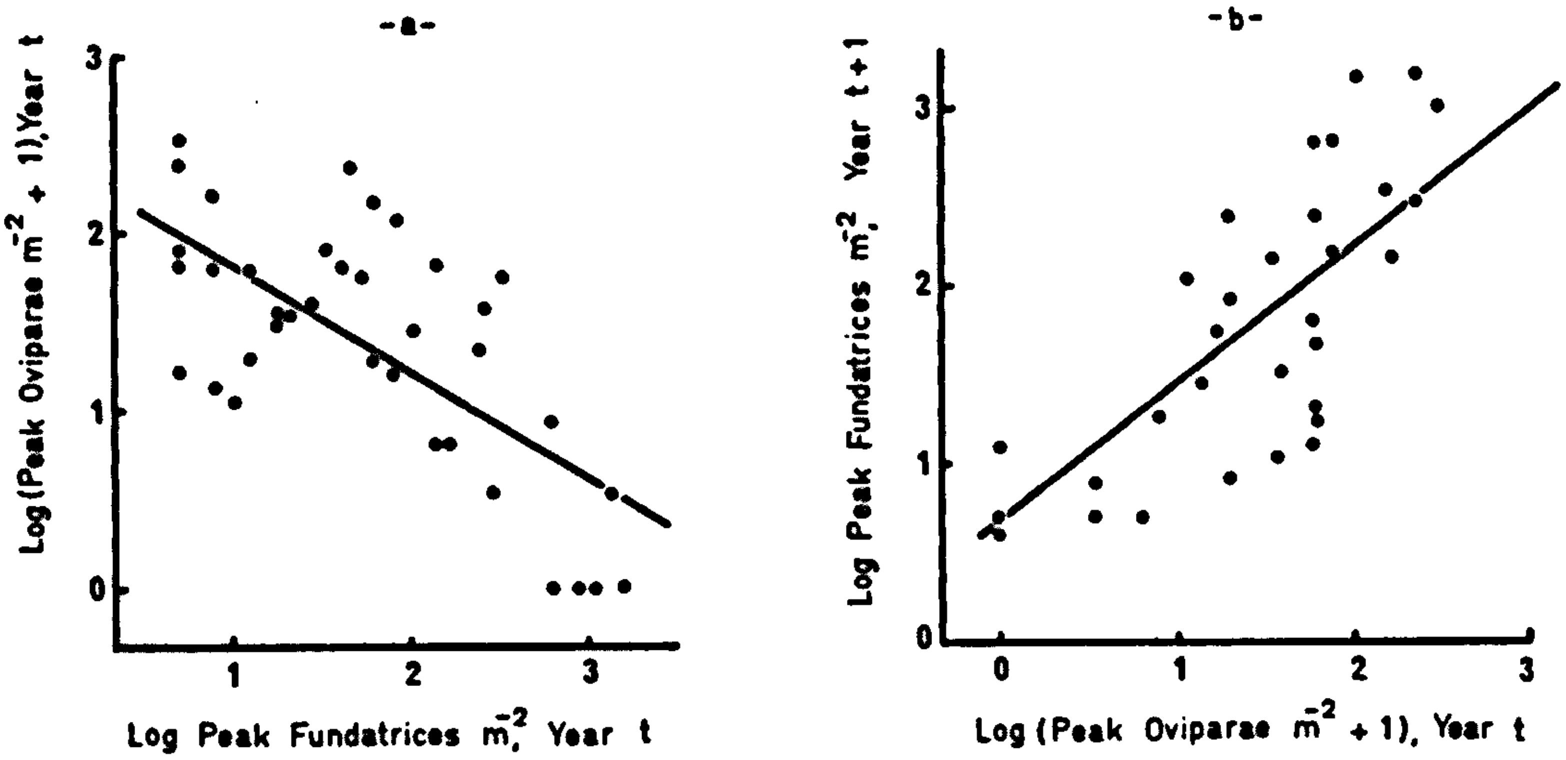


Fig. 8. a) The observed relationship between peak density of fundatrices and that of oviparae in the same year. Each point represents 1 tree in 1 year. b) The observed relationship between peak density of oviparae in one year and peak density of fundatrices in the next.

From the results of Brown (1975), the year-to-year relationship and the summer component can be derived for populations in an insectary, where predators, parasites and the effects of weather are excluded. In this case, since the populations were only monitored over the course of one season, the number of fundatrices in the next year was estimated as the number of eggs on the tree at the end of the season multiplied by an overwintering mortality similar to that occurring in the field (see Section 3.5.10). The relationships in the field and the insectary are compared in Figs 9a and b. The ratio of increase during a season and from one year to the next is more than ten times greater in the insectary than in the field. However, overcompensation still occurs in the insectary giving a theoretical equilibrium population of fundatrices which is also about ten times greater than in the field (Fig. 9a). Although the degree of overcompensation between years is similar, during summer it is less in the insectary than in the field. This reduced overcompensation during summer, together with the generally greater numbers of oviparae in the insectary may be related to the absence of factors such as wind and predation. The reason that the overcompensation is restored over the whole year may be because the oviparae are lighter in weight at high initial fundatrix densities in the insectary than in the field, since the populations reach higher levels during the summer; such light oviparae, as already mentioned, lay relatively few eggs.

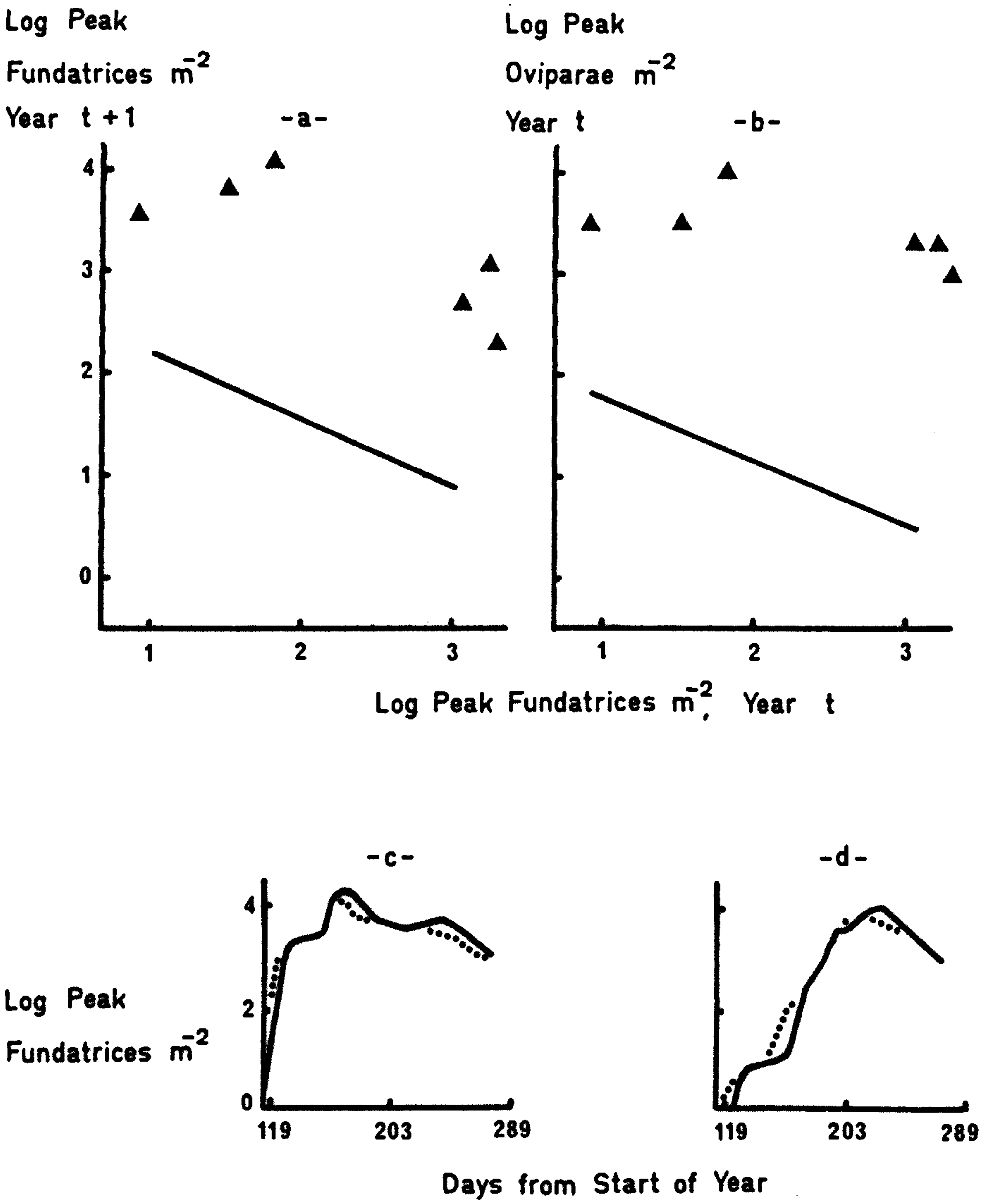


Fig. 9. Observed behaviour of populations in an insectary: a) the relationship between peak fundatrix density and the peak fundatrix density at the beginning of the next year, based on the number of eggs laid at the end of the current year and assuming the same overwintering egg mortality as in the field (▲ points from insectary, — relationship in the field); b) the relationship between peak fundatrix density and peak ovipara density in the same year (legend as in a); c) changes in total population density throughout the season for an initially high-density population (2000/m$^2$) and d) for an initially low-density one (10/m$^2$). Data are from Brown, 1975.

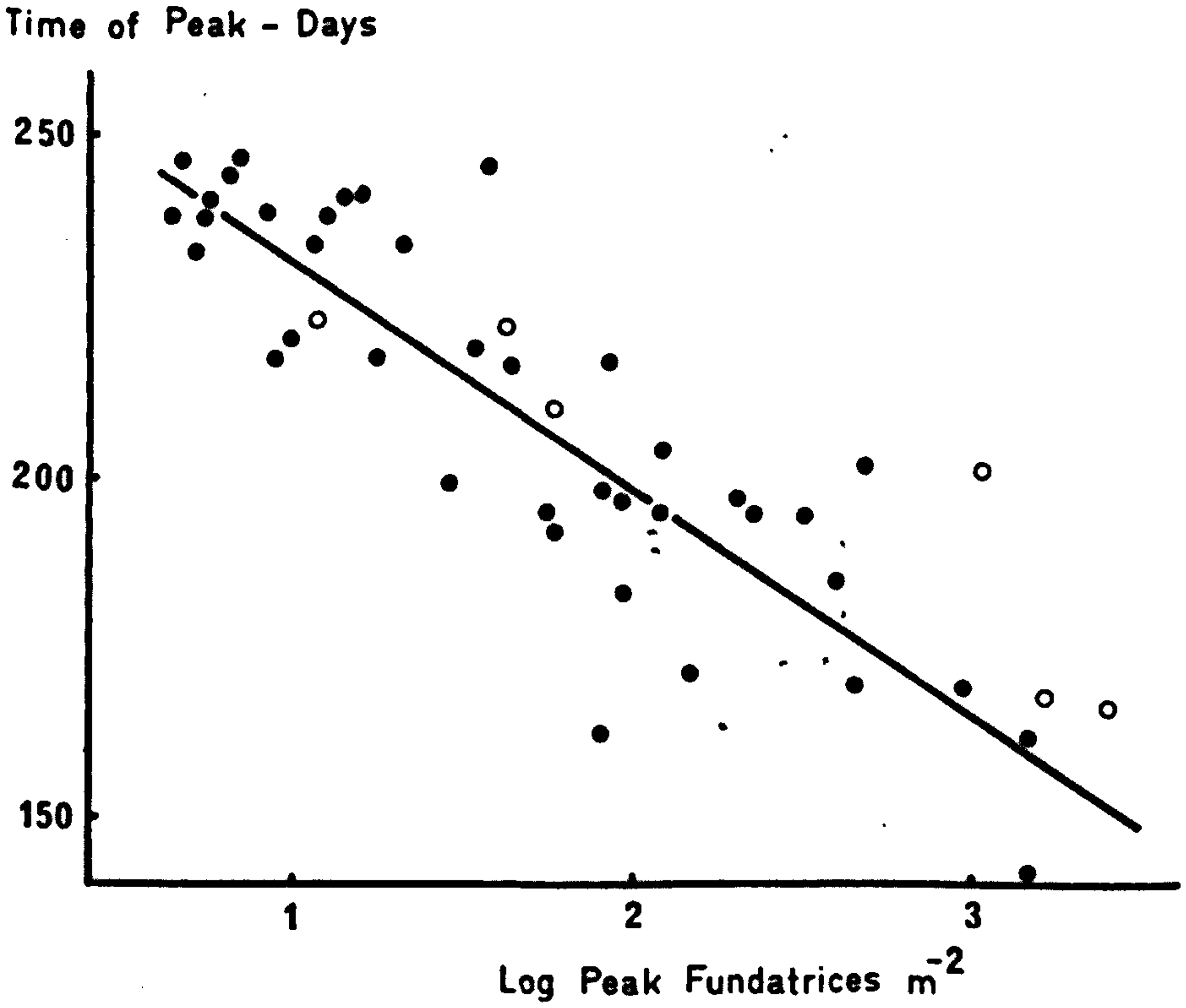


Fig. 10. The observed relationship between peak numbers of fundatrices and the time of the overall peak each year. ● point from the field (1 tree in 1 year); ○ point from Brown's (1975) insectary populations.

Turning now to changes in numbers within a year, lime aphid populations typically have a single peak reached early in the season if fundatrix numbers are high, late if they are low (Fig. 10). The relationship between the time of the peak and the number of fundatrices is

$$T = 266 - 33F_t$$

where

$T$ = time of peak (days from 1st January)

The trends in total numbers throughout each year are shown in Fig. 11, from 1965 to 1972 on trees 1 and 2. Trees 1, 2, 4 and 5 were on one site, tree 3 on another and tree 6 on a third. The populations behaved in a broadly similar way on all trees in any one year but only trees 1, 2 and 3 were sampled continuously for eight years or more. So it was decided to focus attention on the average populations of trees 1 and 2 which formed part of one row, referring to other specific trees and years separately when necessary. Fig. 12 shows the populations in more detail in 1969 and 1970, including

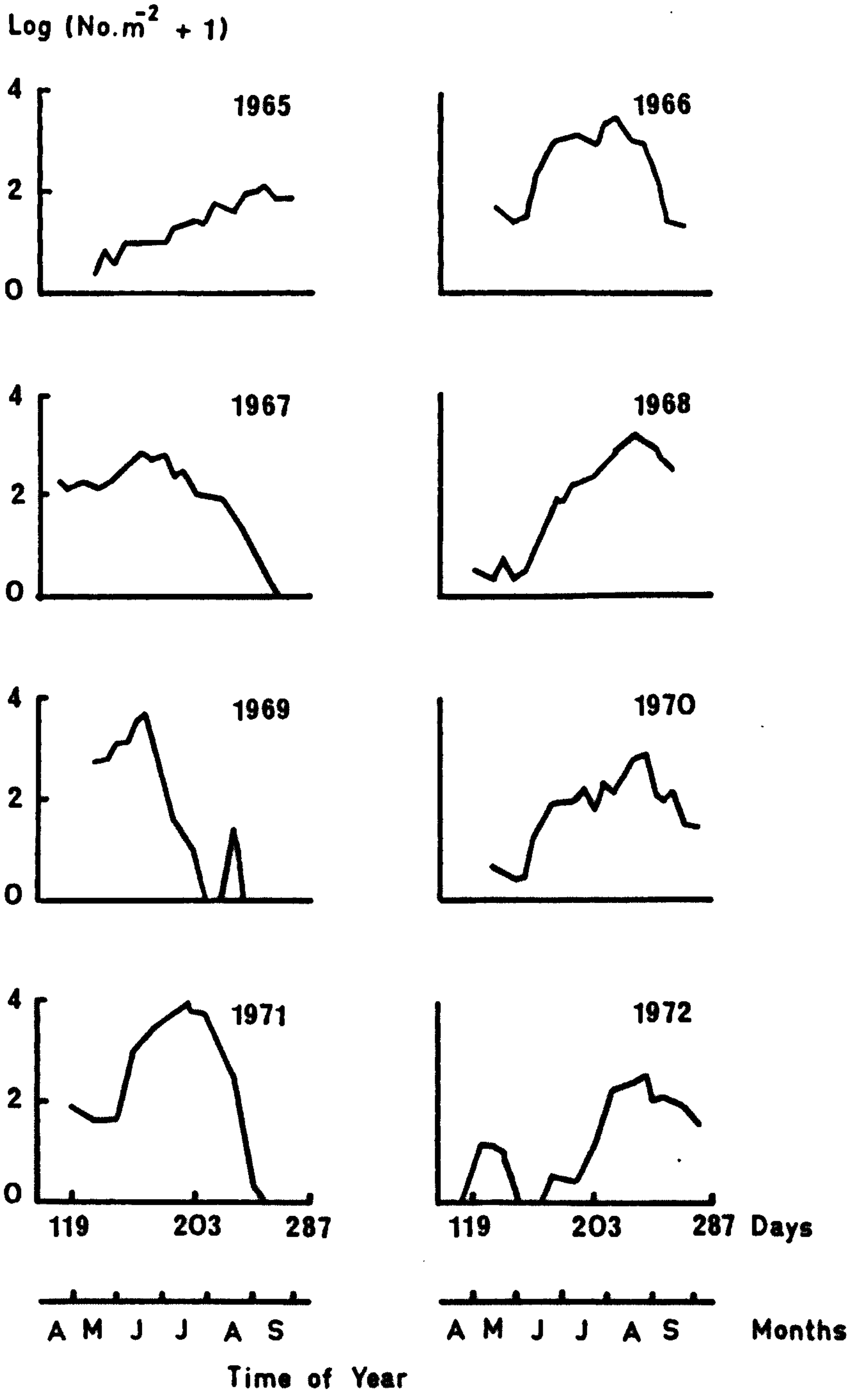


Fig. 11. Observed trends in total population numbers, averaged over tre
1 and 2, during each year from 1965 to 1972.

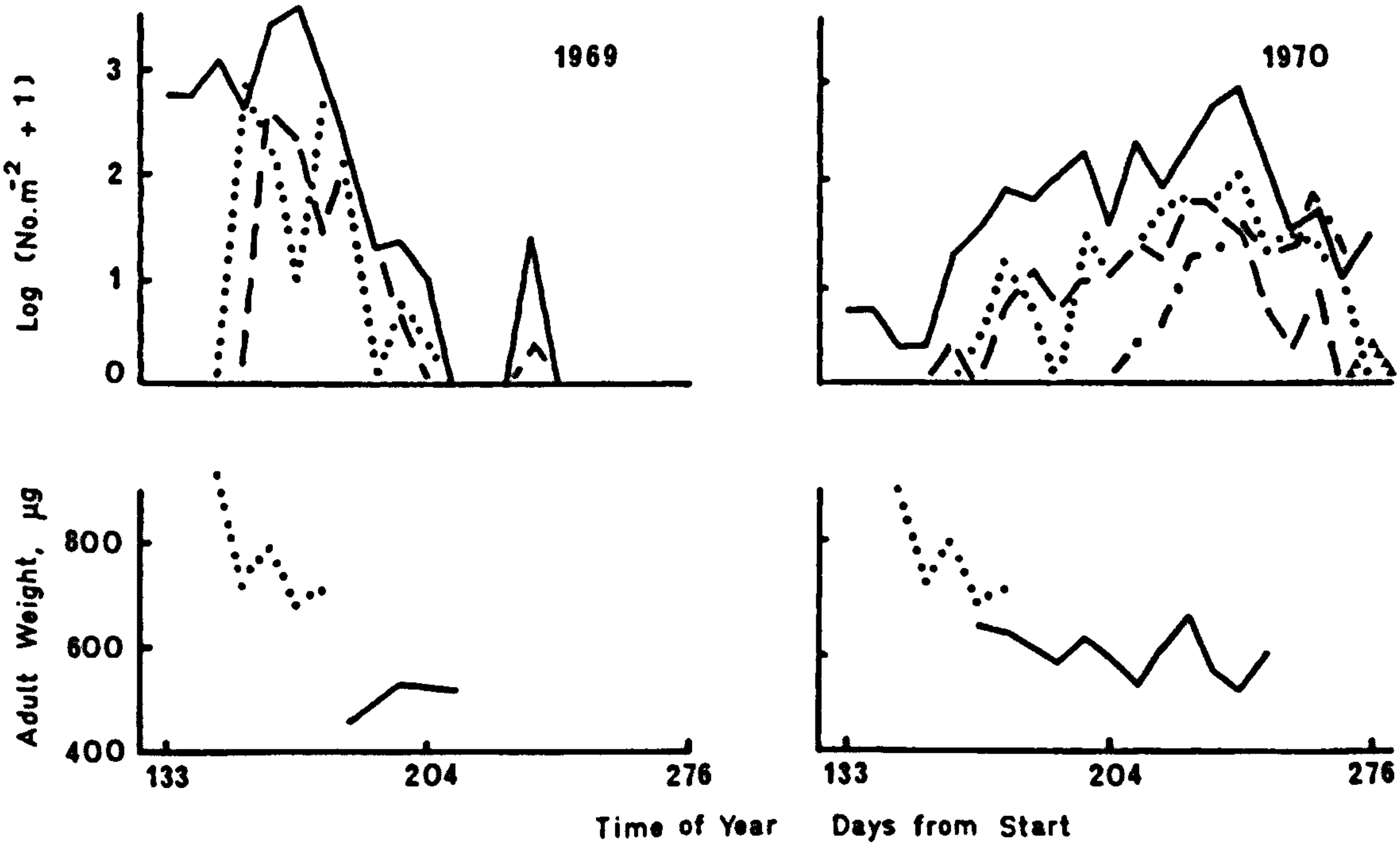


Fig. 12. Detailed population trends and adult weights on trees 1 and 2 in 1969 and 1970. —— young nymphs (instars 1–3); ····· 4th instar nymphs; ––– viviparae; –·–·– oviparae. —— adult weights; · · · · fundatrix weights in 1971.

the various instars and the average weights of the adults. Finally, Figs 9c and d show total population trends during the season in two insectary populations with initial numbers corresponding to the extremes found in the field.

The main results against which the model's predictions are to be tested, therefore, are the general inverse relationship between numbers in successive years (Fig. 7) and the population trends throughout each year on trees 1 and 2 from 1965 to 1972 (Fig. 11). The model will also be used to try to account for the somewhat different pattern of behaviour exhibited by populations in the laboratory (Fig. 9).

# 3 The model

## 3.1 Choice of the model

The appropriate model for this study is one which incorporates a maximum of biological realism while requiring a minimum of computing time to run, in order that a wide range of experiments and sensitivity analyses may be carried out; there is little point in having a model which is so detailed that it is too cumbersome to run. The choices then are between stochastic and deterministic, and discrete or continuous.

Stochastic models were rejected for two reasons; analytical ones would probably require over-simplification of the biology, and simulation ones would require excessive computing time. As Fransz (1974) pointed out in a stochastic model of predation, where non-linear relationships are involved the mean output given varying parameter values will not be identical to the output given the means of the parameter values. It is not possible without comparing stochastic and deterministic models to assess the significance of the difference between them. Probably the difference would not be large enough to warrant the additional information required about the variance of each parameter, the additional complexity of a stochastic model and the additional computing time necessary to run it.

The possibility of a continuous or discrete deterministic model was considered next. If the system can be readily represented as a set of differential equations, then a continuous simulation model is appropriate and there are a number of simulation languages such as CSMP or DYNAMO, which consist of standard sets of functions for describing time-dependent behaviour and will integrate equations over time. These high-level languages are easy to understand, so rendering models readily comprehensible to those not involved in their construction. The approach is described in detail by Goudriaan & de Wit (1974) and in other volumes of this series (van den Bos & Rabbinge, 1976; Fransz, 1974). However, in this case it was decided to use a discrete model written in FORTRAN with a fairly long step-length of operation, in order to retain maximum flexibility and to economise on computing time. The model is thus of the age-class or box-car type with no dispersion (Goudriaan & de Wit, 1974), meaning that the contents of each age-class are shifted bodily to the next at each step corresponding to the duration of the age class. This contrasts with the box-car model with dispersion, in which there is continuous flow of the population from one age class to the next; this generates a Poisson distribution of residence times over a series of age-classes representing an instar if the number of classes is small and a Gaussian distribution if it is large (Goudriaan & de Wit, 1974). The step-length of operation of a model should normally be of the order of 1/10 of the system's time constant, the smallest ratio of the value of a state variable to its rate of change (Goudriaan & de Wit 1974). This is so for models embodying the state variable approach, in which all rates are independent of each other and are calculated according to the current state of the system then used to update the whole system by addition, in a discrete model like the Leslie matrix (Leslie, 1945), or by parallel integration in a continuous model. Where numerical integration is carried out by the Euler or rectangular method, it gives the same result as a matrix operating over the small time interval of integration. The present model, however, is of the type described by Conway and Murdie (1972) in which population processes operate not in parallel but sequentially within each 'iteration'. In this way a correction can be introduced which compensates for the long step-length and large relative changes in numbers which may therefore occur within an interval; in particular, emigration of adults during one iteration may involve up to 50% of those present. The correction involves calculating mortality and emigration first, then basing reproduction on the number of reproductive animals remaining at the end of the interval plus half those dying during the interval. When reproduction is calculated first, before applying mortality, the predicted number of eggs at the end of a year is up to a hundred per cent greater than when mortality precedes reproduction and there is no correction. The correction yielded an intermediate result and the discrepancy would be reduced if the step-length of operation were decreased.

Although the use of a physiological time scale enables a temperature-dependent model to be simplified somewhat it was not employed here for three reasons. Some rates are related non-linearly to temperature so day-degree totals above a threshold are not applicable, different processes are related to temperature in different ways, and some are related to factors other than temperature, such as plant quality.

## 3.2 Structure of the model

The model is deterministic and discrete, written in FORTRAN and operating over a step-length of 1 day. It predicts changes in numbers and growth in size of aphids throughout the season and from one year to the next, while separate submodels described below also mimic changes in numbers of predators and their alternative prey.

Fig. 13 shows the state variables in the model. Numbers of each animal are stored in vectors or arrays by developmental stages (egg, nymphal and larval instars, pupa and adults of different types), together with average weights of the stages in the case of aphids and leafhoppers. In addition, the aphid population is stored in a more detailed form with numbers partitioned among the three morphs and into 50 day age-classes of nymphs and 30 of adults. Associated with each of these age-classes is a mean population density experienced during nymphal development, an average weight and an index of development governing moulting in nymphs and the onset and decline of reproduction in the case of adults. The remaining state variables relate to the tree, being the amino-nitrogen level in the phloem and the cumulative aphid density during the season. Subsidiary variables in the model include the daily mortality experienced by each adult age-class, needed to correct for the model's long step-length, the time of bud-burst, the cumulative proportion of aphid eggs which have hatched, and the accumulated day-degree total above 5°C from 1st March which governs both bud-burst and egg-hatching.

The operation of the model can be described as a series of steps, shown in the flow diagram (Fig. 14). A listing of the actual program is given in Appendix B, and the steps are as follows:

1. Input of parameter values. A set of constants are assigned values by DATA statements at the beginning of each run. These include:

- Cumulative proportion of development achieved at the end of each aphid instar.
- Number of days in each month of the year.
- Initial weights of each aphid instar and weights of each leafhopper instar.
- Maximum weight of prey eaten per day by each predator instar.
- Predator/prey attack coefficients.
- Weekly transition probabilities for leafhopper and predator submodels.

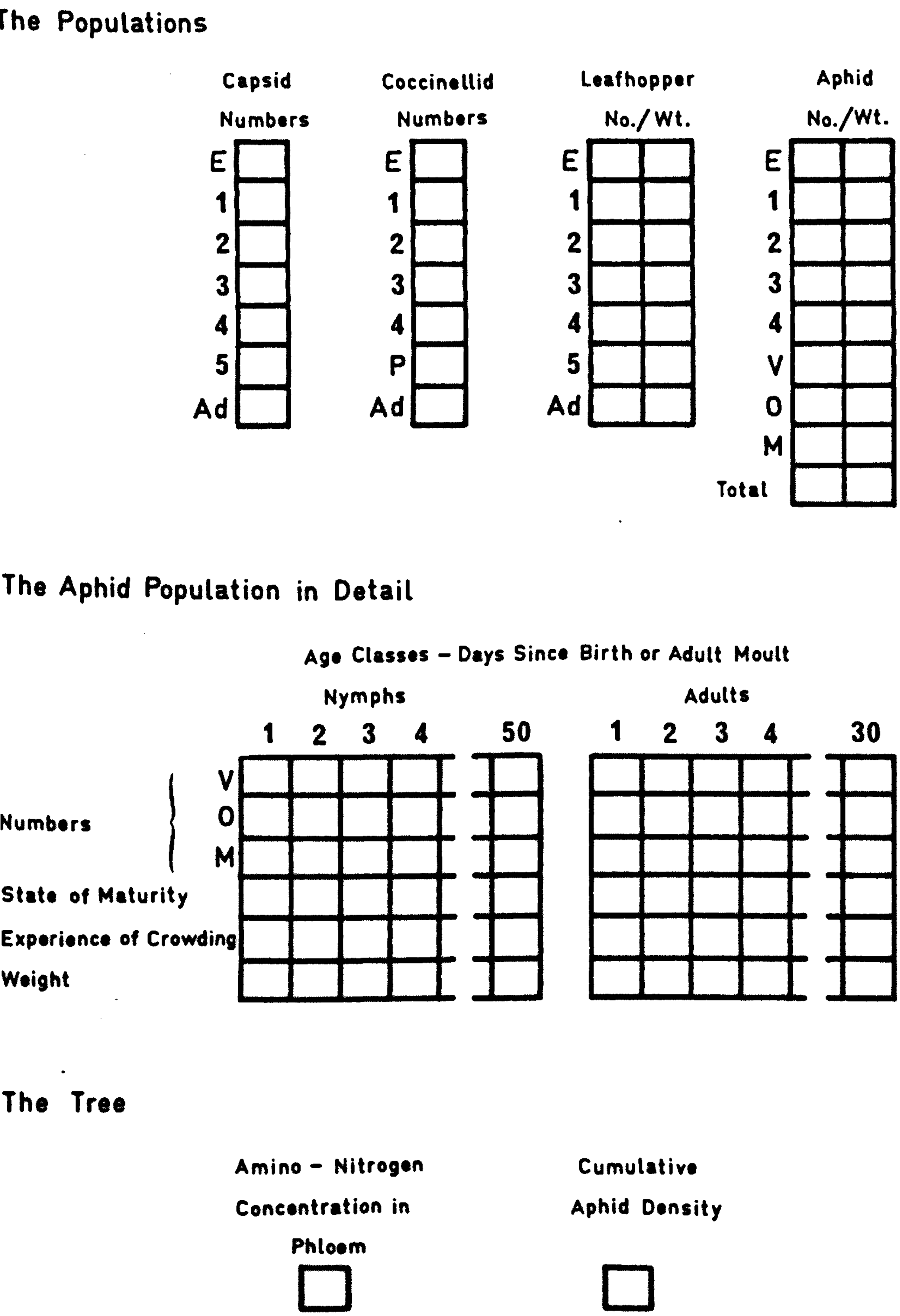


Fig. 13. State variables in the lime aphid model. Figures refer to nymphal instars, E, P, Ad, V, O, M to eggs, pupae, adults, viviparae, oviparae and males, respectively.

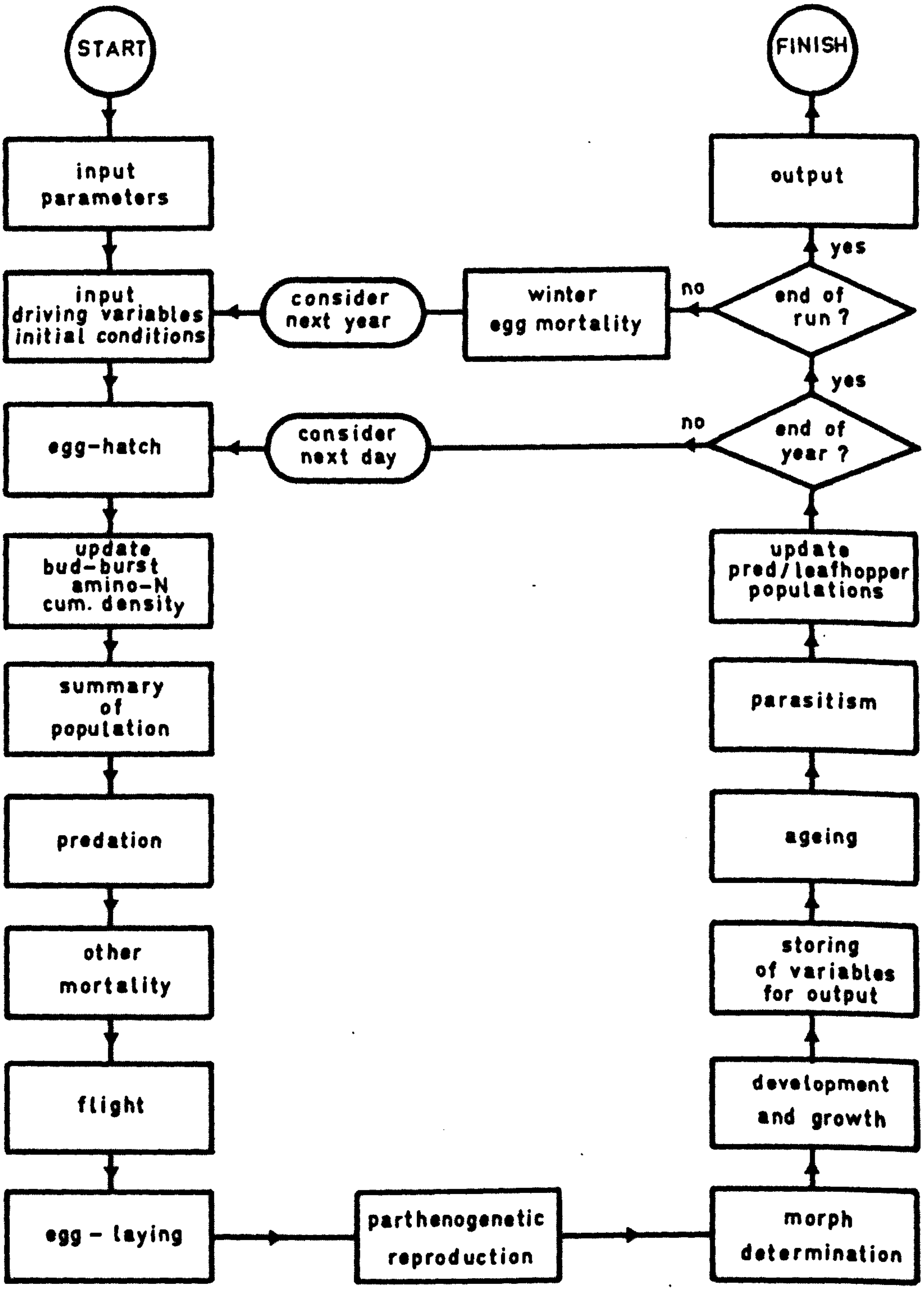


Fig. 14. Flow diagram of the lime aphid model.

— Weekly survival probabilities for leafhopper and predator submodels.

— Arbitrary function values defining relationships between temperature and development rates
  day-degrees above 5°C and cumulative proportions of eggs hatching
  time of year and soluble amino-nitrogen concentrations in the phloem
  time of year and long-term average maximum and minimum temperatures
  time of year and proportion of males among newborn nymphs
  time of year and proportion of oviparae among newborn female nymphs

— The maximum longevity for adults.

— Numbers of aphid, leafhopper and black-kneed capsid eggs at the beginning of each year, and the 'coccinellid multiplier' for each year (see Section 3.3)

— The year (1 to 8 for 1965 to 1972) in which the model starts.

— The year in which the model stops.

2. The first or next year is considered.

3. Initial conditions are established, state variables being zeroed and new initial numbers of eggs assigned. These values are simply the ones set by the previous year's iteration if the model is run continuously from one year to another; otherwise they are re-set according to the year from the DATA statement. The overall day counter is set to 59, giving the first daily iteration of each year on 1st March, and the weekly day counter, which causes the predator/leafhopper submodel to operate with a step-length of 1 week, is zeroed. Daily temperatures for the whole season are from a data file or, if mean conditions are required, they are calculated from the monthly long-term averages (subroutine TEMPS). Daily wind speeds for the year are read in from another data file or set to the long-term average value over the whole season (subroutine WINDS). The dates on which output is required are then assigned (subroutine OBS).

4. Although not shown in the flow diagram, there is provision at this point for running the model repeatedly with the initial conditions and driving variables of any one year, or those representing average values, by returning control to this step from Step 23 as many times as desired.

5. The next day is considered.

6. Egg-hatching (subroutine HATCH). The numbers of eggs hatch-

ing are calculated and the day-degree total above 5°C and proportion of eggs already hatched updated.

7. Updating of variables associated with the tree (subroutine TREE). If the buds have not already broken the expected time of bud-burst is updated, given the day-degree total above 5°C. The daily amino-nitrogen concentration in the phloem is updated, given the time and the time of bud burst, and the accumulated aphid density on the tree updated given the current density.

8. Although not shown on the flow diagram, if no eggs have hatched most of the following processes are by-passed and control passed to Step 16.

9. Summarizing of the aphid population (subroutine SUMP). The vector summarizing the composition of the population by instars, adult morphs and their weights is updated, based on the current numbers in the detailed age-class vector. Weights of males are assumed to be 0.7 times those of females.

10. Predation (subroutine PRED). Given the numbers and weights of predators and prey of various stages and the constants associated with their interactions, this subroutine models the functional response and updates the numbers of leafhoppers and aphids. It also increments a weekly total of number of aphids killed by predation which is output at the end of the run.

11. Mortality, other than predation, parasitism and winter mortality of eggs (subroutine MORTY). This subroutine updates numbers of aphids according to the background daily mortality rate, the wind speed, the time of year relative to the time of leaf-fall and the cumulative aphid density.

12. Flight (subroutine FLIGHT). The number of males and viviparae emigrating from each adult age-class is calculated given the population density, the mean density experienced during nymphal development, the cumulative density and the background emigration rate; numbers are updated accordingly.

13. Egg-laying (subroutine EPROD). The number of eggs laid is added to the total already laid, given the numbers and weights of newly-moulted oviparae; all eggs are assumed to be laid immediately following the moult.

14. Parthenogenetic reproduction and morph determination (subroutine REPROD). Recruitment is calculated and the population vectors updated, given the numbers, weights and developmental stages of adult viviparae in each age-class, and the temperature. New-born nymphs are partitioned among the three morphs according to the time of year and assigned an initial weight.

15. Growth and development (subroutine GROWTH). The proportion of development achieved by each nymphal age-class is updated, given the temperature and the amino-nitrogen concentration in the phloem. Weights of each age-class are also updated given the daily development increment, the population density, the cumulative density, the temperature and the amino-nitrogen concentration.
16. Storing of variables for output (subroutine STORE). If the current day is one on which output is required, the following values are stored: numbers of aphids in different stages, instars 1–3 being grouped together as in the sampling records; average weight of adult aphids; total fresh-weight of the population; and numbers of leafhoppers and predators in the different stages. Otherwise, this step is by-passed.
17. Ageing of the aphid population (subroutine AGE). The numbers in each age-class, and the associated weights, states of development and experiences of crowding, are moved into the next. The contents of any nymphal class for which the development index is greater than or equal to 1 are moved into the first adult class, and no adults are permitted to remain beyond the age-class representing the maximum adult longevity. The daily mortalities suffered by each adult age-class are set to zero.
18. Parasitism (subroutine PARA). Parasitism is assumed to act at the adult moult and the first adult age-class is reduced by the calculated proportion parasitized, given the time of year.
19. Updating of the predator and leafhopper populations (subroutine POP). If the weekly day counter has not reached 7 this subroutine is by-passed. Otherwise, predator and leafhopper populations are updated using modified Leslie matrices operating over the weekly interval. These embody the processes of development, mortality and reproduction which in some cases depend on the time of year or the aphid density. The weekly day-counter is re-set to zero.
20. If the time of year has not reached Day 304 (31 October) control is returned to Step 5.
21. Winter mortality of eggs (subroutine WMORT). The number of eggs laid is reduced by a constant proportion.
22. Output (subroutine OUTPUT). Numbers of leafhoppers, black-kneed capsids, 2-spot coccinellids and aphids of each stage are printed for each date of the year specified in Step 3. The total aphid population on these dates, average adult weight total fresh weight of aphids and the total number eaten by predators are also printed. Finally the logarithms of the aphid egg numbers at the beginning

and end of the year are printed, summarizing the behaviour of the population throughout the year.

23. If additional runs are required with the same initial conditions and driving variables, control is returned to Step 4. If the next year and a new set of these is required control passes to Step 3, otherwise the model stops.

Because of the relatively long step-length of the model, four corrections have been applied, the first of which has already been mentioned, and these are as follows.

1. Mortality and emigration are calculated each day before reproduction; then recruitment is based on the numbers remaining plus half those dying or emigrating.
2. Viviparous adults experience a pre-reproductive delay which is allowed to involve fractions of a day in the model (see p. 59).
3. For nymphs moulting on any day growth factors for the age-class are based not on the whole day but on the calculated fraction of the day for which the cohort remains in the nymphal stage.
4. Predation includes an exploitation component since under certain circumstances a high proportion of prey may be eaten in one day (see p. 3).

This description of the model, taken with the flow diagram in Fig. 14 and the relational diagram in Fig. 3, provides a summary of the population processes included and the factors which affect them. The process submodels will now be considered in more detail.

### 3.3 Initial conditions and driving variables

The initial numbers of aphid eggs, leafhopper eggs and black-kneed capsid eggs, and the 'coccinellid multiplier' for each year from 1965 to 1972 are given in Table 1. The coccinellid multiplier represents the relative abundance of the 2-spot coccinellid in any one year and is explained on p. 97.

The long-term average maximum and minimum daily temperatures are shown in Fig. 15 and the mean weekly temperatures during each season from 1965 to 1972 are given in Fig. 16. These are shade temperatures recorded at Abbotsinch airport five miles from the study area, and Llewellyn (1970) showed that they are approximately 1.5°C lower than the integrated temperatures beneath lime leaves, referred to in the model as corrected temperatures.

Table 1. Initial densities of aphid, leafhopper and black-kneed capsid eggs (number/100 cm$^2$) and the coccinellid multiplier (see text) in each year. *, average values.

| year | aphid eggs | leafhopper eggs | capsid eggs | coccinellid multiplier |
|---|---|---|---|---|
| 1965 | 0.05 | 1.0* | 0.030 | 1 |
| 1966 | 0.45 | 1.0* | 0.063 | 1 |
| 1967 | 1.83 | 1.0* | 0.067 | 1 |
| 1968 | 0.03 | 1.0* | 0.071 | 1 |
| 1969 | 14.00 | 2.1 | 0.118 | 1 |
| 1970 | 0.07 | 0.5 | 0 | 1 |
| 1971 | 1.40 | 0.3 | 0 | 0.3 |
| 1972 | 0.17 | 1.0* | 0 | 1 |

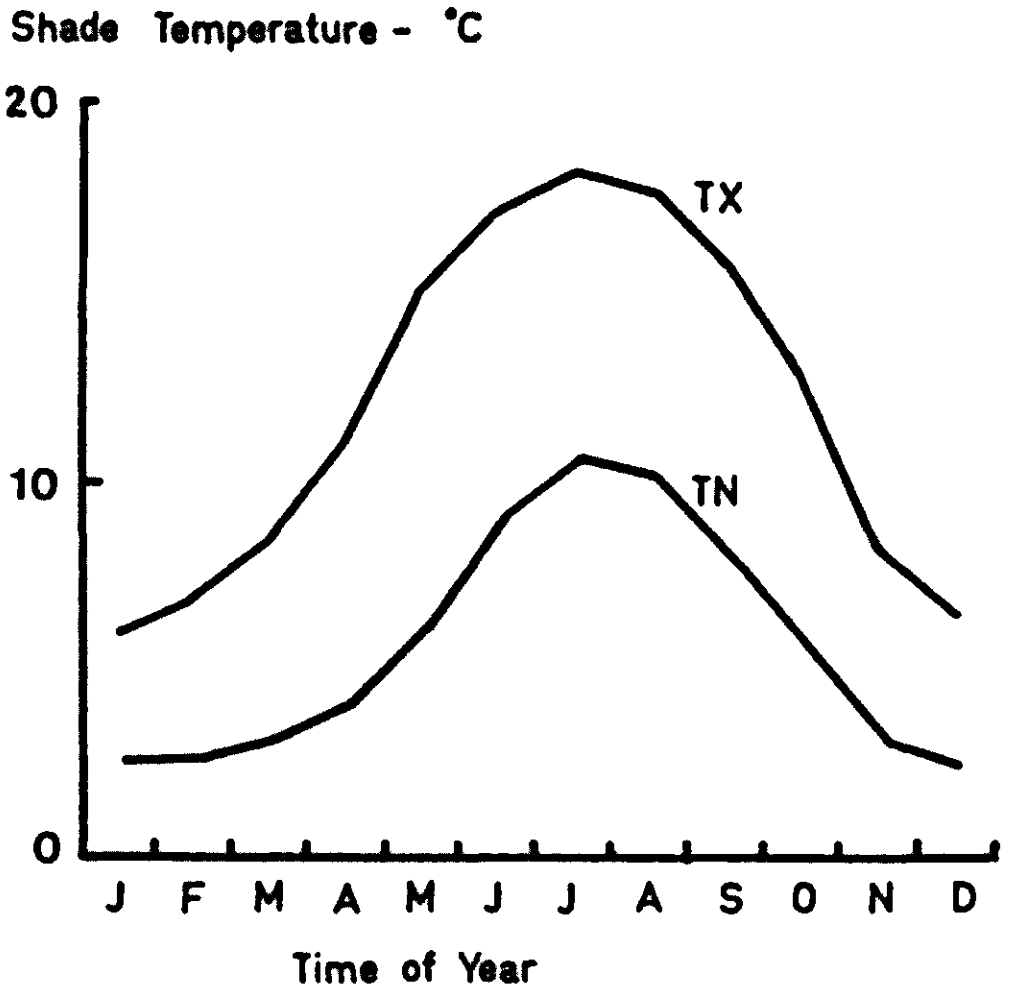


Fig. 15. Long-term average maximum (TX) and minimum (TN) daily shade temperatures throughout the year at Abbotswich airport, Glasgow.

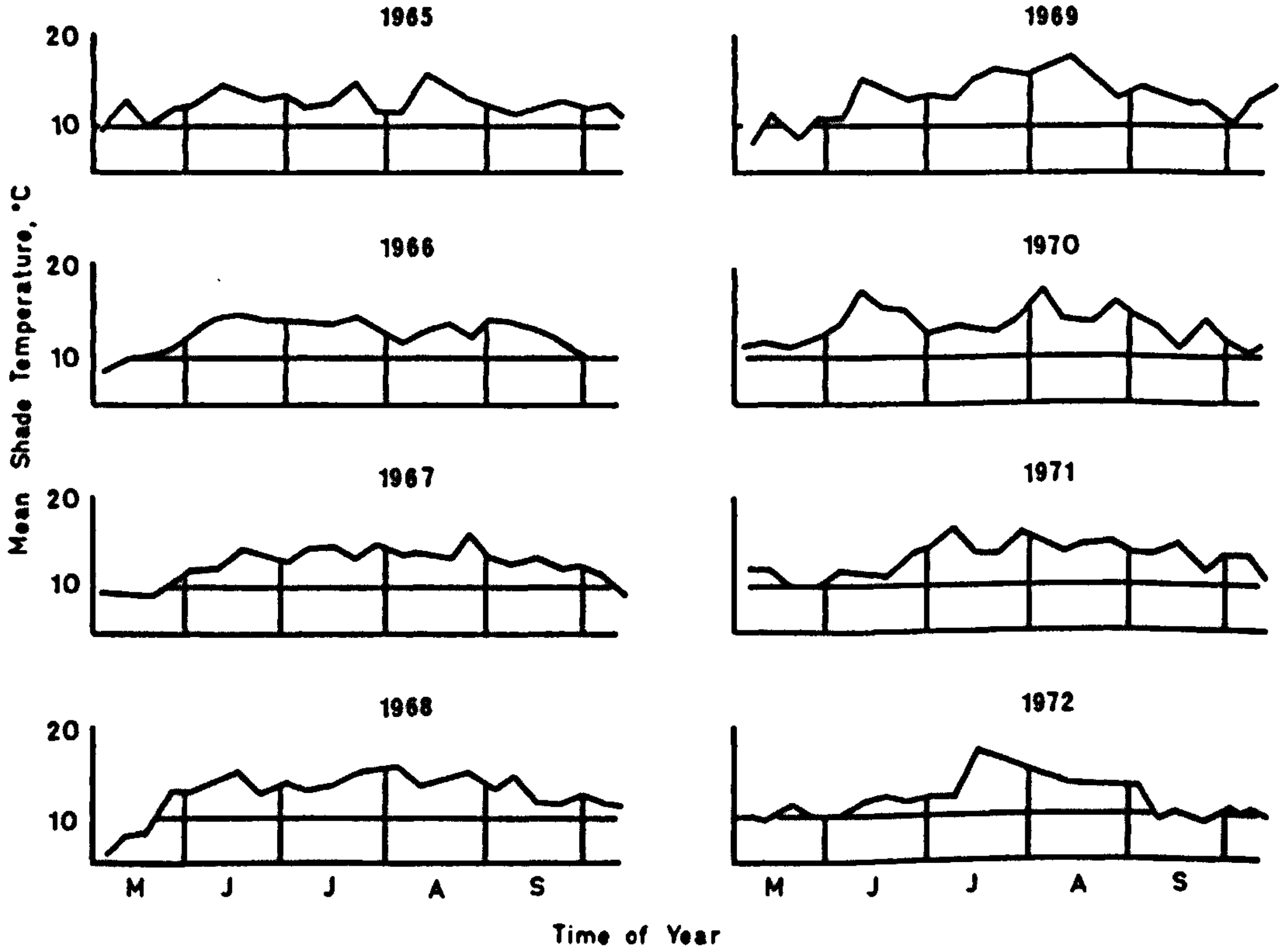


Fig. 16. Mean daily temperatures at Abbotsinch airport, Glasgow, during the seasons 1965 to 1972.

The mean daily wind speeds are shown in Fig. 17, again recorded at Abbotsinch airport and averaged over each week during the season, from 1965 to 1972. The median daily wind speed is 7.74 knots (1 knot = 0.5146 $ms^{-1}$).

Rainfall is not included in the model since it was thought unlikely to cause significant mortality to aphids beneath the leaves, at least in the absence of high winds and pending evidence to the contrary.

## 3.4 The tree submodel

### The model (subroutine TREE)

All buds are assumed to break on the day that the accumulated day-degree total from 1st March, above a threshold of 5°C, reaches 122. In the model the time of bud-burst is then stored in the variable 'BUD', leaf-fall is assumed to occur on 4th October (Day 277) and it is simply treated as a time-dependent mortality factor in the model (subroutine MORTY, Section 3.5.3).

Host plant quality is expressed by the soluble amino-nitrogen

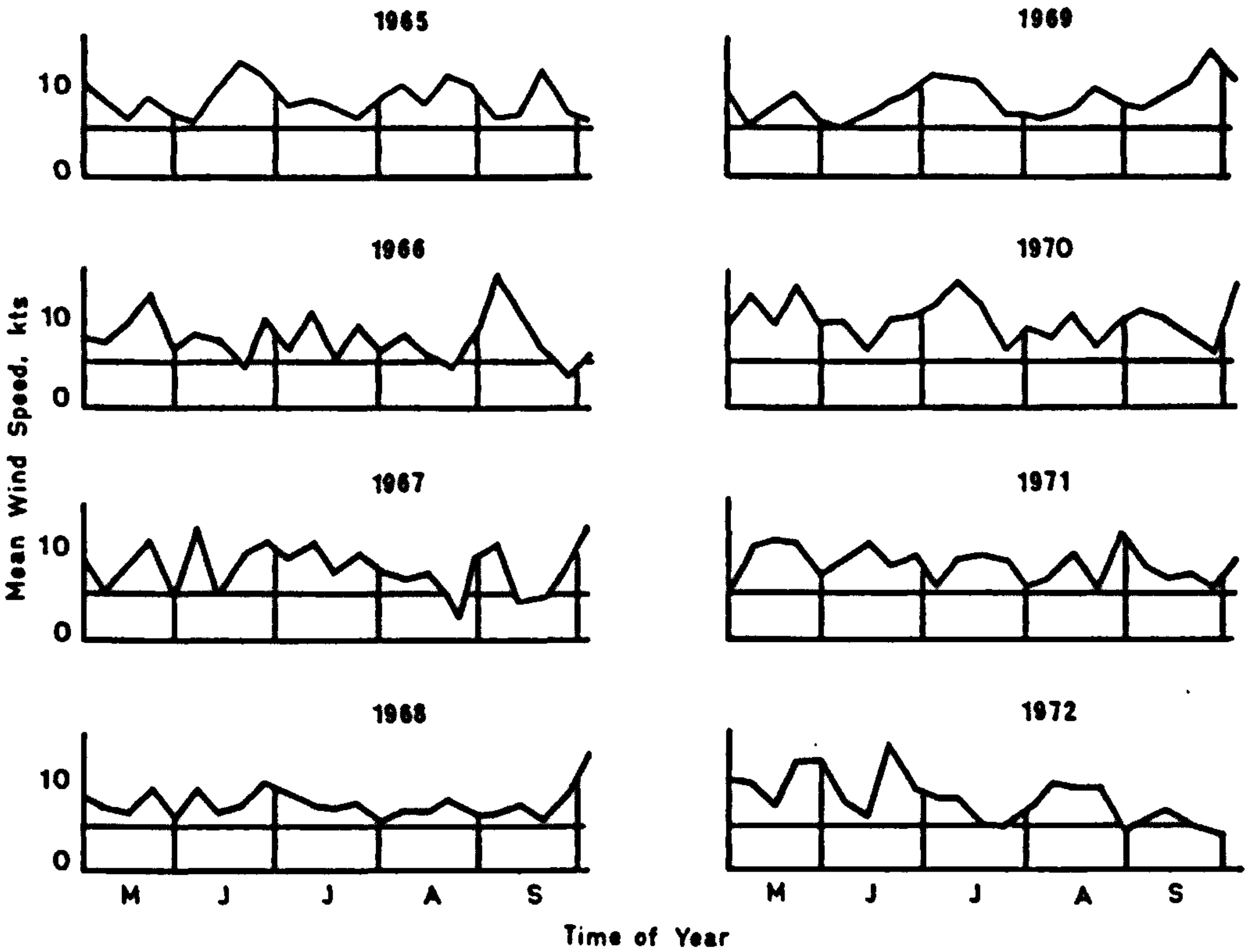


Fig. 17. Mean daily wind speeds at Abbotsinch airport, Glasgow, during the seasons 1965 to 1972.

concentration in the phloem and by the cumulative level of aphid infestation in any one year. Both are updated daily, the first according to the time of year and the time of bud-burst (Fig. 18), the second according to the current aphid density.

## The data

The time of bud-burst varies from year to year and was assumed to do so largely in response to temperature. Approximate times of bud-burst were obtained by back-extrapolating average weekly measurements of leaf width to the point where the widths were 0.2 times the maximum. The day-degree total above 5°C was calculated each year, from the beginning of March to the estimated time of bud-burst and the results averaged over all years. The mean day-degree total, 122, was assumed to be that at which the buds burst, and the calculated times based on this figure accounted for 78% of the variance in those observed. The relationship is (Fig. 19):

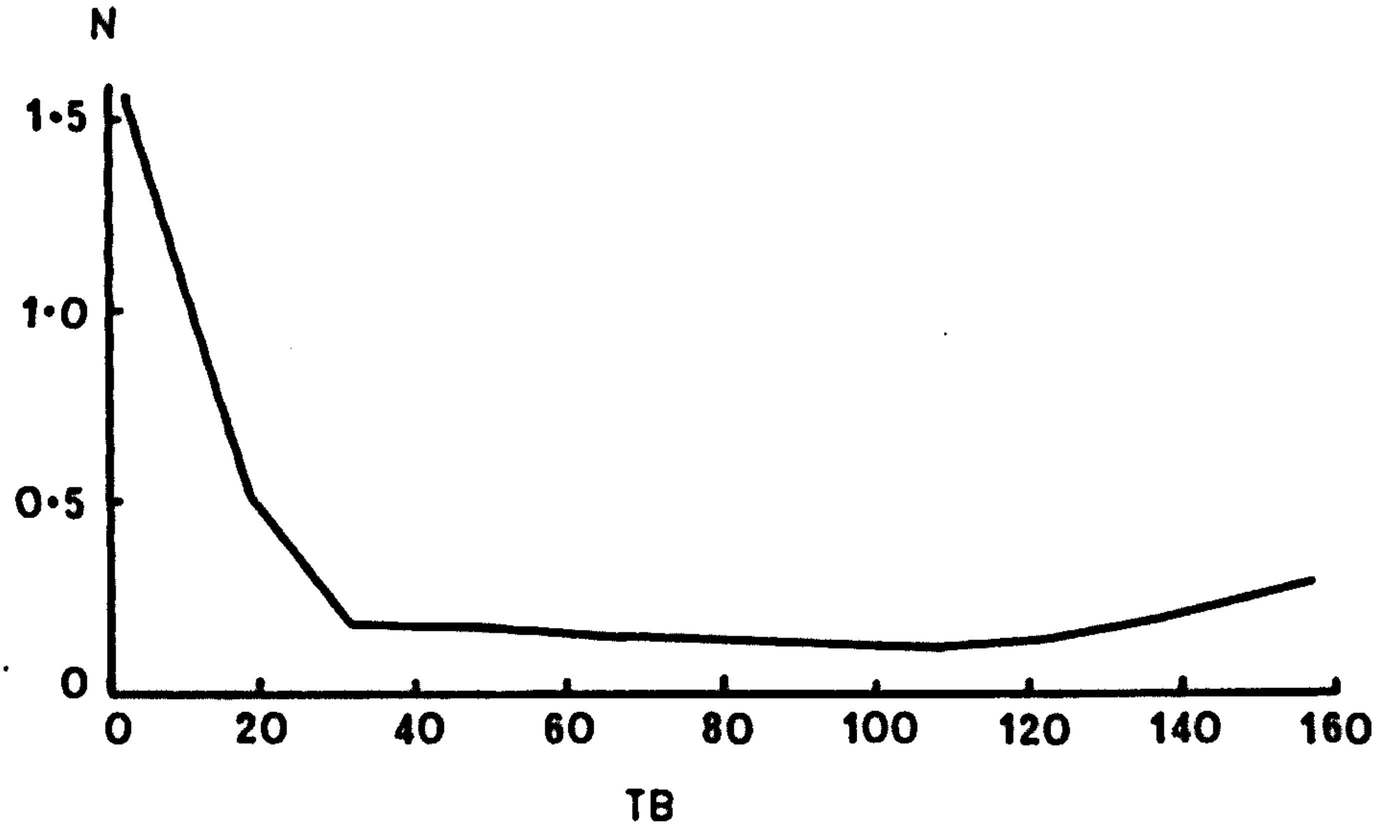


Fig. 18. Soluble nitrogen content of phloem (N, % dry weight) throughout the year (TB, time in days after bud-burst). From Dixon, 1971a.

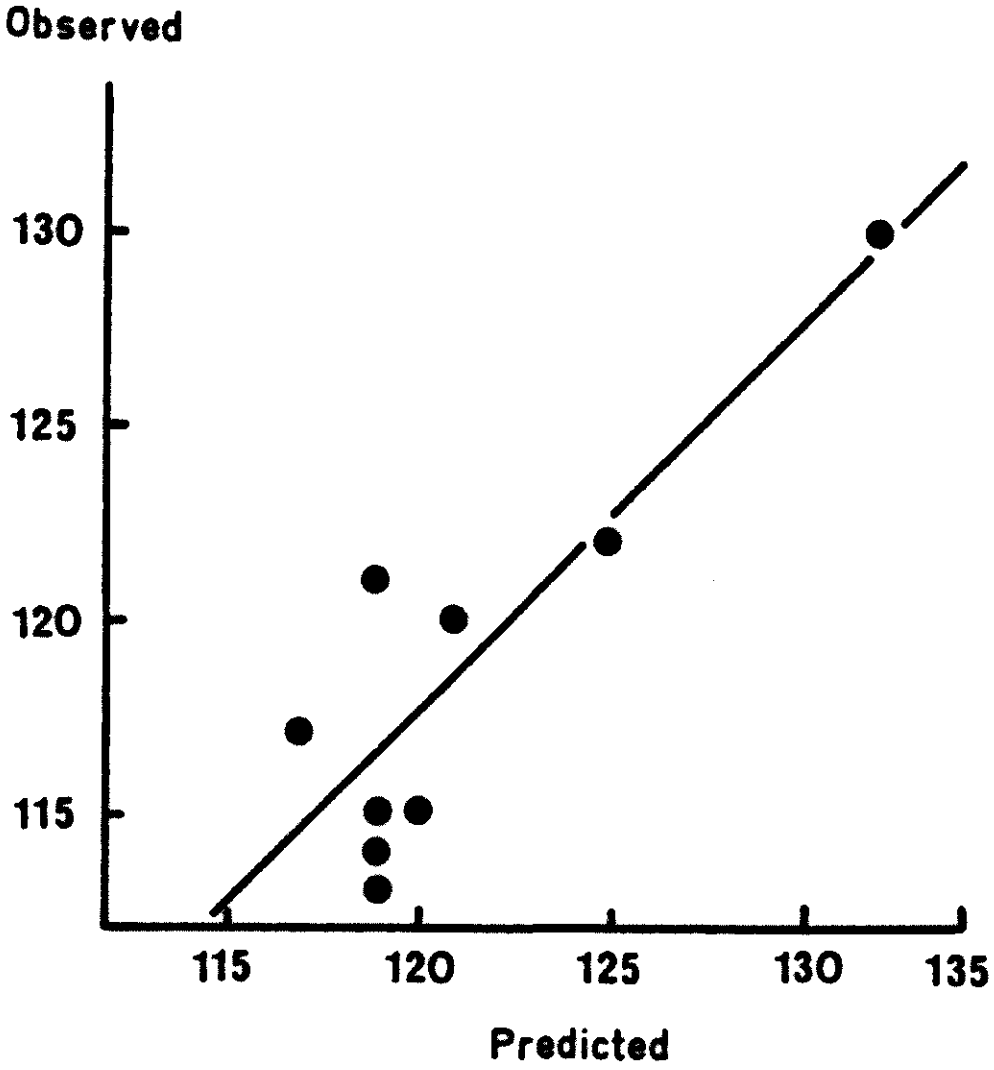


Fig. 19. Relationship between 'observed' and predicted times of bud burst in the field. 'Observed' times are those estimated from measurements of leaf widths; predicted ones are based on accumulation of 122 day-degrees above 5°C. Times are in days from the start of the year.

$$O = 0.9945P - 1.7796 \qquad r = 0.884, \qquad \text{d.f.} = 7, \qquad P < 0.01$$

where

$O$ = estimated time of bud-burst from measurements of leaf width

$P$ = time predicted from a day-degree total of 122.

The same developmental threshold was assumed as applies to egg-hatching (see Section 3.5.1), in the absence of more detailed knowledge about the temperature dependence of bud-burst.

The average time of leaf-fall in the field is 4th October (Day 277). Although the time is variable from year to year it is not known what causes this. High winds in autumn may play a part and White (1970) showed by experiment that leaf-fall was earlier if the leaves had been heavily infested in the current season, but later if aphid numbers had been high in the previous season, than on uninfested plants. However, there is no clear relationship between aphid numbers and time of leaf-fall in the field, where this is taken to be the last sampling date; other factors appear to be more important in determining the variation.

Amino-nitrogen levels in Fig. 18 are those measured by Dixon (1971a) throughout one season. An aphid-induced effect on plant quality, related to cumulative density, is indicated by a reduction in weight of aphids reared on infested tissue and by considerable circumstantial evidence of increased mortality and flight. These effects are considered further in the Sections on growth, mortality and flight.

## 3.5 The aphid submodel

### 3.5.1 *Egg-hatching*

The model (subroutine HATCH)

The submodel predicts the timing and pattern of egg-hatch and their dependence on temperature. It uses a relationship between the cumulative proportion hatching and summed day-degrees from March 1st above a threshold of 5°C (Fig. 20).

If all eggs have already hatched or the date is earlier than March 1st the subroutine is skipped. Otherwise, the day-degree total is updated using Ives' triangulation method (p. 74) and the expected cumulative proportion of eggs hatched obtained from Fig. 20 by linear interpolation. The proportion of remaining eggs hatching

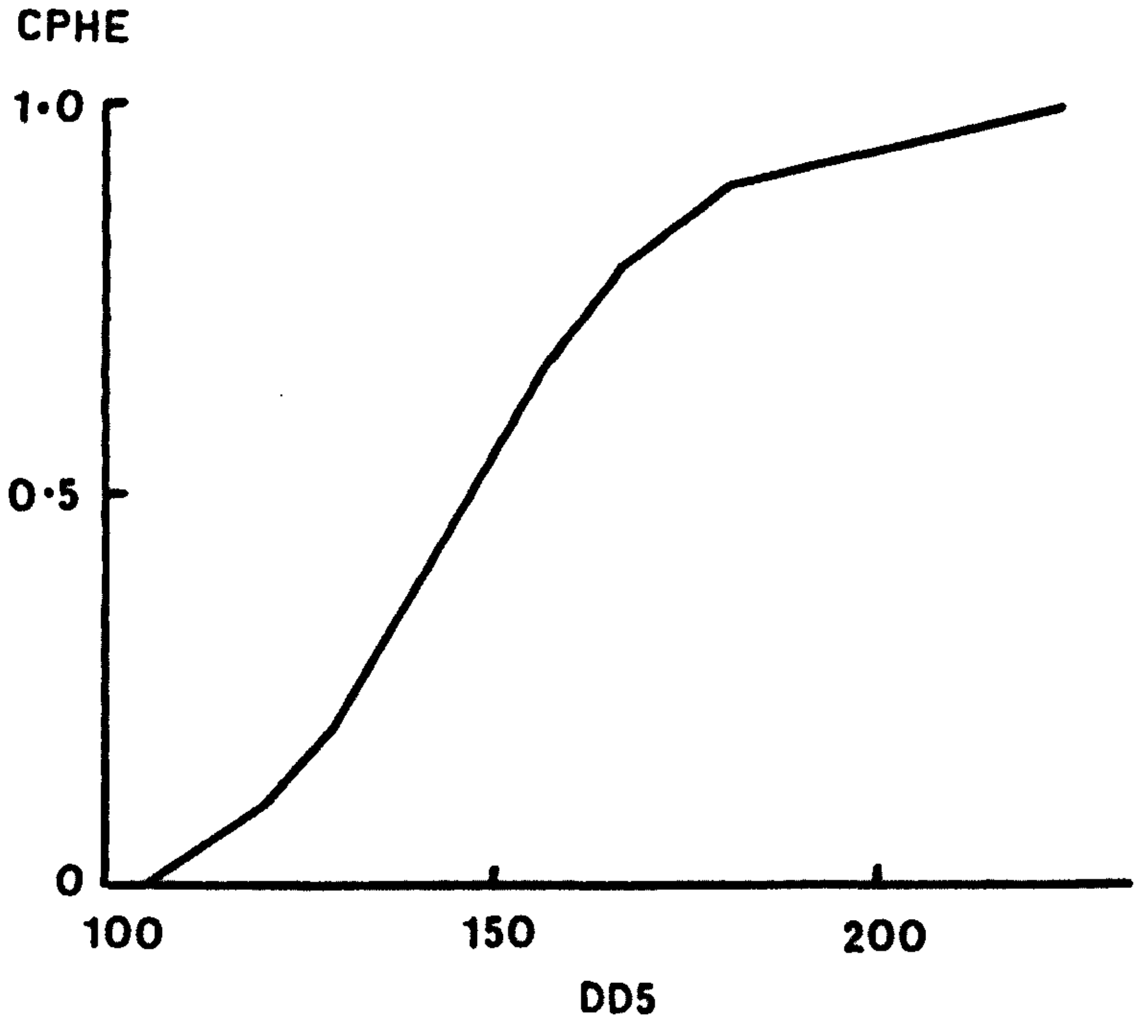


Fig. 20. Relationship between the cumulative proportion of eggs hatching (CPHE) and summed day-degrees above 5°C from 1st March (DD5).

during the current day is then given by:

$$PH = \frac{(CPHE - CPH)}{(1 - CPH)}$$

where

$CPH$ = cumulative proportion hatched

$CPHE$ = the expected cumulative proportion hatched by the end of the day, given the updated day-degree total.

The cumulative proportion hatched is updated and the number hatching subtracted from the egg population and entered into the first nymphal age-class as viviparae with a birth weight of 24 $\mu$g (see p. 57). After reaching 1 the cumulative proportion hatched holds this value for the rest of the year, so no hatching of eggs laid during the current season can occur; the proportion is zeroed at the beginning of the next year.

Fig. 21 shows the cumulative hatching distributions plotted against time for each year and under average temperatures. Temperature differences from year to year before hatching change the position (median) of the hatching curve but not its shape (compare

1968 and 1969). On the other hand, temperature differences during the period of egg-hatching will affect both the median and the shape of the distribution, lower temperatures giving a greater spread of hatching times. This is illustrated by a comparison of the curves in 1966 and 1973 (Fig. 21), the results of experiments described below (Fig. 22) and the difference between observed hatching curves for the lime aphid and sycamore aphid in 1973. Sycamore aphid eggs hatch earlier and over a longer period than those of the lime aphid (Dixon, 1976) and this longer period is explicable in terms of the lower temperatures experienced at the time of hatching. When compared on a day-degree scale, the shapes of the distributions are similar ($\chi^2 = 8.37$, d.f. $= 4$, $P > 0.05$), though the medians differ.

## The data

The time of egg-hatch each year was estimated from the sampling data and assumed to be the date of the first sample. As such, it varies from year to year over a range of about 16 days, from 27 April to 13 May, and it is reasonable to assume that such variations are due to temperature.

The temperature threshold for egg development was obtained from a laboratory experiment, in which eggs on twigs were brought in from the field at the end of February and kept at 4 different temperatures under natural daylengths until all had hatched. Fig. 22 shows the cumulative numbers hatching at 12°C, 16°C, 20°C and 24°C and Fig. 23 the rates of development plotted against temperature. Development rates are reciprocals of the median times between the start of the experiment and hatching. The relationship between development rate and temperature is linear over the range considered and Chambers (pers. commun.) found linearity down to 8°C in the sycamore aphid. The temperature threshold is 5°C.

Development rates of eggs are only relative in the absence of any knowledge of the time at which development starts, and the assumption that the same development process occurs throughout may be invalid (Behrendt, 1973). For these reasons a purely empirical relationship was sought between spring temperatures and hatching times but using the threshold derived from the experiment.

The number of day-degrees above 5°C was calculated for each year using Ives' method, from 1st march to the date of the first sample. The mean of these values was used to give a predicted median hatching time for each year, and the observed times, given by the sampling dates, were regressed on the predicted. The predic-

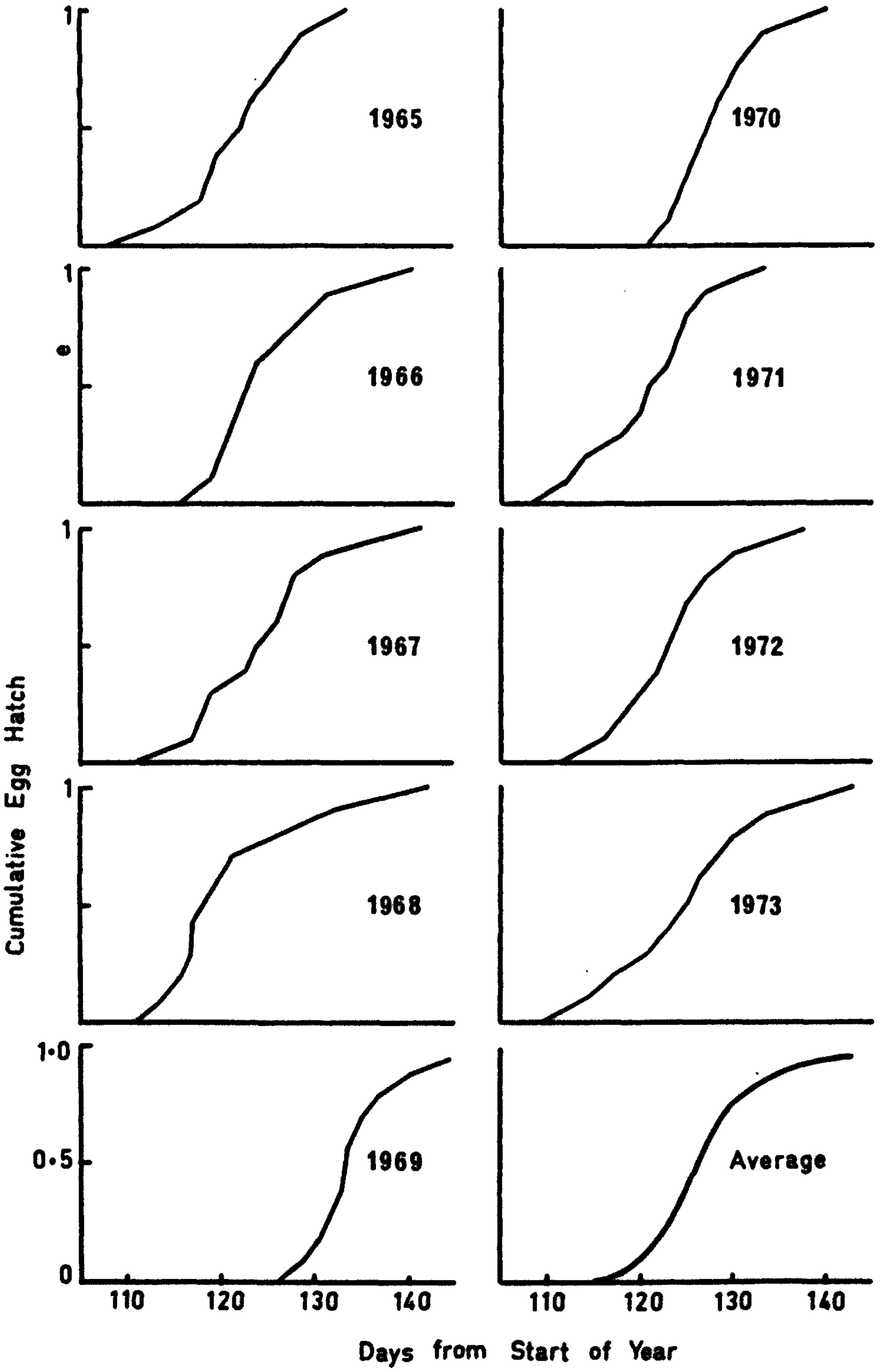


Fig. 21. Cumulative egg-hatching distributions in time, generated by the model for each year in the field and under long-term average temperatures.

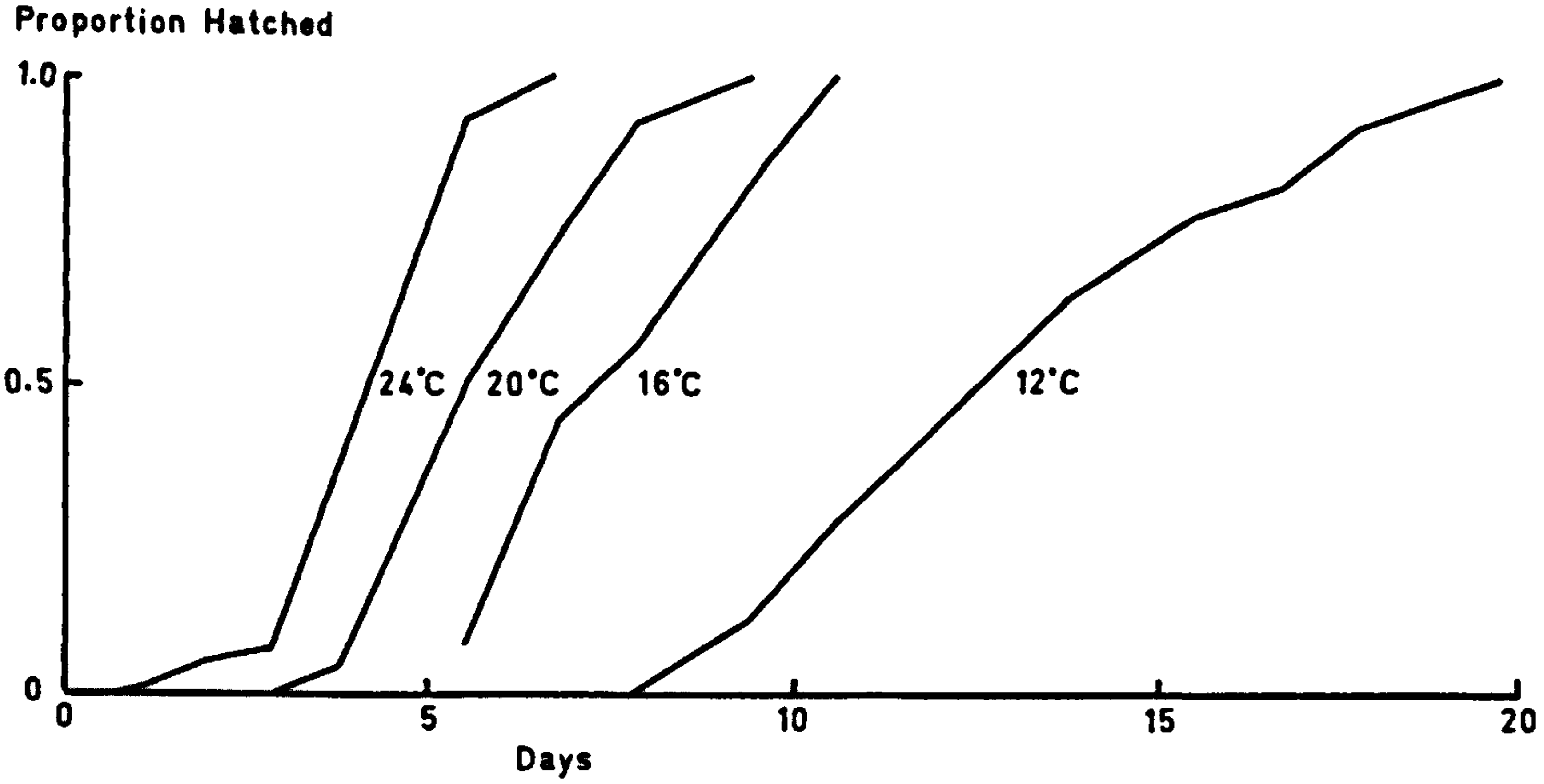


Fig. 22. Distribution of egg-hatching in time at four constant temperatures.

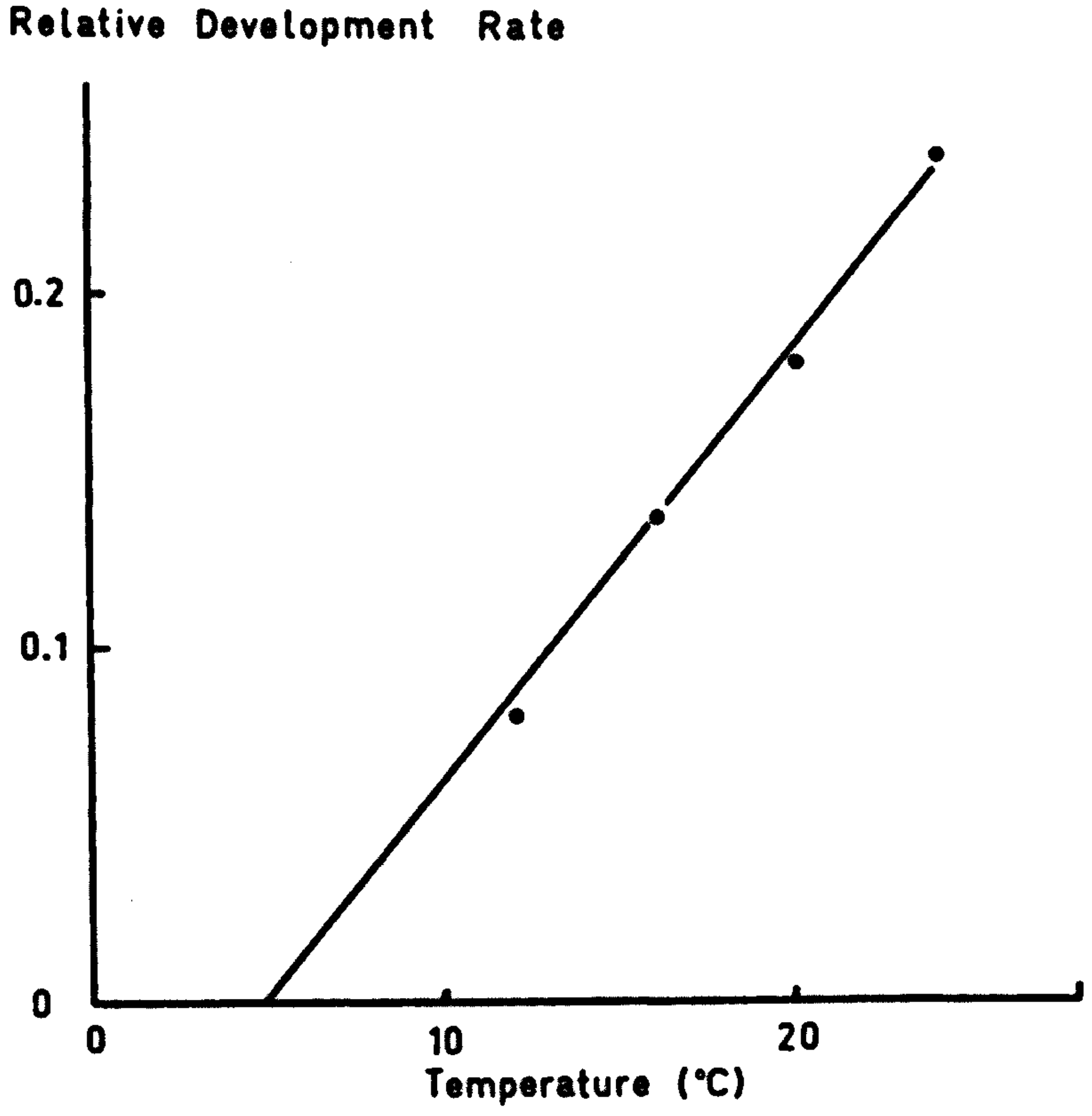


Fig. 23. Relationship between relative development rate of eggs and temperature.

tions ($P$), based on the experience of equal numbers of day-degrees from 1st March (147), accounted for 68% of the variance in the observed hatching times ($O$):

$$O = 1.0113P - 1.5 \qquad r = 0.827, \text{d.f.} = 8, P < 0.01$$

intercept not significantly different from 0

$$t = 0.05, \text{d.f.} = 8, P > 0.05$$

slope not significantly different from 1

$$t = 0.047, \text{d.f.} = 8, P > 0.05$$

Predictions based on corrected temperatures, with 1.5°C added to the mean, gave no better agreement and the correction may be inappropriate in any case at the low temperatures of early spring.

Having established the median of the hatching distribution each year the pattern of hatching within a year, on the same day-degree scale, was derived from Dixon's (unpublished) observations in 1973 on a tree at Glasgow University. The eggs hatched over a period of about 1 month and the distribution showed highly significant kurtosis and positive skew when plotted on the day-degree scale. However, the kurtosis and skew were removed when the scale was transformed to logarithms. The curve of cumulative proportions hatching was therefore smoothed lognormally, though inconsistent departures from the fitted curve indicate that immediate temperatures may have a greater effect than day-degree summation would imply.

### *3.5.2 Predation*

The model (subroutine PRED)

The predation submodel uses a multiple predator/multiple prey functional response equation to calculate the numbers of each prey instar eaten daily. 11 behaviourally distinct predator types and 11 prey types are considered, consisting of

| | | |
|---|---|---|
| Predators | Black-kneed capsids | instars 1–5 and adults |
| | 2-spot coccinellids | instars 1–4 and adults |
| Prey | lime aphids | instars 1–4 and adults (all morphs) |
| | leafhopper | instars 1–5 and adults |

Input consists of data matrices of attack coefficients (Table 2) and weights of prey required to satiate each predator (Table 3), together with numbers of predators and prey generated by the main model and prey weights. Aphid weights are also generated by the model but leafhopper weights are assumed constant for each stage (Table 4).

Table 2. Predator attack coefficients for different predator/prey combinations.

| | | aphid | | | | | leafhopper | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | Ad | 1 | 2 | 3 | 4 | 5 | Ad |
| 2-spot coccinellid | 1 | 0.33 | 0.32 | 0.04 | 0.06 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 1.81 | 0.45 | 0.21 | 0.36 | 0.19 | 0.12 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 2.76 | 2.44 | 0.65 | 1.71 | 0.85 | 0.31 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 4.51 | 6.58 | 3.17 | 2.74 | 2.88 | 0.38 | 0.23 | 0 | 0 | 0 | 0 |
| | Ad | 4.51 | 6.58 | 3.17 | 2.74 | 2.88 | 0.38 | 0.23 | 0 | 0 | 0 | 0 |
| Black-kneed capsid | 1 | 1.27 | 0.47 | 0.16 | 0 | 0 | 0.43 | 0.14 | 0 | 0 | 0 | 0 |
| | 2 | 6.00 | 2.50 | 1.70 | 0.58 | 0.41 | 11.74 | 4.31 | 1.90 | 0.81 | 0.28 | 0 |
| | 3 | 12.58 | 6.98 | 8.73 | 1.68 | 1.65 | 0 | 13.59 | 4.82 | 2.59 | 0 | 0 |
| | 4 | 14.43 | 15.39 | 15.32 | 7.70 | 7.77 | 0 | 23.59 | 15.70 | 10.32 | 4.16 | 0 |
| | 5 | 15.16 | 25.65 | 39.79 | 28.76 | 19.38 | 0 | 0 | 0 | 28.91 | 10.93 | 0 |
| | Ad | 11.38 | 23.55 | 40.64 | 34.25 | 39.25 | 0 | 0 | 0 | 0 | 0 | 3.00 |

Table 3. Maximum weights of prey eaten daily by predators (μg).

| 2-spot coccinellid | | | | | black-kneed capsid | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | Ad | 1 | 2 | 3 | 4 | 5 | Ad |
| 160 | 550 | 1300 | 3470 | 4125 | 20 | 40 | 68 | 113 | 178 | 334 |

Table 4. Average leafhopper weight in the field (μg).

| leafhopper | | | | | |
|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | Ad |
| 40 | 110 | 200 | 360 | 650 | 700 |

The form of functional response assumed is a combination of the models of Thompson (1924) and Nicholson & Bailey (1935) with the number of encounters with prey limited by the predators' searching capacity at low densities and by their maximum rate of ingestion at higher densities. Although originally describing parasite searching behaviour this model is applicable to predators in the present situation since the effects of handling times are negligible (see below); unlike equations of the random predator type (Rogers 1972) it also retains its manageability in a situation where several different predators are eating several different prey. The functional response equation is:

$$N_{at_i} = N_i(1 - e^{-\Sigma_{j=1}^{j=11} a_{ij}P_jS_j})$$

where

$$S_j = VOR_j \Big/ \sum_{i=1}^{i=11} a_{ij}N_iW_i; \qquad S_j \leqslant 1$$

and

$N_{at_i}$ = number of prey $i$ attacked by all predators /100 cm$^2$
$N_i$ = number of prey $i$/100 cm$^2$
$a_{ij}$ = attack coefficient for prey $i$ and predator $j$ (dm$^2$ traversed/day on abaxial leaf surfaces × capture efficiency × correction factor for within-leaf distribution of predators and prey)
$P_j$ = number of predators $j$/100 cm$^2$
$S_j$ = correction factor for satiation of predators $j$
$VOR_j$ = maximum prey weight killed per day per predator $j$ ($\mu$g)
$W_i$ = weight of each prey $i$ ($\mu$g)

and its derivation is described below. Prey numbers in the various population vectors are updated accordingly.

Fig. 24 shows the computed functional response curves for each aphid and predator instar, assuming a high predator density of 1/100 cm$^2$. Lower densities of predators very rapidly reduce the number of prey eaten; if the expectation of survival for a prey is 0.01 at a predator density of 1/100 cm$^2$, for example, this will increase to $(0.01)^{0.1}$ or 0.63 if the predator density decreases to 0.1/100 cm$^2$. Fig. 24 shows clearly that coccinellids are effective at high prey densities because of the amount they can eat, and that although the reverse is true for the black-kneed capsid it is ex-

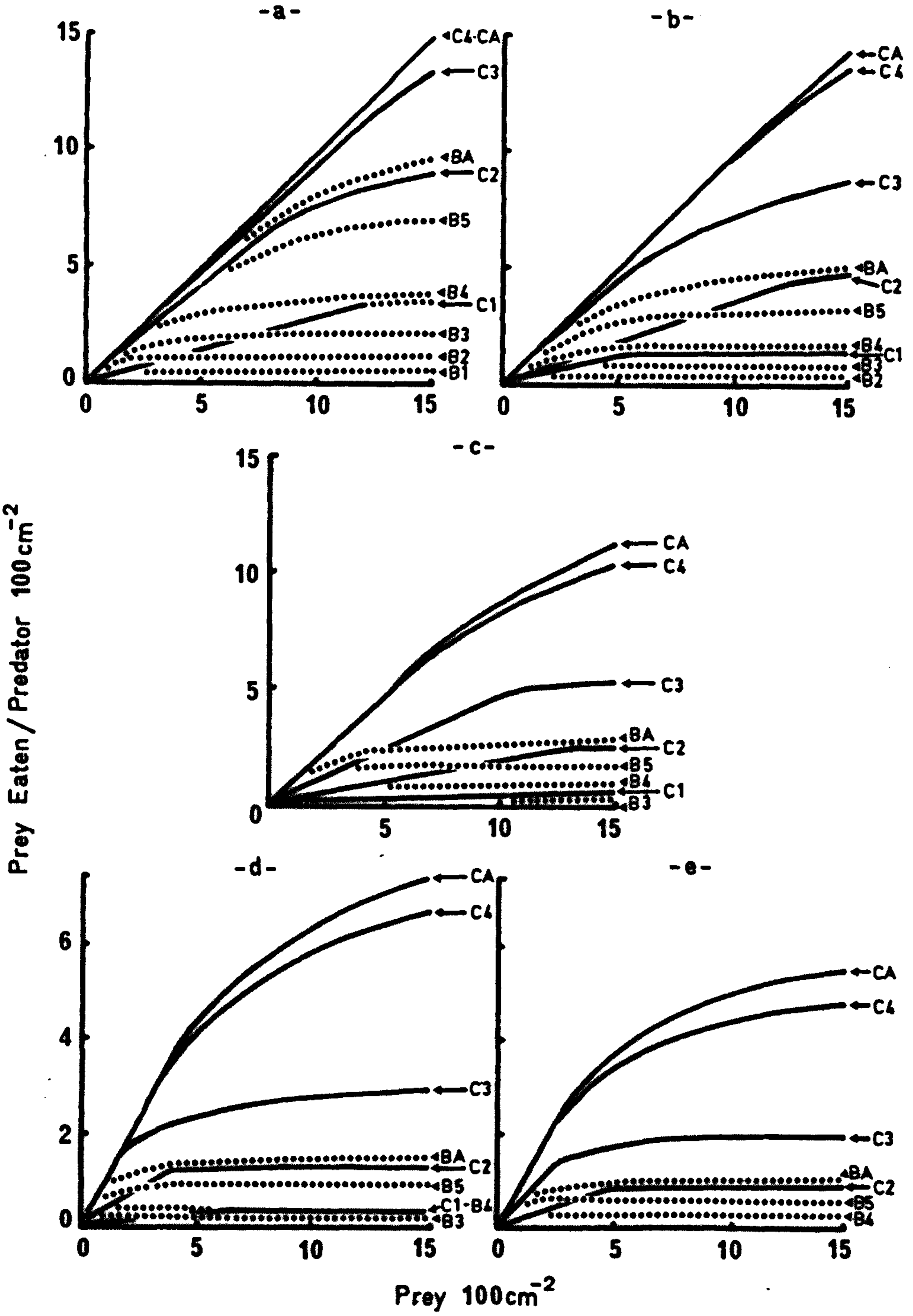


Fig. 24. Functional responses of predators to prey densities, generated by the model. —— 2-spot coccinellid, instars 1–4 and adult (C1, C2, C3, C4, CA); ····· black-kneed capsid instars 1–5 and adult (B1, B2, B3, B4, B5, BA). Predator densities are /100 cm$^2$. a) First, b) second, c) third and d) fourth instar aphid, and e) adult aphid.

tremely effective at low prey densities because of its greater searching ability.

## The data

The actual functional responses of the different predator types to the different prey types have not been observed directly; apart from any other inherent difficulties this would involve 121 separate experiments, each for a range of prey densities and perhaps also for a range of predator densities, while an experimental 'universe' similar to that on the trees would be difficult to devise. Instead, the attack coefficients and the prey weights required to satiate the predators have been determined by experiments and a functional response equation assumed which generates prey death rates, given these parameters and the principle assumptions that predators encounter prey at random and that handling times can be ignored. Attack coefficients are products of the capture efficiencies, the abaxial leaf areas (in dm$^2$) searched per predator per day and factors correcting for the tendency of aphids to aggregate on leaf veins and of predators to search the veins preferentially. Values for these three quantities, for the black-kneed capsid and the 2-spot coccinellid, are taken from Glen (1971, 1975) and Wratten (1973), respectively. The maximum weights of prey killed each day when excess is provided are also taken from Glen's (1971) and Wratten's (1973) laboratory experiments.

The basic equation used is:

$$N_{at} = N(1 - e^{-Enc/N})$$

and

$$Enc/N = aP;\ N < \frac{NMAX_{at}}{a} \quad \text{(as in Nicholson \& Bailey, 1935).}$$

$$Enc/N = \frac{NMAX_{at}P}{N};\ N \geqslant \frac{NMAX_{at}}{a} \quad \text{(as in Thompson, 1924)}$$

where

$Enc/N$ = Successful encounters/prey

$NMAX_{at}$ = maximum number eaten per day per predator

The same equation can be written in Nicholson-Bailey form but with a correction factor for satiation of predators, thus:

$$N_{at} = N(1 - e^{-aPS})$$

where

$$S = \frac{NMAX_{at}}{aN}; \; S \leqslant 1$$

From this it is straightforward to obtain the equation used in the model, for several prey and several predators. The only qualitative difference is that $S$ is now expressed not as the maximum number of prey which can be caught divided by the number encountered, per predator, but by the total prey weight which can be eaten divided by the total weight encountered.

Glen (1971, 1975) and Wratten (1971, 1973) also gave times taken to eat prey and in all cases these are so short as to have a negligible effect on the functional response curve; as Rogers (1972) demonstrated, both the random predator and random parasitoid equations reduce to the Nicholson-Bailey form under these circumstances. It is true that Glen (1971, 1975) has shown that black-kneed capsids may have a greatly reduced speed of searching for as long as 1.5 days after feeding, even when initially hungry, and this is equivalent to a digestive pause hence handling time (Holling, 1966). However, the capsids become satiated at extremely low prey densities, so the range of densities over which the effect may be felt is sufficiently small for it to be ignored in practice.

There is no evidence for switching, interference or sigmoid functional response curves due to reduced searching rates at low prey densities, but neither can these possiblities be rejected; further work would be required to test for their existence. Two other features not included in this submodel of predation are stochastic effects and the effect of temperature changes, the first emphasized by Fransz (1974) and the second by Gilbert et al. (1976) and Frazer & Gilbert (1976). As Fransz demonstrated, a stochastic model of the functional response may give higher predation rates than a deterministic one, since non-linearities are present and 'the expectation of curvilinear functions differs from the function of the expectation value'. The error which results from omitting the chance element from predation, however, is a specific case of the point discussed in Section 3.1. Temperature does affect the searching rate of the 2-spot coccinellid (Wratten, 1973) but it is not known what effect it has on handling times. Moreover, the predator population submodels are less detailed than the aphid one and include little temperature dependence, so for these reasons the effect was omitted from the predation submodel. A more complex version could readily include it by multiplying the number of prey eaten by a temperature-dependent factor.

### *3.5.3. Mortality (other than predation, parasitism and winter losses)*

#### The model (subroutine MORTY)

There is an average daily mortality rate for all members of the population and adults are assumed to have a fixed maximum longevity. Population growth is terminated at the end of the season by mortality of mobile stages resulting from leaf-fall which removes both food and places to live. Prior to this, however, it appears that the food supply may become inadequate through a decline in its quality following high cumulative levels of aphid infestation within any one season; this density-related effect also causes mortality among all aphids on the leaves.

The evidence suggests that variations in the daily mortality rate and its obviously greater average value in the field than in laboratory populations may be due at least in part to an effect of wind in causing leaves and fruit to brush together and aphids to be dislodged. The daily mortality rate is therefore considered to be made up of two components, an intrinsic background mortality, as applies in laboratory populations, and a factor dependent on wind speed which increases the average mortality rate in the field.

The overall daily survival rate applied in the model is then a product of the survival rates associated with these factors, given by the following relationships (Fig. 25):

Adult longevity (age-specific mortality):

$SD = 1$, adult age $<30$ days

$SD = 0$, adult age $\geqslant 30$ days

Intrinsic mortality/effect of wind:

$SW = 0.99(1 - 0.0003W^2)$;   $0.2 \leqslant SW \leqslant 1$

Effect of leaf fall:

$SL = (277 - \text{DAY})/10$;   $0 \leqslant SL \leqslant 1$

Effect of cumulative density:

$SC = 1 - 0.002(C - 250)$;   $0 \leqslant SC \leqslant 1$

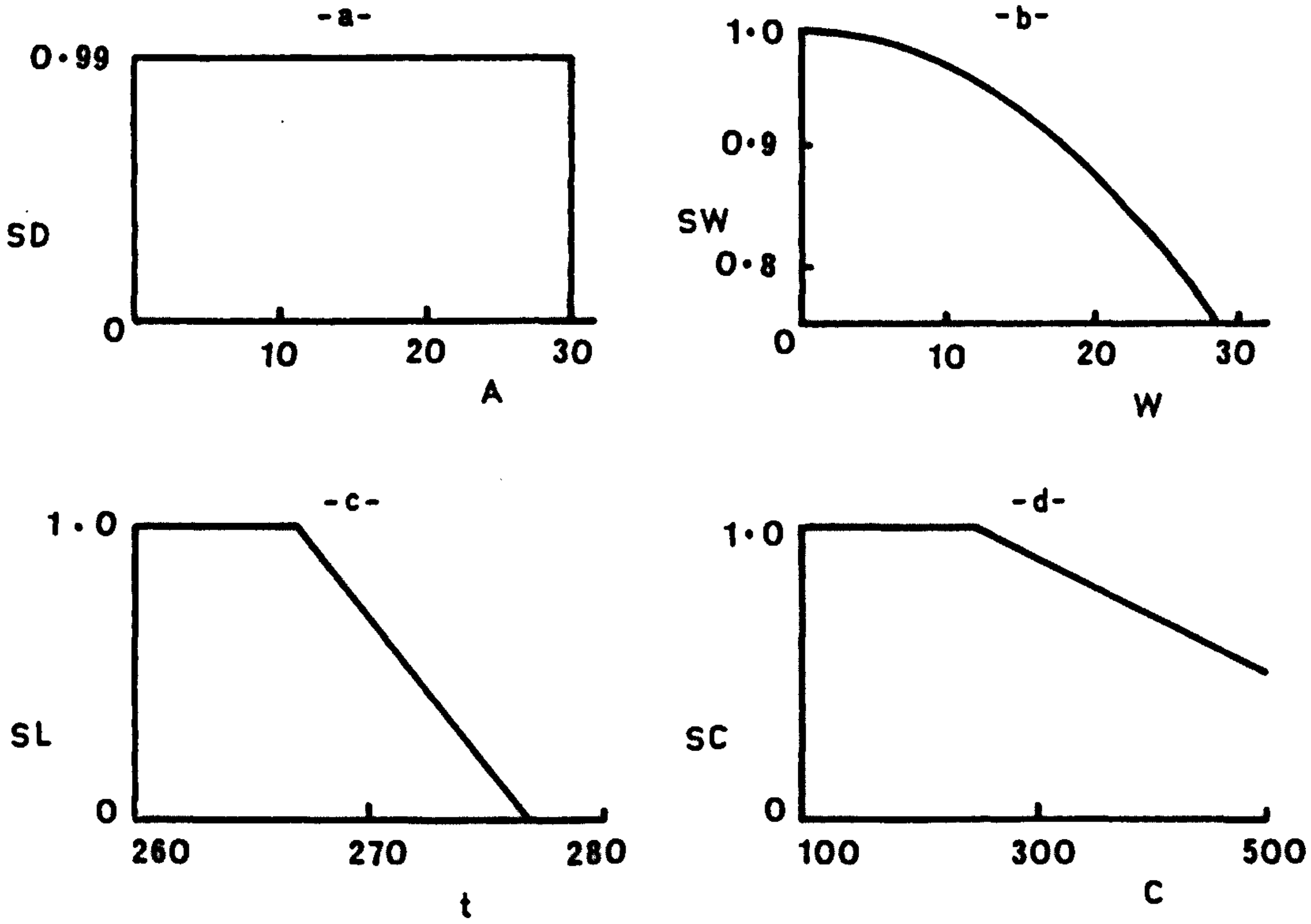


Fig. 25. The components of daily mortality: a) the proportion surviving (SD) dependent on adult age (A); b) the proportion surviving (SW) dependent on mean daily wind speed (W); c) the proportion surviving (SL) dependent on leaf fall hence the time of year (t); d) the proportion surviving (SC) dependent on cumulative density (C, aphid-weeks).

Proportion of population surviving per day:

$$S = SD \times SW \times SL \times SC$$

where

$W$ = mean daily wind speed (kts)
$DAY$ = time of year (days)
$C$ = cumulative aphid density (aphid-weeks/100 cm$^2$)

## The data

The daily background survival rate of 0.99 is an approximate figure obtained from insectary populations under the most favourable environmental conditions, where Brown (1974) recorded numbers of aphids falling from young saplings and dying on the leaves each week. The assumed maximum longevity for adults of 30 days is fairly arbitrary. Adults clip-caged in the laboratory at 15°C live for an extremely long period, on average about 80 days, but in unconfined populations emigration and extrinsic mortality factors determine the pattern of survival and render the potential longevity unimportant. This was confirmed by running the model with two different values (Section 4.2).

The effect of wind was tested by a field experiment. Petioles of leaves bearing a maximum of two large or five small aphids were ringed with 'Stickem' to prevent the aphids walking off. Four trees were used, in different positions, supporting low-density populations so as to minimize the numbers of predators present. These were rarely found on the isolated leaves but when they were the record was omitted. The proportions of aphids disappearing from the leaves each day were then plotted against the daily maximum gust speed at 20 m (Fig. 26). Although wind speeds in general were low and a greater range would have been desirable, nevertheless the relationship between the proportion disappearing and wind speed was highly significant ($r = 0.62$, d.f. $= 38$, $P < 0.01$). This could not be used directly in the model, however, since it was obtained in a different area, it does not cover the full range of wind speeds and it appears to overestimate actual mortality, since running the model with the relationship as it stands rapidly led to extinction of the population. One reason for a possible overestimation of mortality is that aphids are not free to move off leaves which are unfavourably sited. Dixon (1970) found that sycamore aphids left leaves as soon as their surfaces were touched by others. For it is the brushing

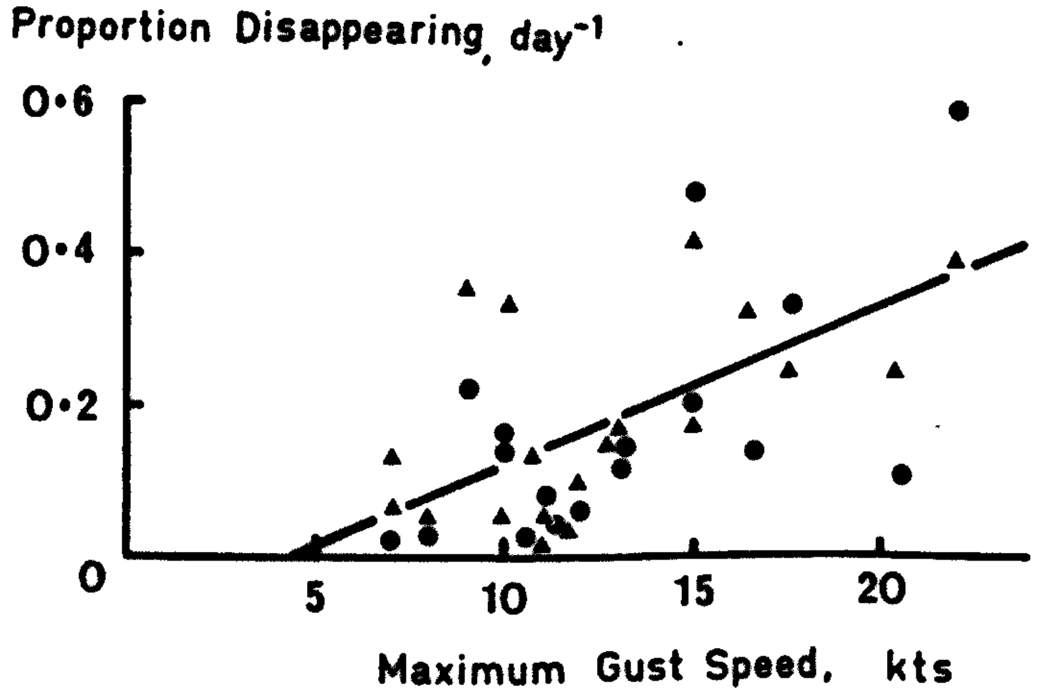


Fig. 26. The effect of wind speed at 20 m on disappearance of nymphs from isolated leaves in the field. ● instars 1–3, ▲ instar 4. kts = knots = 0.5146 m s$^{-1}$.

together of leaves and fruit which is likely to be the actual cause of mortality, and as Dixon pointed out the available space on a sycamore tree is thus limited to a fraction of the total leaf area. Leaves and fruit therefore act as devices converting weather into herbivore mortality. Returning to the model, the effect of wind is assumed to be somewhat less than that observed for aphids on individual leaves, taking the form of Fig. 25 with an arbitrary minimum survival rate of 0.2 per day and an increasingly large effect for very high wind speeds.

Leaf-fall is treated here simply as a time-dependent mortality factor but it is clearly a property of the tree subsystem and as such was considered further in Section 3.4.

Although it has not yet been confirmed by experiment, there is considerable circumstantial evidence for the existence of integrated density-dependent mortality, that is, mortality resulting from a decline in plant quality caused by high cumulative aphid densities. The first indications come from Brown's (1975) painstaking counts of large numbers of aphids falling onto horizontal sticky traps beneath the sampled trees in 1971. This was the year of highest aphid numbers, and mortality increased rapidly towards the end of July when the cumulative density reached 250 aphid-weeks/100 cm$^2$ (Table 5). More significantly, the increase was sustained thereafter, although densities were low by this time and there was no obvious change in weather. Second, adult viviparae were clip-caged on the leaves for 5 days at a time throughout 1971 and also during 1970 and 1972 when numbers were low. The proportions dying each day were plotted against time of year (Fig. 27) and again a large increase in mortality occurred towards the end of 1971 although in the other

Table 5. Effect of cumulative infestation of trees on aphid mortality in the field. Figures are ratios of numbers caught on horizontal sticky traps below the trees, summed over all weeks, to those recorded on the trees per 80 leaves, summed over all weeks. The two time periods correspond to cumulative densities less than and greater than 250 aphid-weeks/100 cm$^2$, respectively, and data are from Brown (1975) for three trees.

| | instars 1–3 | instar 4 | oviparae | alates |
|---|---|---|---|---|
| Before 25/7 | 0.973 | 2.891 | 1.821 | 5.483 |
| After 25/7 | 1.809 | 11.798 | 15.100 | 8.673 |
| $\chi^2$ | 628 | 534 | 43 | 77 |

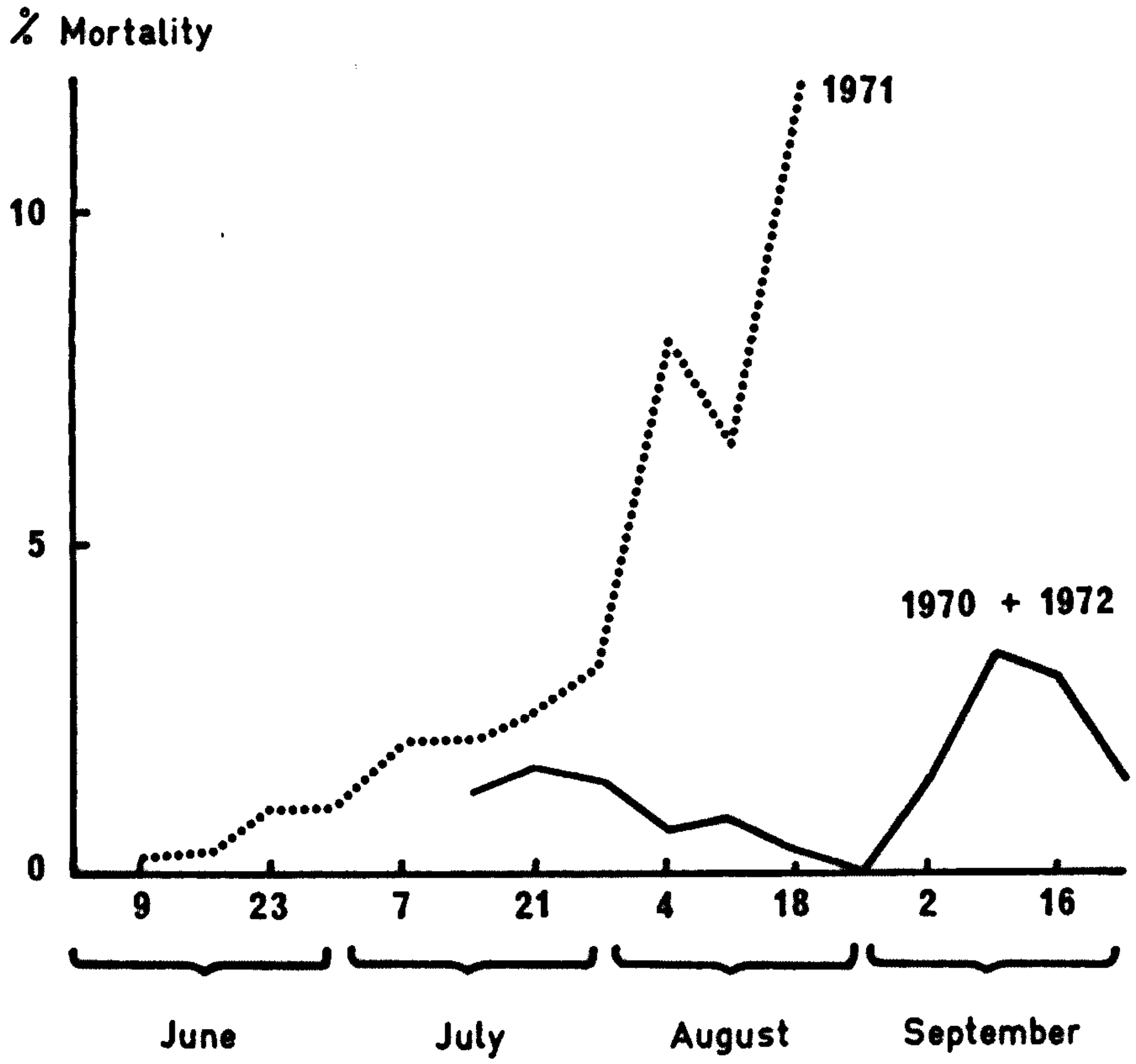


Fig. 27. Adult mortality rate (proportion of clip-caged adults dying per day, taken over all trees) throughout the year in 1971, compared with that in 1970 and 1972.

years it remained constant. The difference between years can only be attributed to two factors, the lower weight of the aphids in 1971, or some equivalent measure of quality, and the state of the tissue, but since adult weight is itself determined partly by cumulative density (p. 75) it must be concluded that this affects mortality either directly or indirectly. However, in Brown's (1975) insectary populations mortality did not increase throughout the season as adult weights declined, suggesting that the effect does not act through the aphid's weight. Since cumulative densities were also extremely high in the insectary populations, their effect on mortality may only be manifested on mature trees. This in turn may explain why it has not yet been possible to confirm the effect of cumulative density experimentally, although Davis (1957) claimed to have demonstrated a conditioning effect for the walnut aphid (*Chromaphis juglandicola* Kalt). The actual mechanism could involve: the injection by aphids of substances into the phloem which inhibit feeding; the progressive occlusion of increasing numbers of vessels as a plant reaction to aphid feeding; or a simple nutrient drain effect. Aphid densities between $28/100\,\mathrm{cm}^2$ (Dixon, 1971) and $78/100\,\mathrm{cm}^2$ (Llewellyn, 1972) throughout a season, depending on the individual tree, would entirely drain the net primary production of the tree in the absence of compensatory growth. In the model a relationship between mortality and cumulative density was used with a fairly arbitrary slope but a threshold of 250 aphid-weeks/$100\,\mathrm{cm}^2$, corresponding to the accumulated total in 1971 at the time that mortality of the clip-caged adults began to rise.

Table 5 suggests that adults and 4th instar nymphs have a much higher overall mortality rate in the field than do younger nymphs, but when rates of disappearance from individual leaves were monitored the mortalities of 4th instars and of younger nymphs were similar. However, making the mortality instar-dependent proved to have very little effect on the model's output, even in terms of instar-distributions, so for simplicity the factors considered in this submodel were assumed to affect all instars equally.

There is a suggestion based on catches from sticky traps in 1971 of density-dependent mortality (Barlow, 1977). However, there is no experimental evidence for the effect which must in any case be slight, since observed instar distributions during July and August are the same in years of high and low density at this time; it was therefore ignored in the model.

### 3.5.4 *Flight*

The model (subroutine FLIGHT)

All viviparae are winged and may fly at any time, before or after reproducing. The proportion flying each day depends on the current weighted population density, the mean total density experienced during nymphal development and, though this is less well established, the accumulated total density over the season. There is also a constant background level, even at low densities, and flight is independent of adult age. The first two components are known to be additive while the others are assumed to be so. The quantitative relationships used in the model are (Fig. 28).

Effect of current density:

$$FA = 0.005\,WD$$

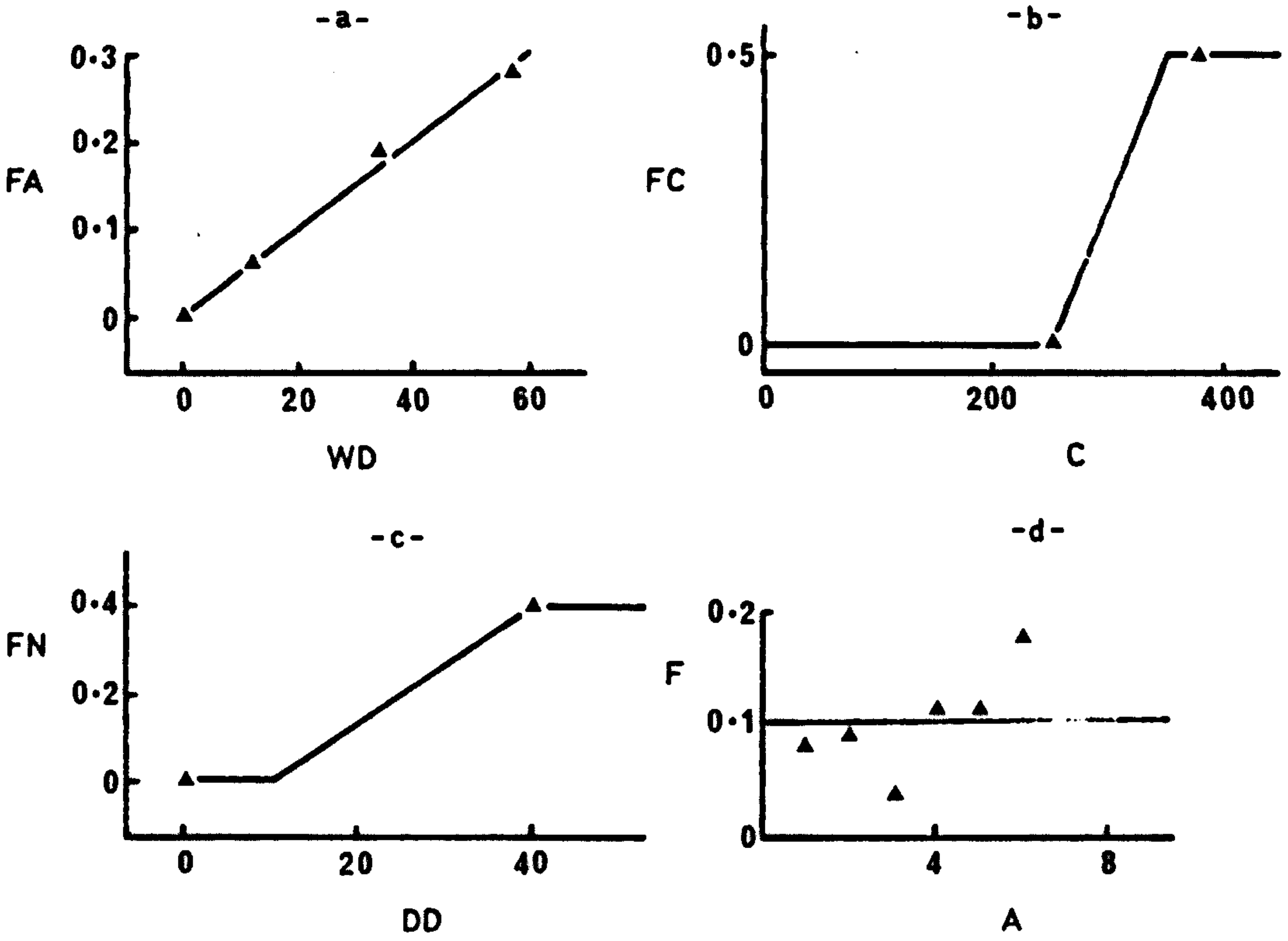


Fig. 28. The components of daily adult flight: a) the proportion flying (FA) dependent on current weighted population density (WD, see text); b) the proportion flying (FN) dependent on mean total density experienced during nymphal development (DD); c) the proportion flying (FC) dependent on cumulative density (aphid-weeks, C); d) the background level of flight (F) relative to adult age (A).

Effect of nymphal crowding:

$$FN = 0.02(DD - 10); \quad 0 \leqslant FN \leqslant 0.4$$

Effect of cumulative density:

$$FC = 0.005(C - 250); \quad 0 \leqslant FC \leqslant 0.5$$

Background level

$$F = 0.1$$

Total proportion flying per day:

$$FLT = FA + FN + FC + F$$

where

$WD$ = weighted density (adults + 4th instars + $\frac{1}{4}$(instars 1–3) per 100 cm$^2$)

$DD$ = mean density during development (aphids/100 $cm^2$)
$C$ = cumulative density (aphid-weeks/100 $cm^2$)

The data

The effect of current density on flight was based on a laboratory experiment of Dixon (1971a) and his results are reproduced in modified form in Table 6. To obtain the relationship in Fig. 28, proportions flying were expressed as increments and the densities used in the laboratory transformed to equivalent densities in the field in the following way. Aphids in the field are aggregated between leaves (Dixon, 1971a) so the average density experienced by each aphid, or mean crowding (Lloyd, 1967), is higher than the average number per unit area. Following Lloyd, the two can be related using the variance/mean equation given by Dixon (1971a), and the resulting expression for mean crowding is:

Table 6. Effect of current density on flight in the laboratory. Modified from Dixon (1971a).

| adults/100 $cm^2$ in lab. | adults/100 $cm^2$ in field | proportion flying/day | prop. flying – basic level |
|---|---|---|---|
| 1 | $\approx 0$ | 0.17 | 0 |
| 30 | 12 | 0.23 | 0.06 |
| 60 | 34 | 0.36 | 0.19 |
| 90 | 57 | 0.45 | 0.28 |

$$\dot{m} = m(1+7.283m^{-0.63})$$

where

$\dot{m}$ = index of mean crowding (aphids/aphid/100 $cm^2$)
$m$ = mean density (aphids/100 $cm^2$)

or, with $\dot{m}$ and $m$ expressed as numbers per leaf

$$\dot{m} = m(1+4.615m^{-0.63})$$

and both forms are shown in Fig. 29. The laboratory densities were taken as mean crowding values and the corresponding mean densities for an aggregated population derived from these using the above expression (Table 6). Since the population in the field consists of stages other than adults, this also must be taken into account.

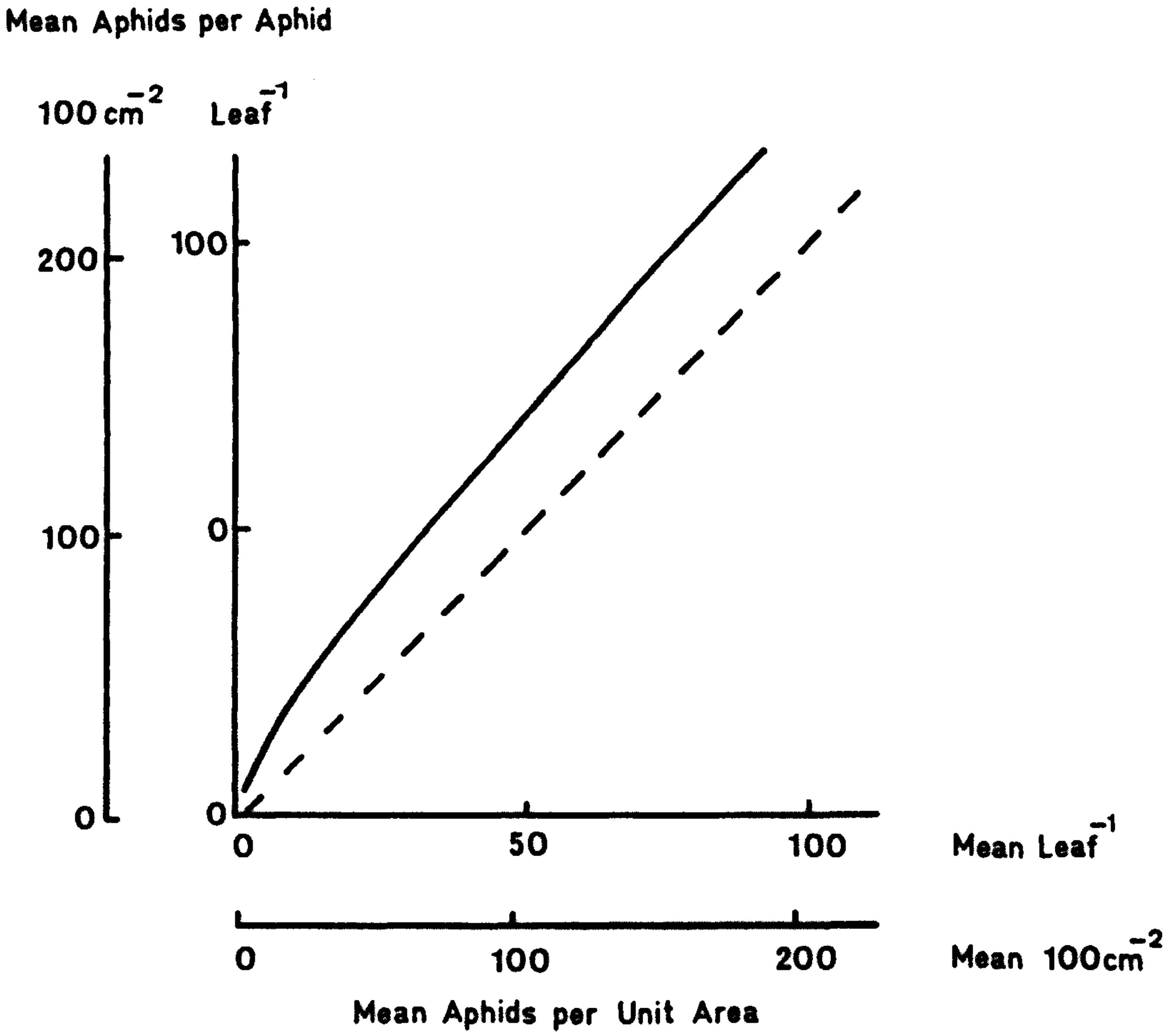


Fig. 29. The relationship between mean density of aphids and mean crowding. —— as observed; – – – for a random distribution.

Fourth instar nymphs were assumed to be equivalent to adults but a weighting factor of 0.25 was applied to densities of younger nymphs since these are less active (Brown, 1975) and the adult flight component depends largely on direct interactions between aphids on the leaves (Kidd, 1975, 1977).

The effect of density during nymphal development was also established by laboratory experiments (Table 16 in Kidd, 1975) in which a maximum additional proportion flying of 0.4 per day was associated with nymphal experience of crowding. The latter cannot be related directly to densities in the field since aphids in Kidd's experiments were reared in small clip-cages. However, these aphids were about 100 $\mu$g lighter in weight than aphids reared in isolation and such a decline in weight in the field in 1969 was associated with a density during development of about 40 aphids/100 cm$^2$. The nymphal component of 0.4 is therefore activated at levels of crowding between 0 and 40/100 cm$^2$ and is assumed in the model to act over the range 10–30/100 cm$^2$ (Fig. 28). The nymphal experience and current density components were shown by Kidd (1977) to be additive.

Evidence that flight depends also on accumulated density, through conditioning of leaf tissue, comes from two sources. Kidd (1977) transferred aphids isolated during rearing to previously infested tissue, where the proportion flying per day was 0.54 greater than for aphids transferred to uninfested tissue. This observation does not preclude the possibility that increased flight was due to the change in tissue quality experienced by the adults, and that aphids reared from birth on previously infested tissue would fly no more readily than those reared from birth on uninfested tissue. However, flight in the field during 1971 increased dramatically at the beginning of August after prolonged heavy infestation of the tree corresponding to a cumulative density of about 250 aphid-weeks/100 cm$^2$. It remained high thereafter, even when the population had crashed to very low levels (Fig. 30). Flight in this case was based on Brown's (1975) counts of aphids caught on horizontal sticky traps beneath one of the sampled trees, and measured as the number caught each week divided by the average number present on the tree that week. Similar data are not available for other years when cumulative densities were low, so the effect may be one of the time of year or the aphid generation; no sustained change in weather was apparent. However, data on mortality are available for other years, when a large increase in mortality recorded at the end of 1971 did not occur (Section 3.5.3). This suggests that flight, an active alternative to death, probably is related to the high infestation levels in 1971 rather than to the time of year or generation, a conclusion reinforced when one considers years like 1968 where rapid population growth and presumably, therefore, little flight was occurring among the same generations of aphids at the same time of year (see Fig. 11). Returning to the model, the relationship in Fig. 28 uses the observed cumulative density threshold of 250 aphid-weeks/100 cm$^2$ and Kidd's figure rounded to 0.5 for the maximum likely flight increment; the slope is arbitrary but its precise value was found to be unimportant in practice.

The background level of flight was estimated in the field using the method described in Section 3.5.3 for mortality. The index of daily flight was determined by the difference between the recorded proportion of adults and nymphs disappearing daily from marked, isolated leaves on the trees. The average value spanning two different

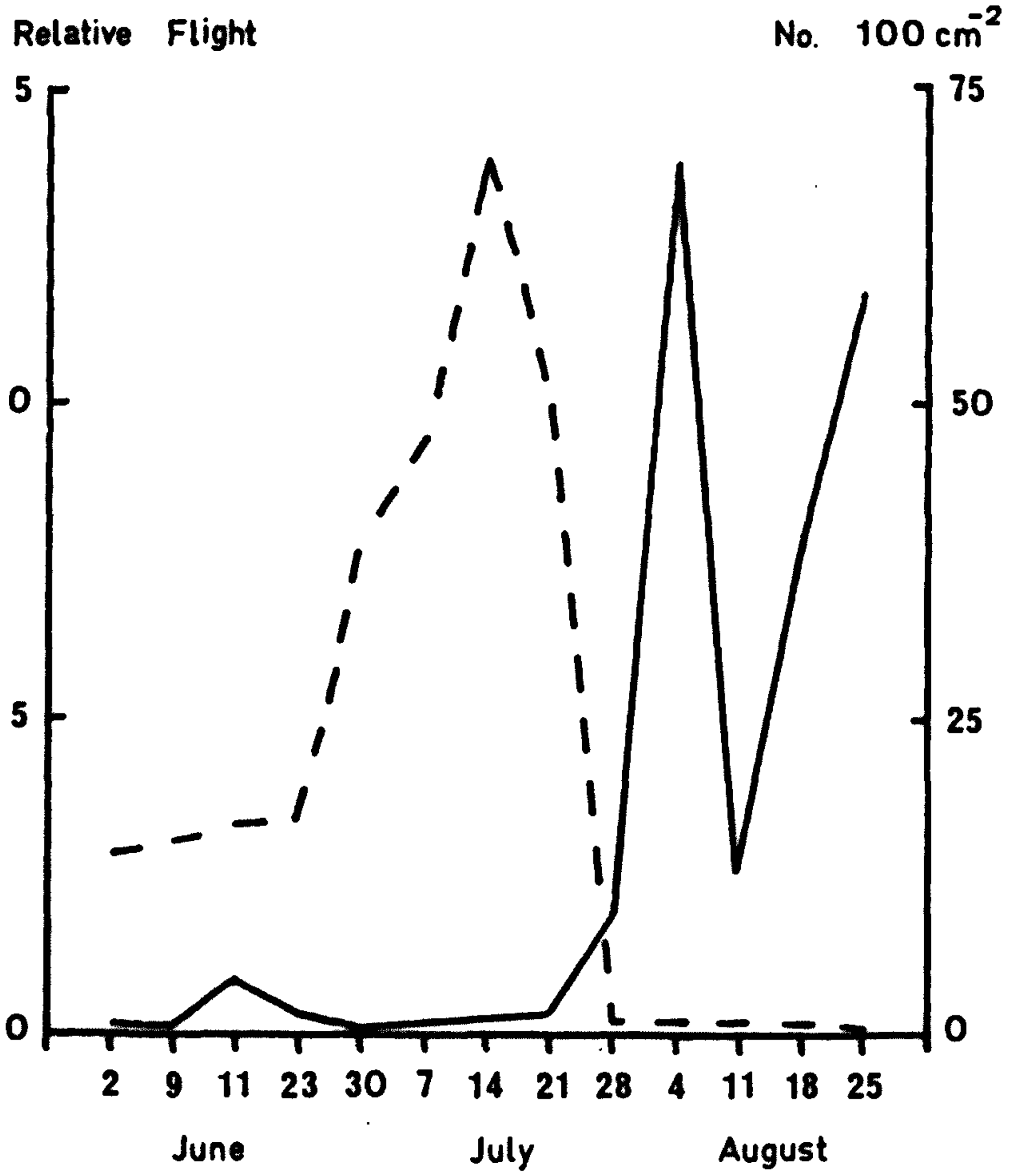


Fig. 30. Variations in relative flight (——, ratio of alates caught on suspended sticky traps to those present per unit area on one tree each week) compared with the variations in population density (----) during 1971.

periods of successive observations was of the order of 0.1 per day. The points in Fig. 28 represent measured proportions of adults flying at different ages, taken from laboratory observations and with the points standardized to the background level of 0.1; there is no significant effect of age over the initial period of adult life.

A laboratory experiment has shown that no flight occurs below 12°C and field observations suggest that higher maximum temperatures result in increased flight (Barlow, 1977). Presumably it is also inhibited by high winds or prolonged rain, but the full extent of the action of weather was felt to be, as yet, insufficiently understood to warrant its inclusion as a factor affecting the average level of flight.

The whole process of flight initiation in the lime aphid is highly complex and the present submodel is a simplified, high-level representation of the underlying behaviour. Kidd (1975, 1977) in particular has studied this in more detail, and Fig. 31 illustrates conceptually the factors priming adult flight. The probability of

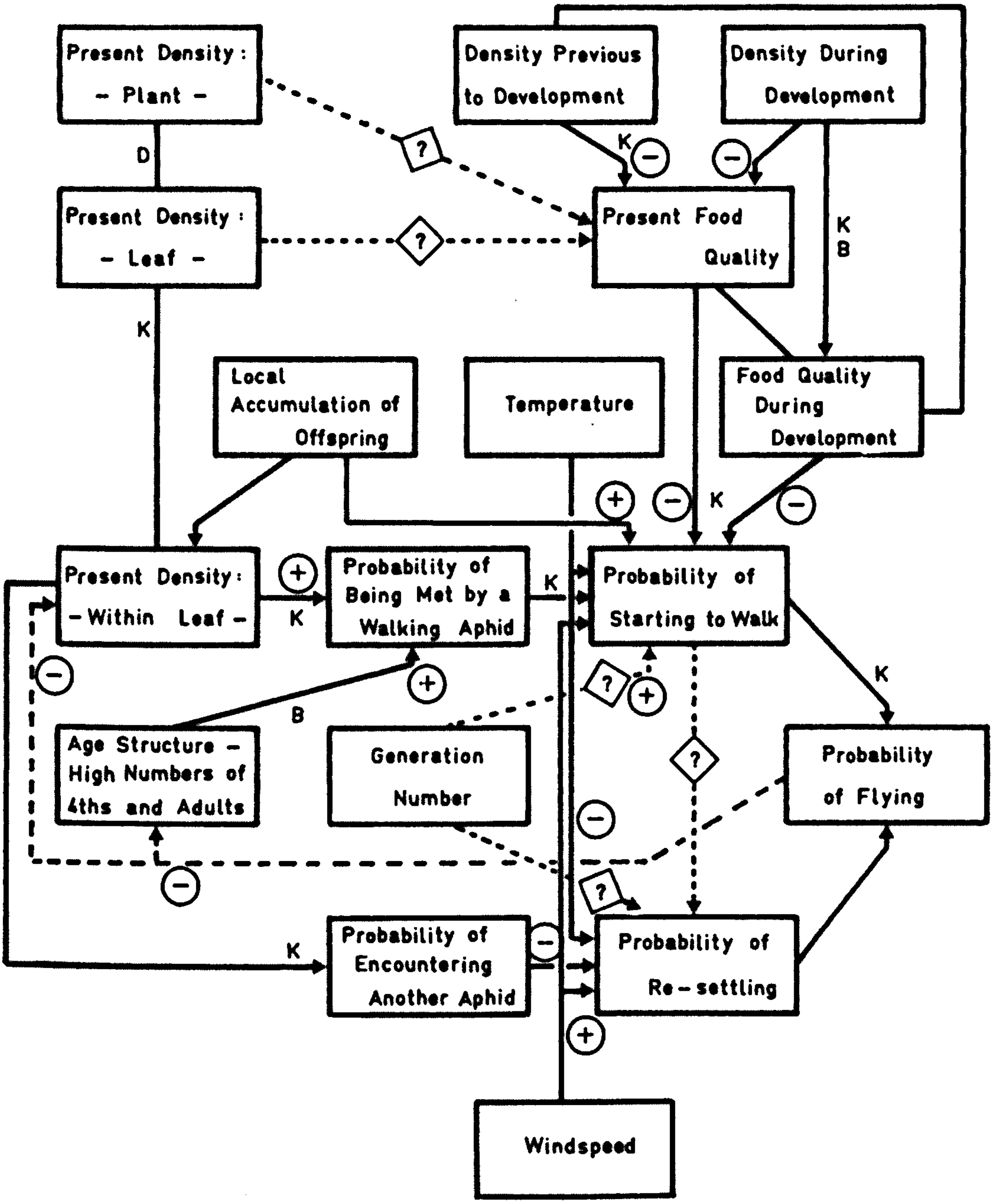


Fig. 31. Diagram of a detailed flight model. ⟶ a relationship indicating that one factor affects another; - - -→ a tentative relationship; —— a link or correspondence; - - -→ feedback from flight. D, K, B, authorities for relationships already established (Dixon 1971a, Kidd 1975, 1976, 1977, Brown 1975).

flying is shown on the right and the pathways represented in the model can be recognized as the effects of immediate density and age composition, perceived through direct interaction, nymphal experience of density, perceived through tissue quality at that time, and past accumulated densities, perceived as the present state of the leaf tissue. Weather and a possible generation effect are included, and all factors appear to act through their effects on movement of the adults; there is a constant probability of flying for an adult given that it has started to walk (Kidd, 1977).

### *3.5.5 Egg-laying*

The model (subroutine EPROD)

The number of eggs laid by each ovipara is related to its size (Fig. 32), thus:

$$E = 0.0162W - 2.736$$

where

$E$ = eggs laid/ovipara produced
$W$ = weight of ovipara ($\mu$g)

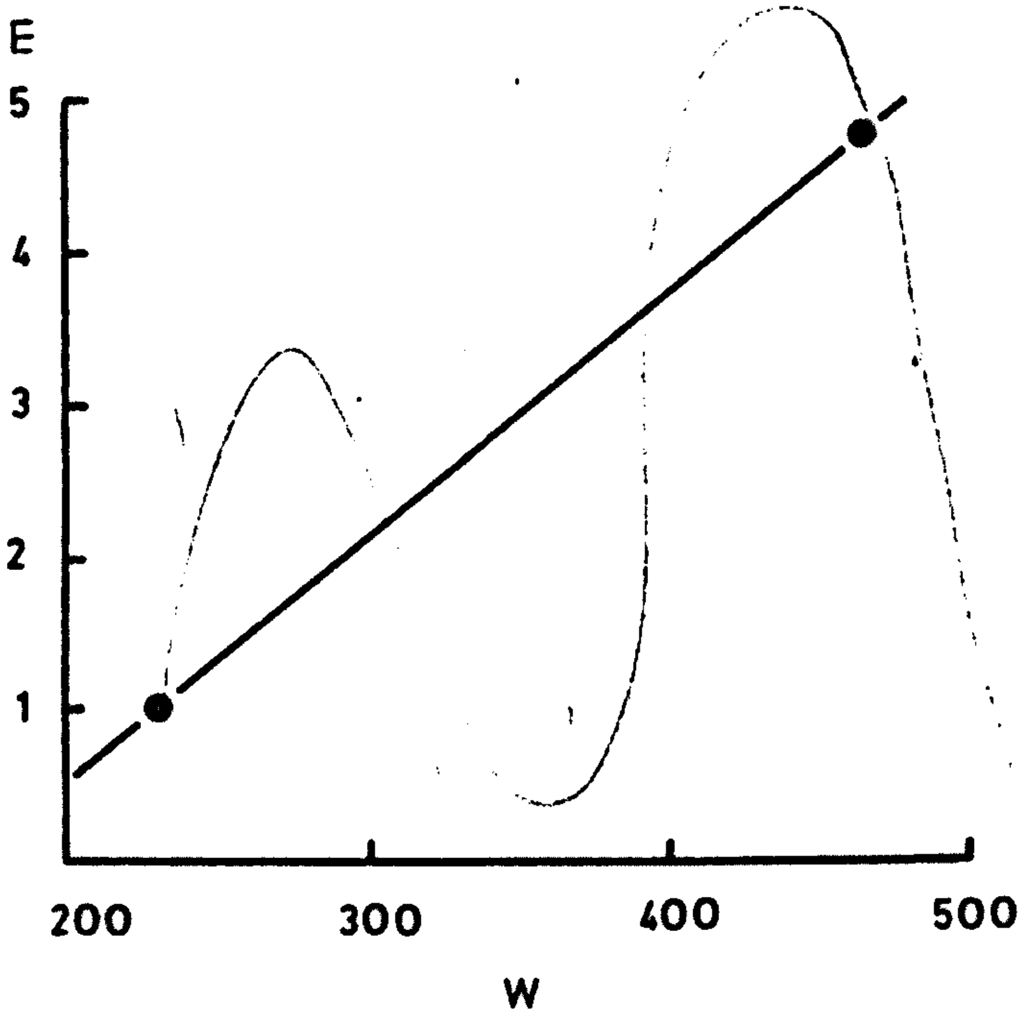


Fig. 32. The relationship between weight of oviparae (W, $\mu$g) and the number of eggs laid by each (E).

Multiplying this by the number of newly-moulted oviparae gives the total number of eggs laid each day, which is added to the current egg population.

### The data

Brown (1975) gave figures for the numbers of oviparae produced in 6 populations reared in an insectary and the numbers of eggs laid on the 6 trees. These fell into two groups corresponding to the two initial population densities employed. The ratios of mean eggs laid/mean oviparae produced for the two groups relate to the mean weights of oviparae in those groups (Fig. 32) and a linear relationship is assumed between the points. The number of eggs laid by each ovipara of the heavier group is approximately 80% of its total egg complement, using Brown's (1975) results from dissections of oviparae of similar weight. Very little more is known about ovipara behaviour and it may be that even less of the potential egg complement is laid in the field. Infertility of eggs is treated along with winter mortality in the model (p. 86) and an average value is assumed for the combined effect. It is interesting to note, in this context, that the sex ratio varies widely throughout the season and that there are up to 7 times as many oviparae as males during August and September.

## *3.5.6 Parthenogenetic reproduction*

### The model (subroutine REPROD)

This submodel computes recruitment to the first nymphal age-class, assigns an initial weight to the nymphs and updates the state of maturity of adults.

The pattern of reproduction by viviparous adults involves a pre-reproductive delay following the moult, an initial constant reproductive rate, and a decline in reproductive rate with increasing age. The pre-reproductive delay and the initial rate of reproduction depend on adult weight and temperature (Figs 33 and 34) thus:

$$D = \frac{1652000}{(W-100)T^{2.68}}$$

$$R = \frac{WT^{1.5}}{14817}$$

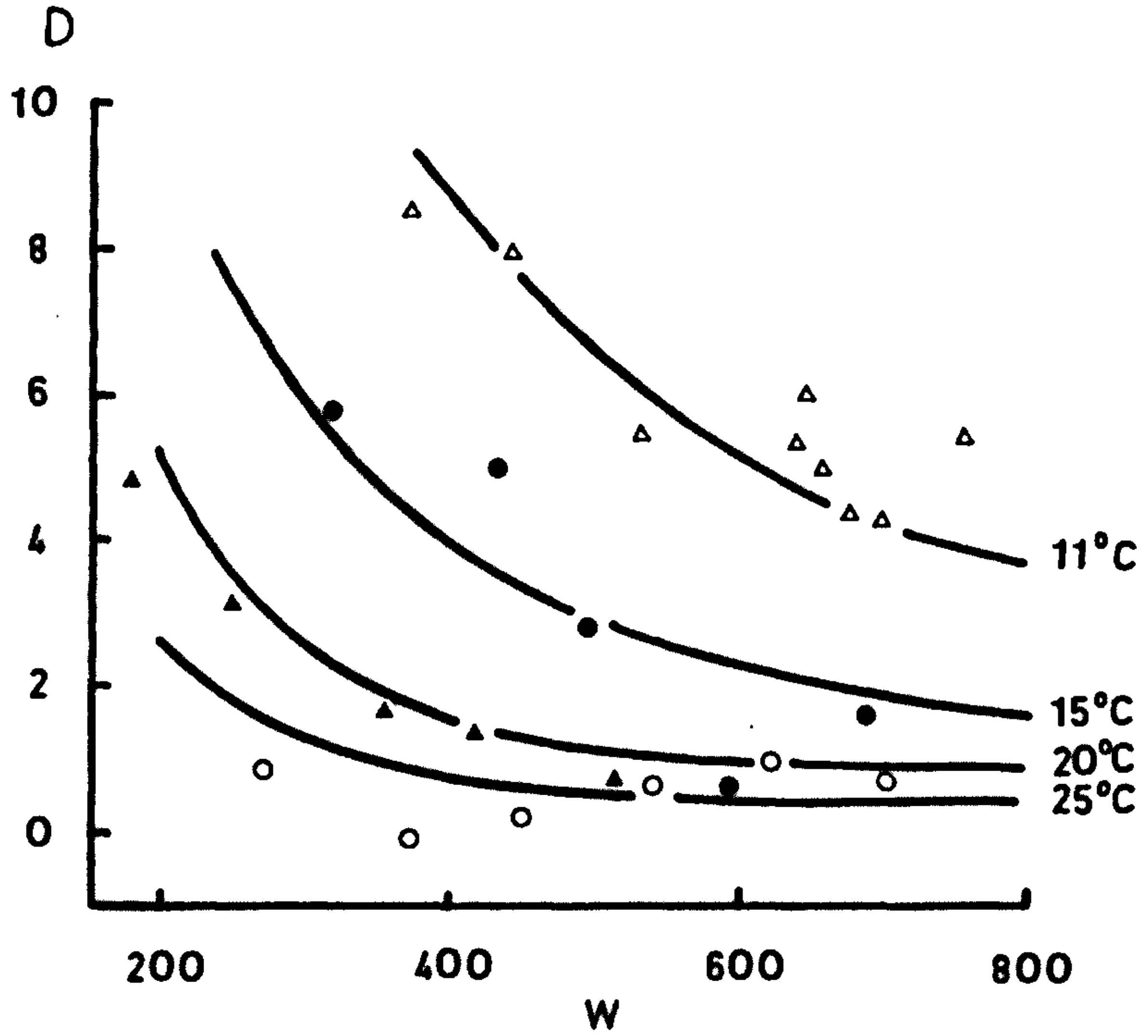


Fig. 33. The effect of temperature and adult weight (W, $\mu$g) on the pre-reproductive delay (D, days). △ 11°C, ● 15°C, ▲ 20°C, ○ 25°C.

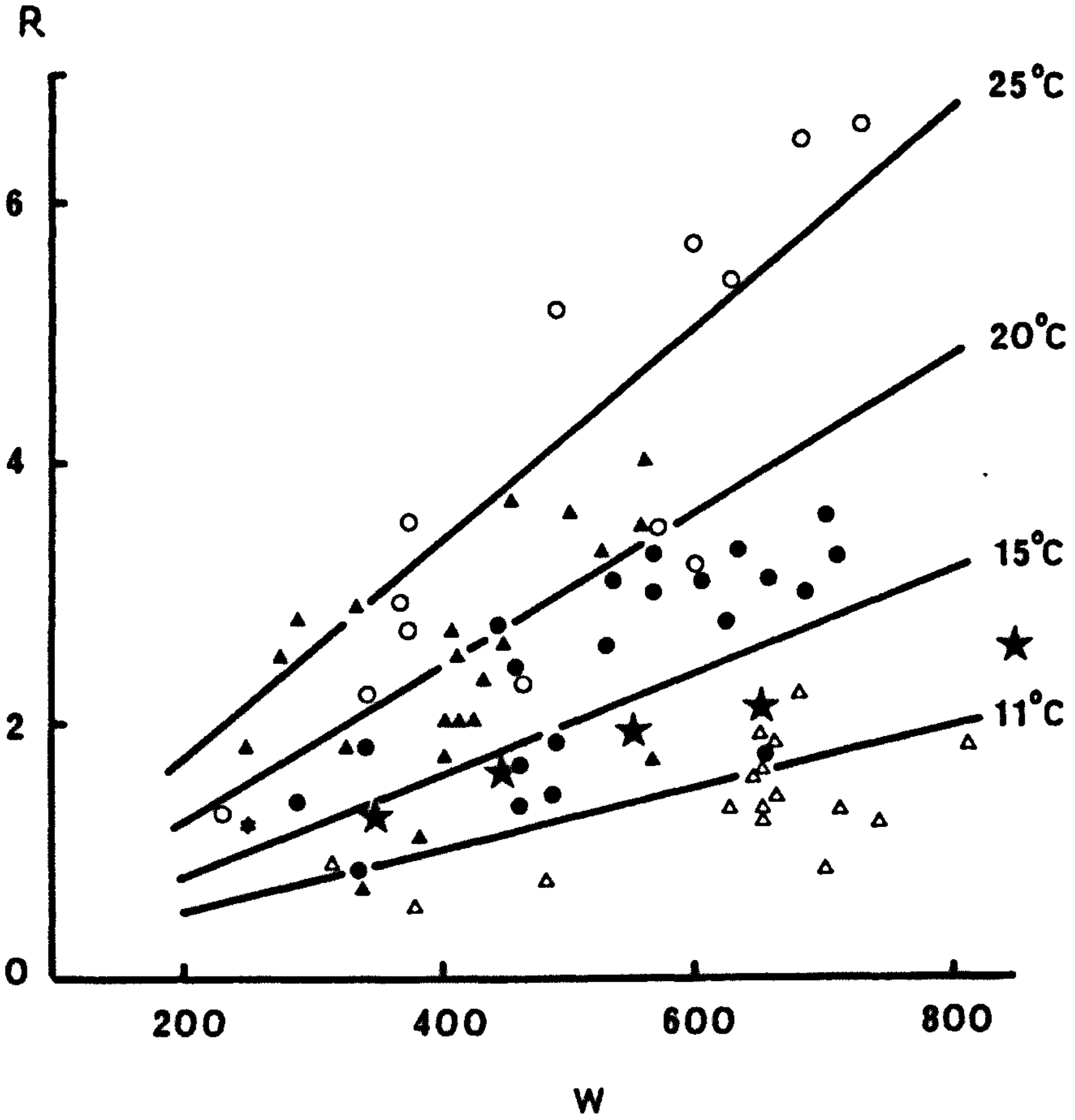


Fig. 34. The effect of temperature and adult weight on reproductive rate (nymphs/adult/day). △ 11°C, ● 15°C, ▲ 20°C, ○ 25°C, ★ points from field taken over all temperatures.

where

$D$ = pre-reproductive delay in days
$R$ = nymphs produced per adult per day
$W$ = adult weight ($\mu$g)
$T$ = actual (corrected) temperature (°C)

The decline in reproductive rate depends on the accumulated temperature experience of the adult since the start of reproduction (Fig. 35):

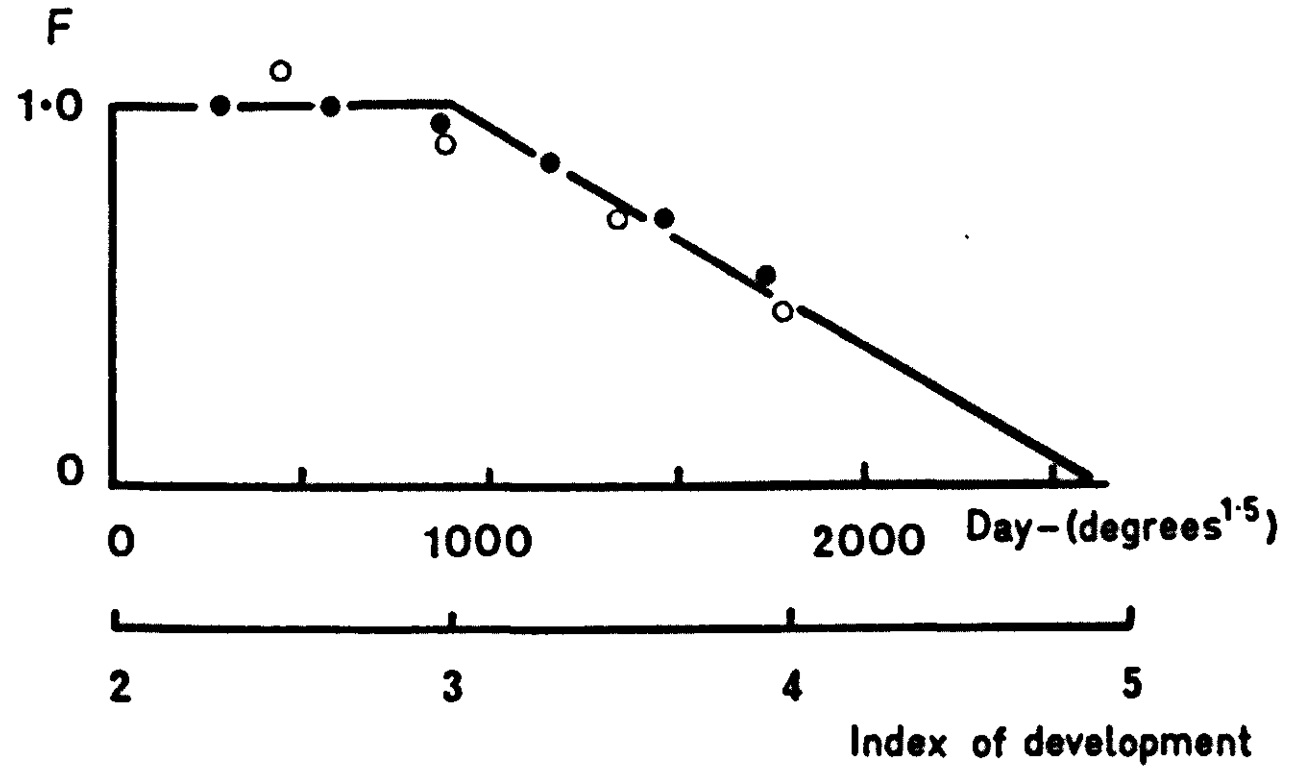


Fig. 35. The factor (F) modifying reproductive rate according to adult age, expressed as accumulated temperature experienced ($\Sigma$(mean daily temperature)$^{1.5}$) or an index of development achieved since the start of reproduction, and based on experiments at 20°C (○) and 15°C (●).

$$RF = 2.578 - 0.526ID \qquad 0 \leqslant RF \leqslant 1$$

where

$RF$ = factor multiplying reproductive rate
$ID$ = temperature experience or index of development (see below)

New-born nymphs are assigned an initial weight depending on that of the parents, assumed to be the average weight of viviparae present at the time, thus (Fig. 36):

$$Wo = 24 - 24.8e^{-0.0077W}$$

where

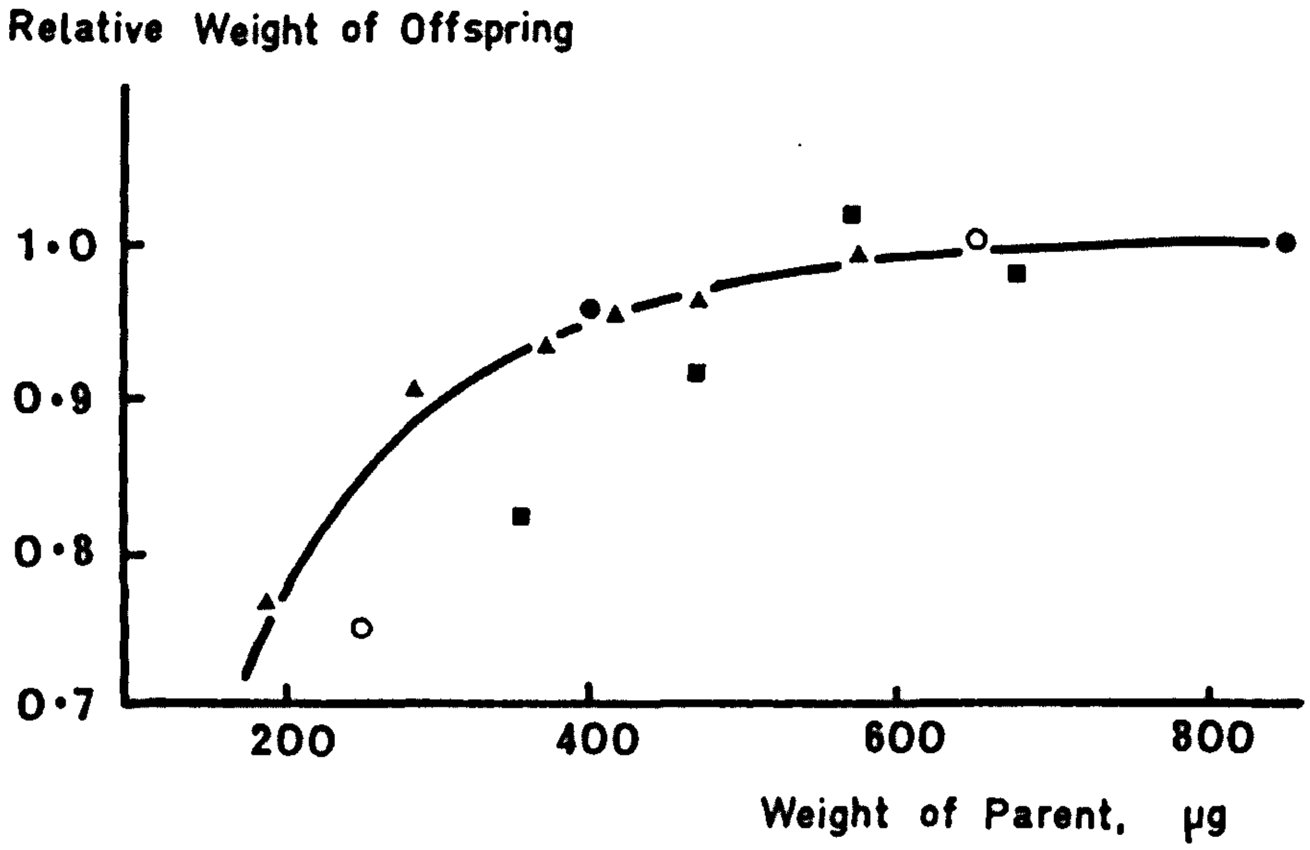


Fig. 36. The relationship between parent weight and relative weights of offspring, at birth (●, ○, ■) and at maturity (▲). Relative weights are actual weights divided by the maximum for each experiment (see text and Table 14).

$Wo$ = weight of nymphs at birth (μg)
$W$ = weight of parents (μg)

These features of reproduction are simulated in the following way. First, each age-class has associated with it an index of accumulated development similar to those of nymphal classes but in this case controlling reproduction. Values between 1 and 2 correspond to the pre-reproductive period, those between 2 and 3 to the period of initial high reproductive rate ($R$) and values greater than 3 to the period of gradually waning reproductive output.

The submodel computes recruitment to the first nymphal age-class from each adult age-class in turn depending on its index of development. If this is between 1 and 2, the basic reproductive rate $R$ is reduced by a factor $RD$ and the index incremented by the reciprocal of the calculated pre-reproductive delay given the weight of the age class and the corrected mean temperature. $RD$ is calculated as:

$$RD = 1 + \frac{ID-2}{I}; \quad 0 \leqslant RD \leqslant 1$$

where

$ID$ = index of development already achieved
$I$ = increment for the current day

allowing account to be taken of delays involving fractions of days. If the calculated pre-reproductive delay is a constant 2.8 days, for example, the reproductive rate is set by the model to zero on the first two days and 0.2 times the maximum on the third. The development index is re-set to 2 when it first exceeds this value. If the development index is 2 or more the daily increment is now a function of temperature alone, given by:

$$0.0011\,(\textit{corrected mean temperature})^{1.5}$$

If it exceeds 3 the reproductive rate is reduced by the factor RF given above. Total reproduction by the age-class is then calculated as the product of the corrected reproductive rate and the number of viviparae in the class plus half the mortality from that class.

Though it is not explicitly used in the model it is worth noting that the above relationships imply a total potential fecundity for any adult independent of temperature and equal to 0.12 times its teneral weight.

## The data

The data come from two sources, laboratory experiments and measurements in the field. Fourth instar-aphids were clip-caged on 20 cm high lime seedlings (*Tilia cordata*) in constant-temperature cabinets and under natural daylengths at 11°C and 20°C. Once adults had moulted the nymphs produced were removed and counted daily for 10 days after the start of reproduction, when the adults were weighed. The results were combined with those of Dixon (1971) and Brown (1975), carried out at 15°C and 20°C, respectively, to give the expressions for pre-reproductive delay and initial reproductive rate. Ad hoc methods were used initially to fit these expressions, then as a check the actual values were regressed on the estimates. Correlation coefficients were highly significant (for reproductive rate $r = 0.83$, d.f. $= 71$, $P < 0.01$; for pre-reproductive delay $r = 0.89$, d.f. $= 20$, $P < 0.01$), while slopes and intercepts were not significantly different from 1 and 0, respectively.

The effect of parental age on reproductive rate was obtained from Dixon's (1972) experiments on morph-determination. These yielded the numbers of nymphs produced at intervals during the lives of adult viviparae, at constant temperatures of 15°C and 20°C. Pre-reproductive delays were estimated by back-extrapolation of the curves of cumulative offspring production, and the mean numbers of nymphs produced per day of reproductive life were expressed as proportions of the initial reproductive rate, over the first 10 days of reproductive life. The rates of decline in relative reproductive rates appeared to be the same for rates initially high and for those initially low, hence, presumably, for large and for small adults. When the grouped results are graphed on a scale of accumulated temperatures the 15°C and 20°C figures approximately coincide (Fig. 35). The same temperature transformation was used as that involved in the reproductive rate, namely $(\text{temperature})^{1.5}$, scaled so that values of 2 to 3 correspond to the period of constant reproductive rate. The straight line relating decline in reproductive rate to values greater than 3 was fitted by eye.

The potential total fecundity of any adult is calculated as:

$$\sum R = \frac{W}{14817} \sum FT^{1.5}$$

where summation is over all days of the adult's reproductive life, $R$ is the reproductive rate, $W$ the weight, $T$ the temperature and $F$ the correction factor for accumulated temperature experience. $\sum FT^{1.5}$ is the area under the line in Fig. 35, equal to 1750 on the $(\text{day-degree})^{1.5}$ scale, which gives the value for $\sum R$ of $0.12W$.

The above estimates of reproductive rate from the laboratory were then compared with those from the field. Daily reproductive rates of weighed, clip-caged adults have been recorded in the field throughout each season from 1969 to 1973, each adult being caged for a 5-day period. Random number tables were used to select a single day's record for each adult, but zero reproductive rates were ignored unless the adult had produced nymphs on any previous day. Pre-reproductive delay was thus excluded from the estimates. The data were grouped and the relationship between reproductive rate and adult weight is indicated by the stars in Fig. 34. The overall mean corrected temperature in the field was 15°C so it appears that the reproductive rate in the field is slightly less than that in the laboratory at a similar temperature. Probably the rates in the field are lower because the field estimates include the effects of age or accumulated temperature experience which lower the reproductive rate, or because of stressing effects of wind and rain. However, regression analysis indicated an effect of temperature on the reproductive rate of these clip-caged adults but no effect of wind or rain.

Wind and rain could well affect adults exposed on the leaves, however.

The derivation of the relationship between offspring weight and parent weight is discussed in Section 3.5.8.

### *3.5.7 Morph determination*

The model (in subroutine REPROD)

The three morphs of the lime aphid are viviparae and the sexual males and oviparae. Their proportions among new-born nymphs are related to the time of year as shown in Fig. 37. The proportions on any particular day are calculated in the model by linear interpolation and the nymphs produced that day assigned to the appropriate subclasses of the first nymphal age-class (Fig. 13).

The data

The data come from Dixon's (1972) laboratory experiments.

Male production

Fig. 37 gives the average proportions of males produced at different times of year by parents less than 20 days old as adults; the results are from two experiments, one at approximately 15°C under natural daylengths, the other at 15°C under a 17-hour daylength. In both experiments the trends in male production with time of year are similar and probably due to the operation of an 'interval timer' (Lees, 1966).

At a finer level of resolution, male-production is also affected by the age of the parent and to a lesser extent by temperature and daylength, which are not included in the present submodel because of uncertainties about their action. The effect of parental age is illustrated in Fig. 38 which gives results for generations 3, 4 and 5 combined under natural daylengths. Males are produced during the middle of a parent's reproductive life and their appearance is as closely related to time since the moult as to time since the start of reproduction or to the cumulative number of offspring produced, judged by a comparison of standardized variances of these quantities between individuals. However, including the effect in the model gave fewer males than actually observed in the field, presumably because of losses, mainly by flight, over the period of the

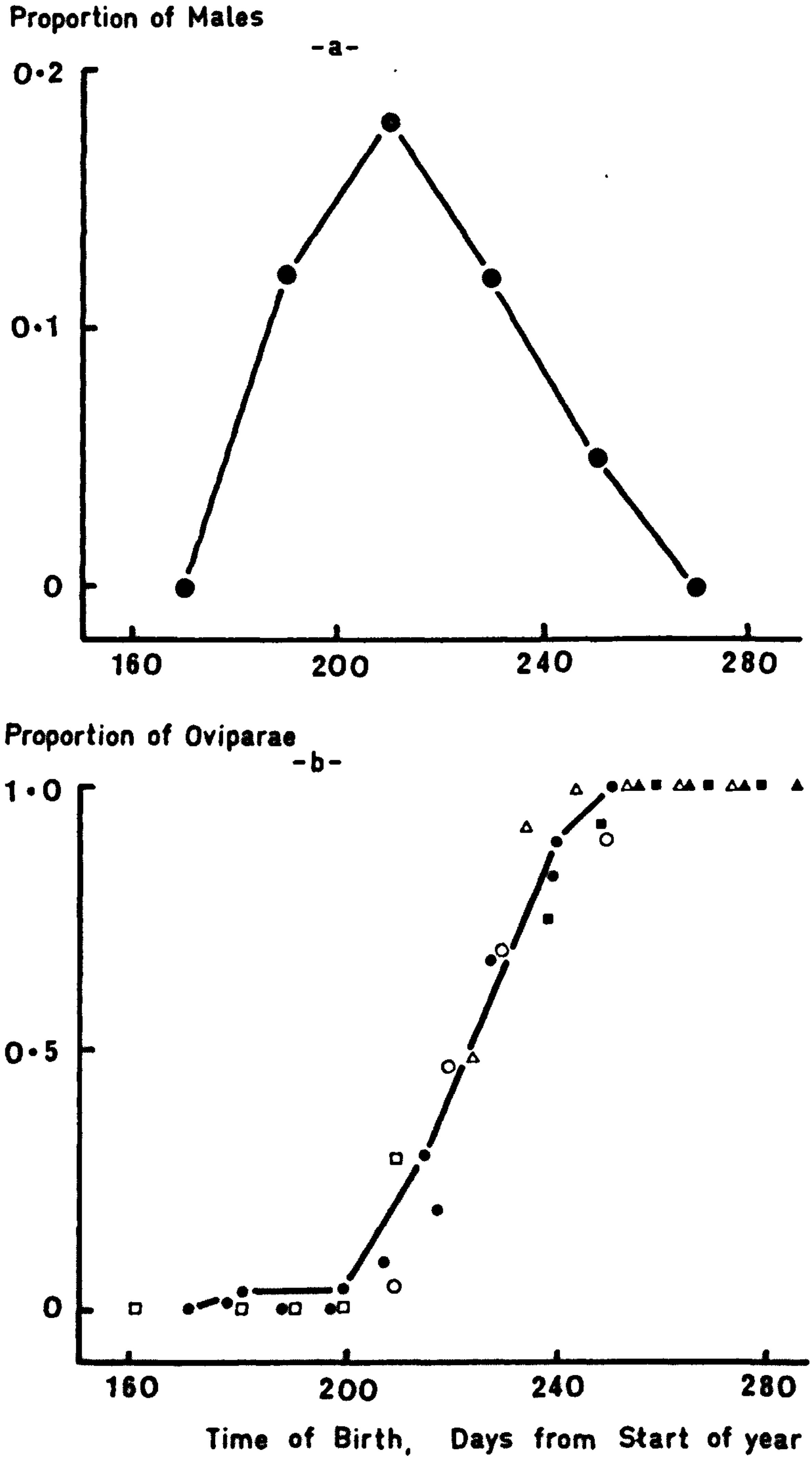


Fig. 37. a) Effect of time of year on the proportion of offspring which are males, averaged over generations 3 to 5. b) Effect of time of year on the proportion of female offspring which are oviparae, under natural daylength. □ generation 2, ● generation 3, ○ generation 4, △ generation 5, ■ generation 6, ▲ generation 7.

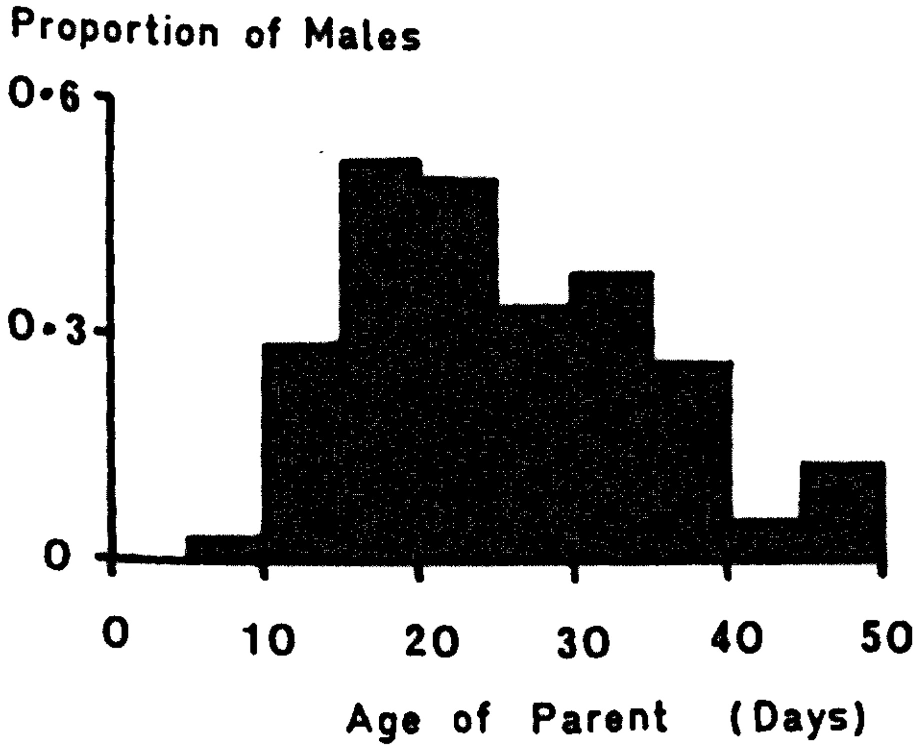


Fig. 38. Effect on male production of age of the parent as an adult, under natural daylengths and taken over generations 3–5.

parent's life before male-production begins. A possible explanation for the anomaly might lie in the strong suggestion of a clonal effect in Dixon's experiments. Fig. 39 shows the distribution among clones

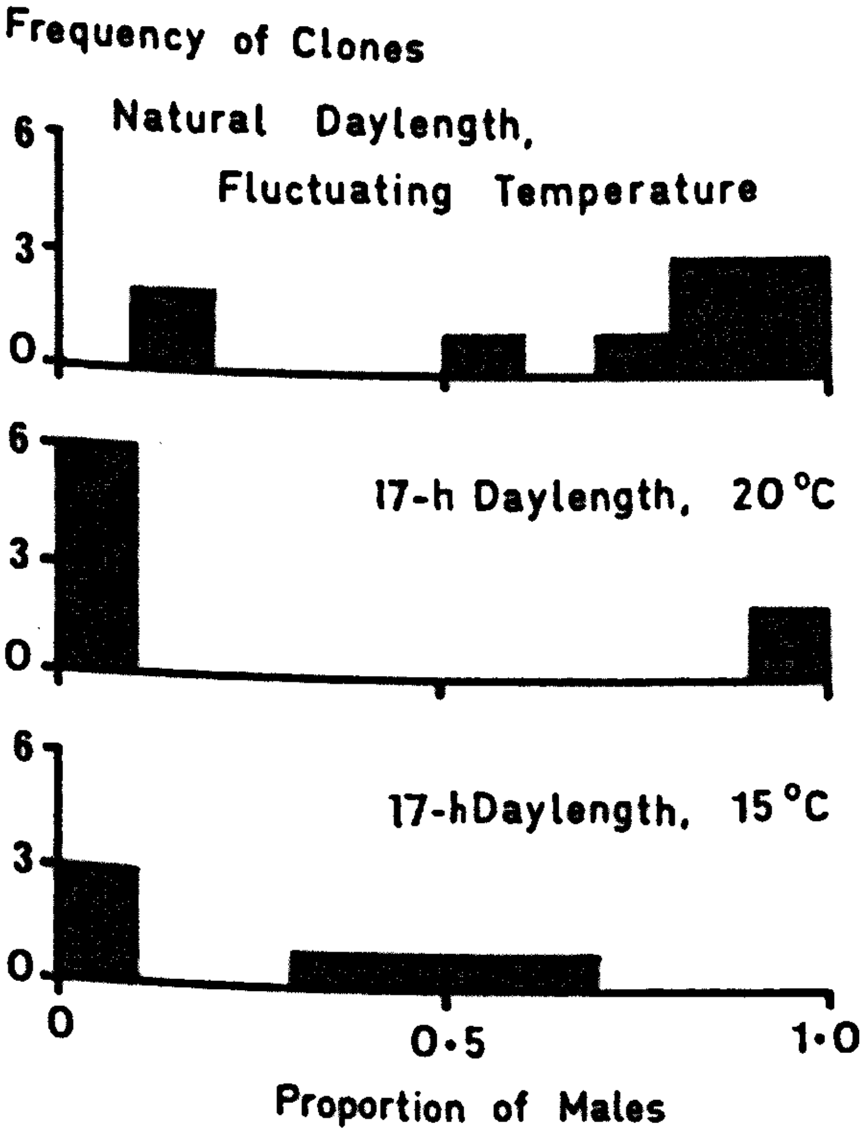


Fig. 39. Clonal variability in the production of males. Proportions of males are the maximum in any generation for each clone, among offspring produced by parents aged 10–40 days from the adult moult.

of the maximum proportions of males produced in any generation, for parents aged between 10 and 40 days as adults. Perhaps viviparae from clones which tend to produce many males fly less readily than those from clones which produce few. An effect of temperature on male-production is indicated by the fact that a greater proportion of offspring were males at 20°C than at 15°C, taken over all generations and from the same clone reared under a 17-hour daylength in both cases (0.74 and 0.30, respectively; $\chi^2 = 62.2$, d.f. = 1, $P < 0.01$) At the higher temperature males also tend to appear sooner in the parent's reproductive life. As regards daylength, long photoperiods do not inhibit male-production but short ones appear to do so (Dixon, 1972).

### Ovipara production

The points in Fig. 37 are for 11 clones reared under natural daylengths. The proportions of oviparae produced relate well either to daylength or to the time of birth, and neither parental age nor generation number need be considered in addition; high temperatures have an inhibiting effect (Dixon, 1972) but this is insignificant in the present context. Results from rearing clones under 8-hour and 17-hour daylengths at 15°C (Fig. 40a) indicate that ovipara production actually depends on an interaction between daylength and time, probably of the form shown in Fig. 40b. If the stimulus (short daylength) is weak the effect is still felt but the response takes longer, a situation partly resembling dependence of egg-hatching or nymphal development on temperature and time but with the important difference that the time dependence of sexual production spans several generations. A more detailed submodel of ovipara production might therefore relate ovipara production to a time-photoperiod scale, with largest increments for shortest photoperiods. However, daylength is linearly related to the time of year in the range over which it acts and for the given latitude, about 54°N, so in the present submodel ovipara-production is simply related to the time of year and the effect of daylength implicitly rather than explicitly included.

## *3.5.8 Growth and development*

### The model (subroutine GROWTH)

This submodel simulates growth in size and physiological maturation of nymphs, the two being considered as related but distinct

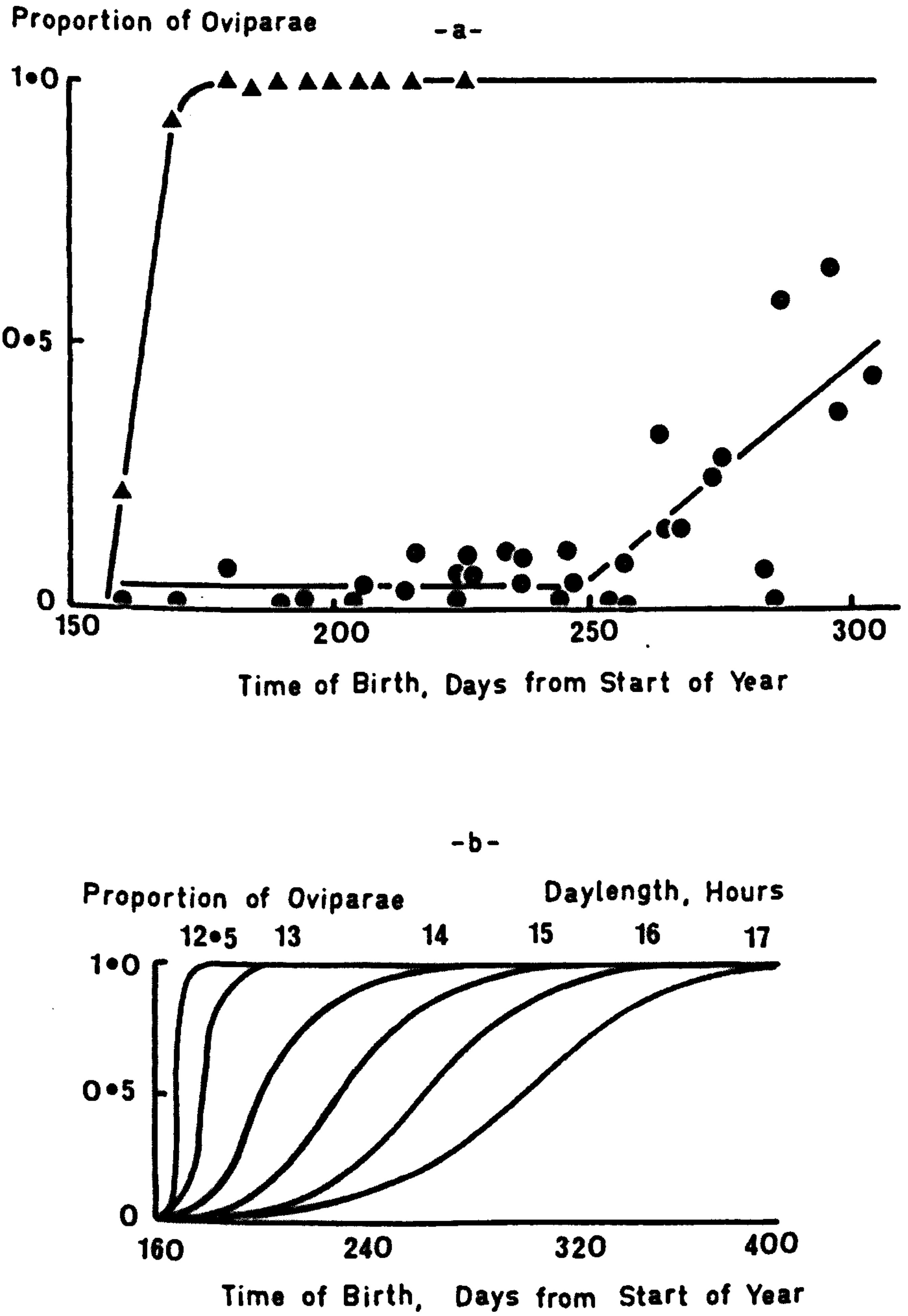


Fig. 40. a) Relationship between ovipara production (proportion of female offspring which are oviparae) and time of birth at two constant daylengths, 8 h (▲) and 17 h (●). b) The supposed functional relationship between the proportion of female offspring which are oviparae, the time of year and daylength.

processes. Exponential growth is assumed and each day the weight of every nymphal age-class is multiplied by a growth factor. At the same time, the proportion of development achieved by the age-class is incremented by the development rate, equal to the reciprocal of the calculated development time given the conditions that day. The adult moult occurs when the proportion of development achieved reaches 1, while values between 0 and 1 determine the instar of the age-class according to Table 7. The resulting weight of the adults is therefore a function of the initial weight at birth, the growth rate and the development time.

### Development

The development rate of nymphs depends on temperature and plant quality (Fig. 41). It is calculated each day as:

$$DV=(DX+DN+DM)/3$$

where

$DX$ = development rate at the maximum corrected temperature
$DN$ = development rate at the minimum corrected temperature
$DM$ = development rate at the mean corrected temperature

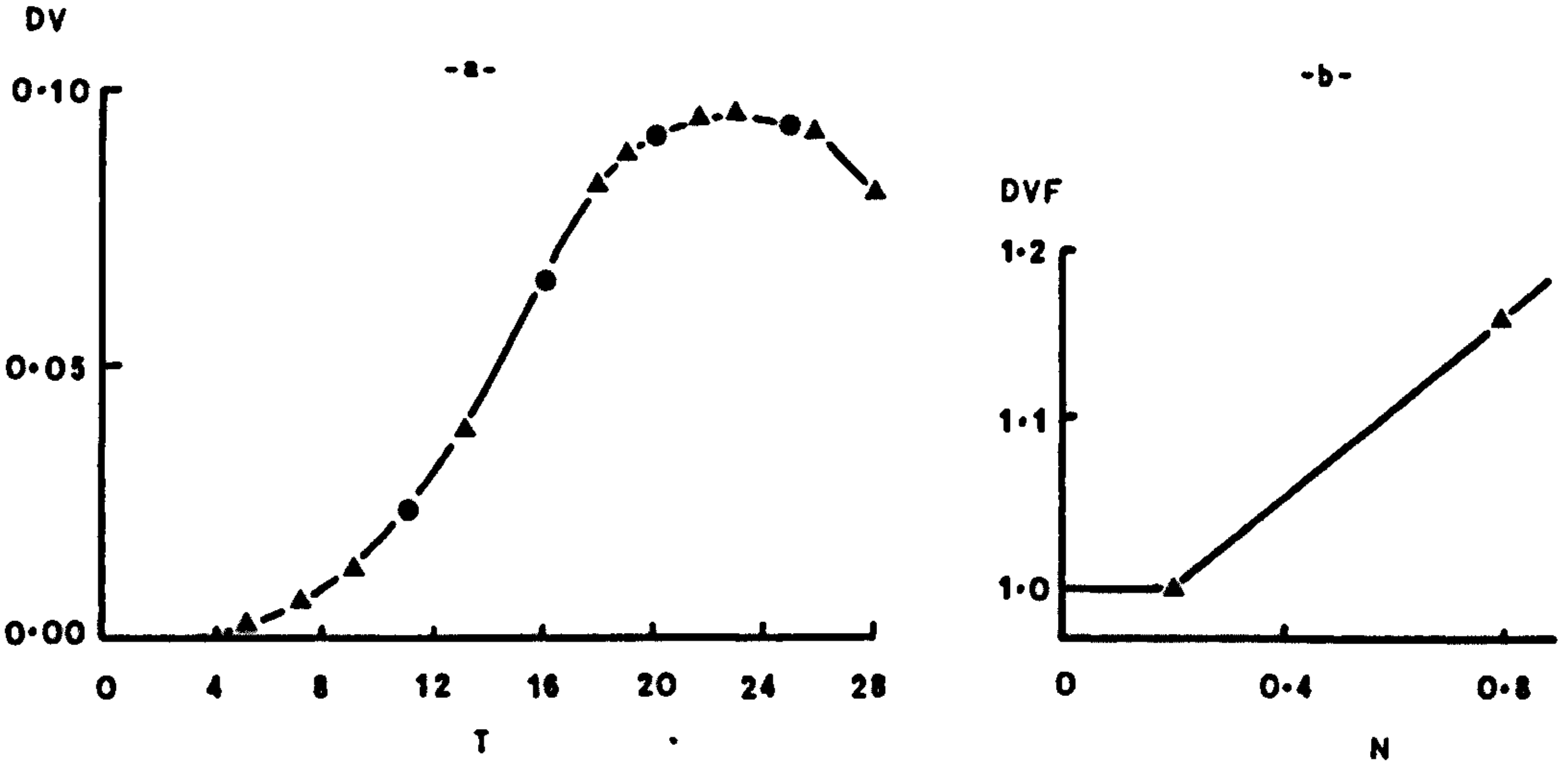


Fig. 41. a) Effect of temperature (T, °C) on development rate (DV, proportion of nymphal development achieved per day) ● experimental points, ▲ points used in linear interpolation. b) The factor (DVF) modifying development rate according to the amino-nitrogen concentration in the phloem (N, % dry weight).

and the rates are obtained by linear interpolation from Fig. 41a. The daily development rate, $DV$, is then multiplied by the plant quality factor, $DVF$, given by:

$$DVF = 1 + 0.27(N - 0.2): \quad DVF \geqslant 1$$

where

$N$ = soluble amino-nitrogen concentration in the leaves (%)

## Growth

The growth factor for each day is related in the model to density, cumulative density (aphid-weeks), temperature, plant quality and the calculated development rate, thus (Fig. 42):

$$LR = 1.5373 - 0.00064C - 0.00174D - 0.00809T + 0.24(N - 0.2)$$

where

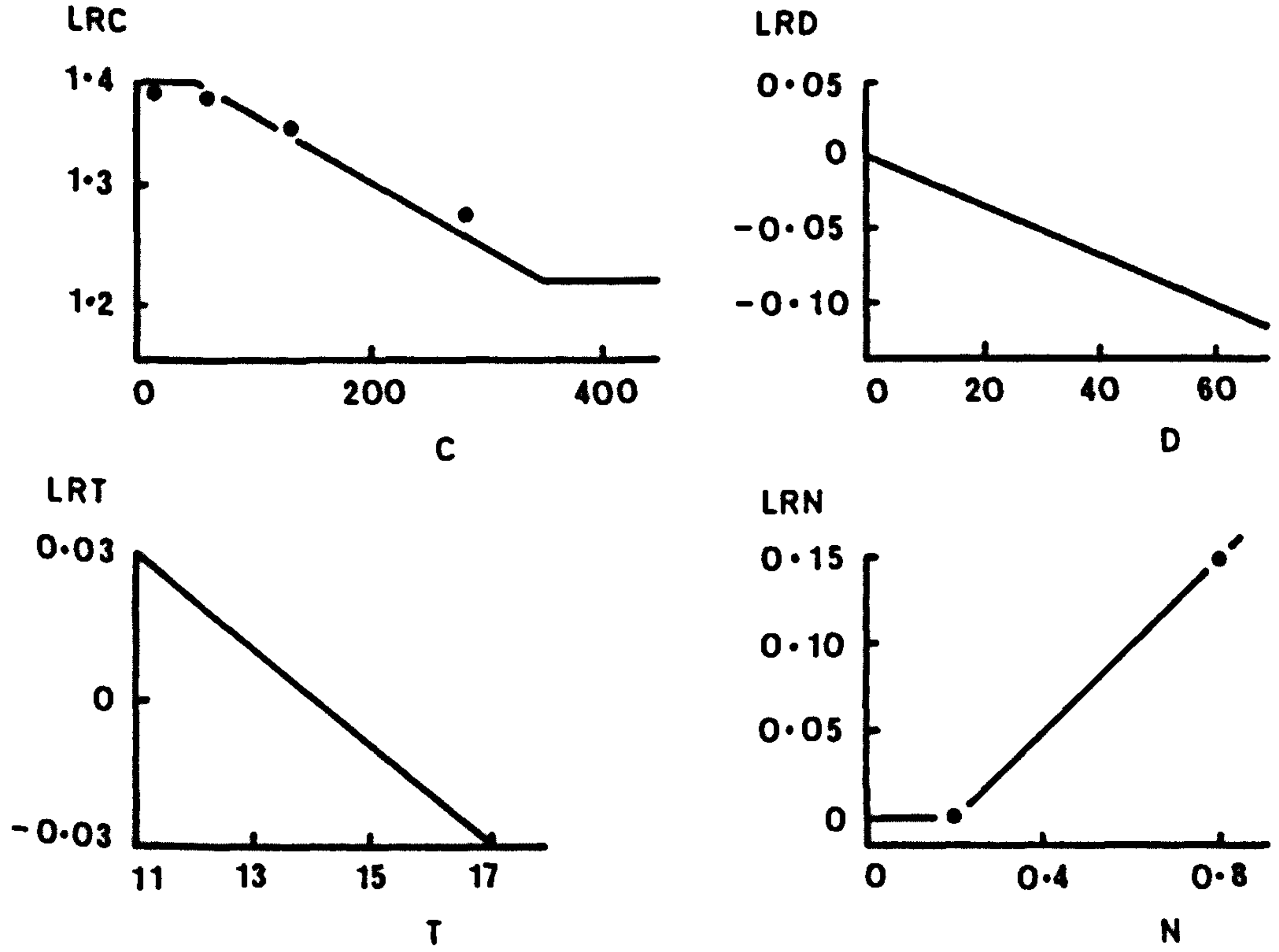


Fig. 42. The components of aphid growth: a) the effect of cumulative density (aphid weeks 100 cm$^{-2}$) on log (adult weight/birth weight) (LRC); b) the additional effect (LRD) of density (D, numbers 100 cm$^{-2}$); c) the additional effect (LRT) of mean temperature (T, °C); and d) the additional effect (LRN) of amino-nitrogen concentration (N, % dry weight).

$LR$ = log (weight at the adult moult/weight at birth)
$C$ = cumulative density (aphid-weeks/100 cm$^2$) within the range 50–350
$D$ = density (aphids/100 cm$^2$)
$T$ = mean daily shade temperature (°C)
$N$ = soluble amino-nitrogen concentration in the leaves (%)

and

$$GF = 10^{LR \times DV}$$

where

$GF$ = factor by which weights are multiplied each day
$DV$ = calculated development rate that day

## The data for development

To obtain the relationship between development rate and temperature aphids were reared at 11°C, 16°C, 20°C and 25°C under a 17-hour daylength in climatic cabinets. They were clip-caged on 20 cm-high lime seedlings (*Tilia cordata*) and inspected daily, giving development times (Table 8) and approximate times spent in the various instars at the 4 temperatures; instar lengths were then converted into proportions of total development achieved (Table 7).

Table 7. Proportions of development (P) and cumulative proportions of development (C) achieved during the various instars.

| instar | P | C |
|---|---|---|
| 1 | 0.230 | 0.230 |
| 2 | 0.300 | 0.530 |
| 3 | 0.155 | 0.685 |
| 4 | 0.315 | 1.000 |

When aphids were reared isolated and crowded at 10 per clip-cage, the crowded ones took no longer to develop than the isolated ones (Table 9, $P > 0.05$). However, when reared on growing tissue aphids took 14% less time to develop than those reared on mature tissue (Table 10, $P < 0.01$). The quantitative relationship between development rate and plant quality was based on an increase of 16% in the rate for an increase in soluble nitrogen concentration

Table 8. Aphid development times at constant temperatures on mature tissue.

| Temperature (°C) | mean devt time (days) |
|---|---|
| 11 | 42.9 |
| 16 | 15.3 |
| 20 | 11.0 |
| 25 | 10.7 |

Table 9. Mean development times for aphids reared, crowded or isolated, at 2 temperatures on mature tissue.

| temperature | development time (days) | |
|---|---|---|
| (°C) | isolated | crowded |
| 15 | 20.2 | 21.21 |
| 20 | 11.0 | 11.23 |

Table 10. Mean development times for aphids reared on mature and growing tissue at 12°C.

| development time (days) on | |
|---|---|
| mature tissue | growing tissue |
| 36.0 | 30.4 |

from 0.2% to 0.8%, where 0.8% is the greatest mean value likely to be experienced by an aphid over the course of its development in spring and 0.2% is the average level for summer and autumn (see Fig. 18).

Development times predicted by laboratory experiments were then compared with those in the field. Table 11 shows development times and overall mean temperatures measured on a tree at Glasgow in 1974, and the development times and corrected mean temperatures quoted by Llewellyn for the field in 1967. The results differ very little from those predicted by the laboratory experiments,

Table 11. Aphid development times in the field.

| mean temperature °C. | development time (days). | source | |
|---|---|---|---|
| 14.6 | 20.0 | June | corrected field temperatures, 1967, from Llewellyn (1970). |
| 15.5 | 17.5 | July | |
| 15.8 | 16.0 | Aug | |
| 15.0 | 19.1 | Glasgow Univ. tree | |
| 15.1 | 20.5 | Glasshouse | |

any discrepancies due to temperature fluctuations being relatively insignificant in the region of 15°C as shown in Fig. 43.

Although not included in the present submodel there is clearly a distribution associated with mean development times and development rates. Measured in the laboratory, development rates are normally distributed with mean 1.0 and standard deviation 0.117 ($\chi^2 = 9.95$, d.f. $= 8$, $P > 0.25$, comparing frequencies of rates lying

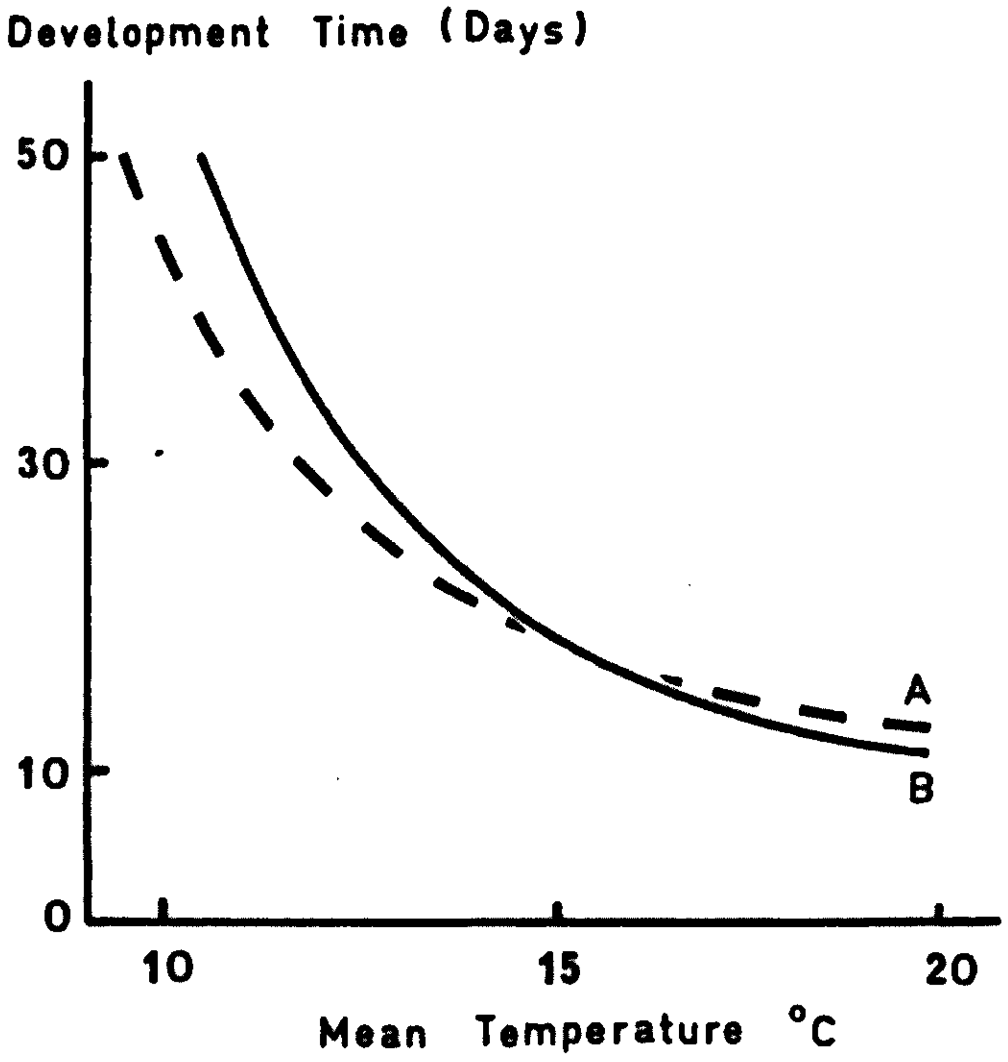


Fig. 43. Comparison of relationships between development time and mean temperature when the temperature is constant (observed, Line B) and fluctuating with an amplitude of ±5°C (generated by the model, Line A).

within given intervals with those expected from a normal distribution).

## The algorithm for predicting development rates

Perhaps the most widely used algorithm in insect simulation models involves a physiological time scale based on accumulated day-degrees above a threshold (Hughes, 1962; Gilbert et al., 1976). However, this algorithm assumes a linear relationship between development rate and temperature and in many cases ignores effects of fluctuating temperatures within each day. Watt (1968) and Howe (1967) discussed the effects of fluctuating temperatures on rates of activity and development. If the rates are related to temperature non-linearly then integrating or summing them over the range of fluctuating temperatures experienced gives a total increment less than or greater than that for a constant mean temperature, depending on whether the rate curve is convex or concave. There appears to be no convincing evidence for any additional physiological effects of temperature fluctuations on development rates of aphids, with the possible exception of Messenger's (1964) study on development rates of the aphid *Therioaphis maculata* Buckton. He quoted a discrepancy at low temperatures between observed development times and those calculated by hourly summation using a relationship based on a rather puzzling extrapolation (Messenger's Table 5), and it is possible that development rates at low temperatures are underestimated. If so, such underestimates could account for the discrepancy since calculated development times are extremely sensitive to additive errors in their reciprocals (the rates) when the latter are small.

At medium or low temperatures, therefore, development under alternating temperatures will be at least as rapid as implied by hourly summation. The question then is how significant are temperature fluctuations in the case of the lime aphid, and what is the appropriate algorithm?

A non-linear curve of development rate with temperature was assumed in the first instance. It is clearly so at high temperatures, and Chambers' (1979) results for the sycamore aphid suggest that this is also the case at low temperatures. A simple simulation was then carried out to compare several possible algorithms on the basis of their predicted development times over a range of constant and alternating temperatures. In each case the assumed standard was the development time predicted by hourly summation, given a sine curve of temperatures fitted to the maximum and minimum each day, and the relationship between development rate and constant temperatures shown in Fig. 41a. The algorithms are as follows:

1. Summation of daily development increments based on the mean temperatures. This takes no account of temperature fluctuations during each day.
2. Summation of integrated daily development using maximum and minimum temperatures and the trapezoidal integration rule, to give

$$DV = (D_{TX} + D_{TN} + 2D_{TM})/4$$

where

$DV$ = proportion of development achieved daily
$D_{TX}$ = development rate (proportion achieved daily) at the maximum temperature
$D_{TN}$ = development rate at the minimum temperature
$D_{TM}$ = development rate at the mean temperature

The method assumes a symmetrical curve of temperatures between the 24-hour maximum and minimum each day. Development rate then varies throughout the day as illustrated in Fig. 44 and the daily increment is obtained by integrating the rate. In this case the integral is approximated by the trapezoidal rule with the day divided into 4 equal parts, giving the above formula for the area under the

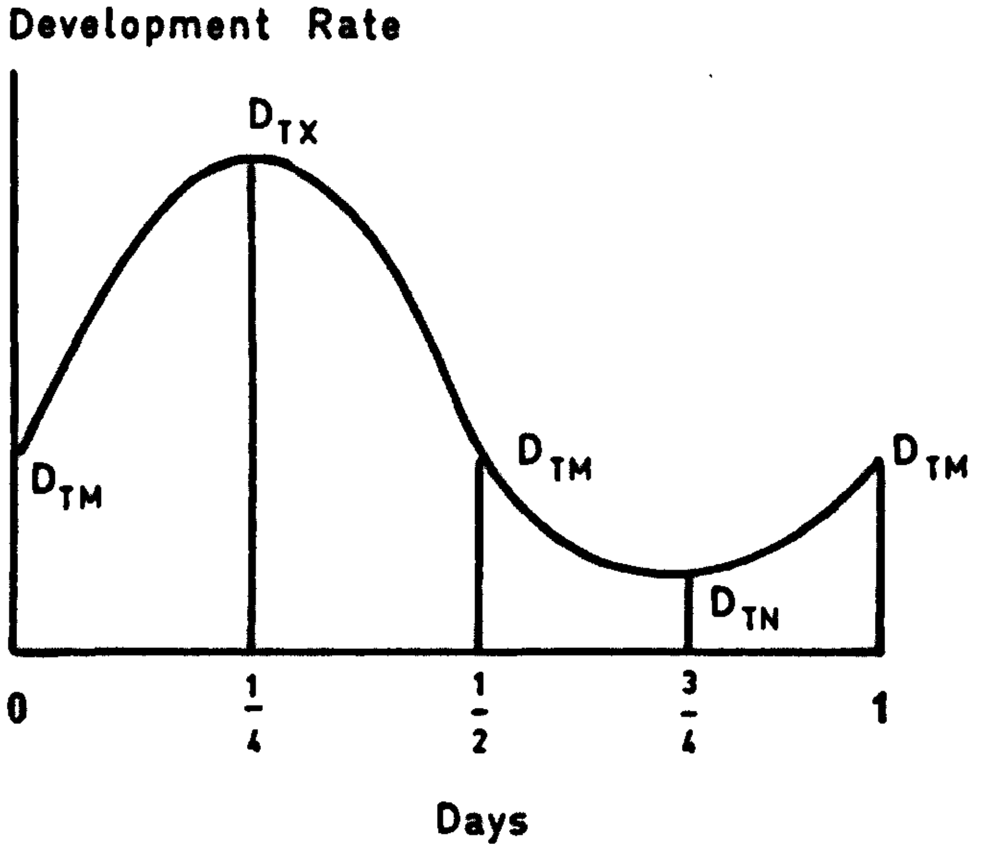


Fig. 44. The assumed sine curve of instantaneous development rates (D) throughout each day, the four points of inflexion corresponding to the maximum (TX), minimum (TN) and mean (TM) daily temperatures.

rate curve and the development achieved per day.

3. Summation of integrated daily development using maximum and minimum temperatures and Simpson's rule for integration, to give:

$$DV = (D_{TX} + D_{TN} + D_{TM})/3$$

where

$DV$, $D_{TX}$, $D_{TN}$ and $D_{TM}$ are as above.

In most respects the method is the same as the previous one, the only difference being that in calculating the area under the development rate curve, Simpson's rule assumes a curve between each pair of ordinates while the trapezoidal rule assumes a straight line.

4. Hourly summation of proportions of development achieved using maximum and minimum temperatures, the non-linear relationship between development rate and temperature, and a sine curve of temperatures throughout each day. The temperature $T_h$ in hour t is thus:

$$T_h = (TX - TM)\sin(2\pi h/24) + TM$$

where $TX$ and $TM$ are the maximum and mean daily temperatures. The proportion of development achieved per day is the mean of the calculated rates for each of the 24 hours.

The results of these simulations are given in Table 12. Algorithm 1 based only on daily mean temperatures considerably overestimates development time at low alternating temperatures (by 60% for a temperature of 10±5°C).

Development integration using the trapezoidal rule and Simpson's rule both give results very close to those obtained by hourly summation, the trapezoidal rule yielding marginally better agreement than Simpson's rule, but with a slightly more complex formula. The characteristic features, that development at low temperatures is accelerated by temperature fluctuations while at high temperatures the reverse occurs, are well reproduced by both. Moreover, the computing time required for their execution in a large simulation program is clearly less than that for hourly summation. Development integration by Simpson's rule was therefore chosen as an appropriate algorithm for the model.

Given the widespread use of physiological time scales based on day-degree summation, it is interesting to compare the results obtained with those of the methods described above. Day-degree summation implies a linear relationship between development rate ($DV$) and temperature ($T$), given in this case by:

Table 12. Development times (days) predicted by different simulation algorithms for constant and alternating temperatures. The algorithms are: 1) summation of daily proportions of development based on mean temperatures 2) integration of daily development using the trapezoidal rule 3) integration of daily development using Simpson's rule 4) hourly summation of development increments 5) summation of day-degrees using mean temperatures 6) summation of day-degrees using maximum and minimum temperatures and Ives' method. Algorithms 1) to 4) assume a non-linear development rate/temperature relationship, 5) and 6) a linear one. For further explanation see text.

| temperature (°C) | | | algorithm | | | | | |
|---|---|---|---|---|---|---|---|---|
| Mean | Max | Min | 1 | 2 | 3 | 4 | 5 | 6 |
| 10.0 | 10.0 | 10.0 | 56 | 56 | 56 | 56 | 48 | 48 |
| 10.0 | 12.5 | 7.5 | 56 | 52 | 51 | 52 | 48 | 48 |
| 10.0 | 15.0 | 5.0 | 56 | 44 | 41 | 43 | 48 | 45 |
| 10.0 | 20.0 | 0.0 | 56 | 32 | 28 | 30 | 48 | 34 |
| 15.0 | 15.0 | 15.0 | 19 | 19 | 19 | 19 | 18 | 18 |
| 15.0 | 17.5 | 12.5 | 19 | 19 | 19 | 19 | 18 | 18 |
| 15.0 | 20.0 | 10.0 | 19 | 19 | 19 | 19 | 18 | 18 |
| 15.0 | 25.0 | 5.0 | 19 | 20 | 21 | 20 | 18 | 18 |
| 20.0 | 20.0 | 20.0 | 11 | 11 | 11 | 11 | 11 | 11 |
| 20.0 | 22.5 | 17.5 | 11 | 12 | 12 | 12 | 11 | 11 |
| 20.0 | 25.0 | 15.0 | 11 | 13 | 13 | 13 | 11 | 11 |
| 20.0 | 30.0 | 10.0 | 11 | 15 | 16 | 16 | 11 | 11 |
| 25.0 | 25.0 | 25.0 | 11 | 11 | 11 | 11 | 8 | 8 |
| 25.0 | 27.5 | 22.5 | 11 | 12 | 12 | 12 | 8 | 8 |

$$DV = \frac{T-7}{143}$$

and the algorithms are:

5. Summation of day-degrees above 7°C to a total of 143 using daily mean temperatures only.

6. Summation of day-degrees above 7°C to a total of 143, using 24-hour maximum and minimum temperatures and Ives' (1973) triangulation approximation. Each day's increment, $DV$ is now:

$$DV = (Mean - 7) \qquad (7 \leqslant min)$$

$$DV = \frac{(Max - 7)^2}{2(Max - Min)} \qquad (min \leqslant 7 \leqslant max)$$

$$DV = 0 \qquad (max \leqslant 7)$$

Summation of day-degrees in the normal way yields considerably shorter development times at high constant temperatures than implied by the non-linear relationship between development rate and temperature (Table 12). The predicted development time at low constant temperatures is extremely sensitive to the position of the threshold, and there is no reduction in development time under fluctuating temperatures; it is overestimated by 12% for a low temperature with a 5°C amplitude and by 60% if the amplitude increases to 10°C. Ives' method is a clear improvement under low fluctuating temperatures but still underestimates development time at high constant ones. Whether the linear or non-linear relationships are assumed, temperature fluctuations can clearly be significant, especially at low mean temperatures which are nevertheless well within the range experienced by the aphid. Fig. 43 summarizes the effect, showing development times at different constant temperatures and at temperatures fluctuating with a 5°C amplitude, similar to that in the field. There is still a need for experimental data not only for temperatures covering the range of mean values in the field, but for those near the maxima and minima.

### The data for growth

As a first stage in modelling growth, the factors affecting adult weights were determined by laboratory experiments. The growth process is then considered, and the quantitative effects of the above factors on growth assessed by regressions of field data.

### The factors affecting adult weight

Aphids reared clip-caged in groups are smaller than those reared in isolation (Dixon, 1971a) and the effect appears to act through the leaves (Brown, 1975; Kidd, 1975). Recent experiments have shown that not only crowding during development but also conditioning of leaves by previous aphid infestation can cause weight reductions, up to 60% in the latter case.

First generation aphids in the field are up to 50% heavier than those of later generations, but develop on good quality tissue at relatively low temperatures. To assess possible effects of temperature, plant quality and generation number, aphids from the first and second generations were reared at 12°C and 20°C, on mature and growing seedlings (*Tilia cordata*) about 20 cm high. Some of the plants were subjected to room temperatures 6 weeks before the emergence of fundatrices in the field to give mature tissue for first generation rearings. Others were kept at 5°C to provide growing leaves for the second generation.

Mean aphid weights were compared between generations for each of the 4 categories: mature tissue at 20°C; mature tissue at 12°C; growing tissue at 20°C; growing tissue at 12°C. Bartlett's test indicated homogeneity of variance between the mean weights ($P > 0.05$ in all cases), and there was no significant difference between the weights of adults of generation 1 and of generation 2 under any of the above 4 regimes ($P > 0.05$ in all cases). Pooling the generations and considering individual aphid weights, we compared the effects of plant condition and temperature. Weights were significantly higher ($P < 0.001$) on growing tissue than on mature tissue, both at 12°C and at 20°C, and significantly higher ($P < 0.001$) at 12°C than at 20°C both on growing tissue and on mature tissue. The resulting weights are shown in Table 13.

Table 13. Effects of temperature and the state of the leaves of lime saplings on aphid weights achieved in the laboratory (weights in $\mu$g, confidence limits are for $P = 0.01$).

| temperature (°C) | state of leaves | |
|---|---|---|
| | growing | mature |
| 12 | 872±36 | 756±43 |
| 20 | 658±33 | 526±33 |

The conclusion, therefore, is that experience of low temperatures and growing tissue during development significantly increases adult teneral weights in an approximately additive way. Further, the effects are the same for fundatrices and for aphids of the second generation indicating that the high fundatrix weights observed in the field are environmentally, not inherently determined. Therefore they can be modelled in the same way as those of later generations, though this does not imply that fundatrices are similar in all respects, rather that any differences are likely to be more subtle. For instance, small fundatrices reared under crowded conditions on mature tissue, a situation not occurring in the field, reproduced as adults at a rate higher than predicted from the equations based on results from later generations.

Finally, Brown (1975) showed that small parents produce offspring which are also small as adults. A curve was fitted to her data by a non-linear least-squares program, with offspring weight standardized to a maximum of 1 to allow comparison with other experiments under different rearing conditions. The curve is (Fig. 36):

$$A = 1 - 1.0333\,e^{-0.0077P}$$

where

$A$ = relative weight of offspring ($0 \leqslant A \leqslant 1$)
$P$ = actual weight of parent ($\mu$g)

Such a result implies either that the growth rates of offspring are in some way pre-determined by the mother during embryogenesis or that the weight of the mother determines the weight of the nymph at birth, which in turn influences the final weight it achieves as an adult. There is no evidence for the former but a strong indication that the latter may be true since small parents do produce nymphs which are small at birth. Offsping from parents of known weight were weighed in groups of 3 or 4 on a Kahn electric micro-balance, within 24 hours of birth. The results are shown in Table 14 together with some data of Simpson's (unpublished); significance levels refer to weights of groups. The weights are not those at the actual instant of birth, but are treated as birth weights for the purposes of modelling. They were expressed as proportions of the maximum, for each experiment, and are plotted against parent weights in Fig. 36. There is an obvious similarity in the relationships between weight of offspring at birth and parent weight, and weight of offspring when adult and parent weight. However small nymphs become larger adults than would be expected if adult weight were a constant multiple of birth weight. That is, the effect of parent weights on weights of the offspring at birth is greater than on their weights at maturity. It would be reasonable to expect compensation of this kind, given what is known about the regulatory nature of growth (Hubbell, 1971; Calow, 1973). However, it is unlikely that significant errors would result from considering birth weights to be constant proportions of the final weights attained and specific growth rates to be similar for small and large nymphs. Maximum birth weights are

Table 14. Weight ($\mu$g) of offspring within 24 h of birth from parents of different weight

| weight of parent | offspring weight | | | |
|---|---|---|---|---|
| | rel. | actual | | |
| 675 | 0.98 | 23.67 | 24.17 | $P<0.025$ (data from Simpson unpublished)<br>$n=24$ |
| 570 | 1.02 | 24.67 | | |
| 468 | 0.92 | 22.33 | 21.08 | |
| 356 | 0.82 | 19.83 | | |
| 850 | 1.00 | 25.02 | | $P>0.05$<br>$n=15$ groups of 4 |
| 400 | 0.96 | 24.04 | | |
| 650 | 1.00 | 26.70 | | $P<0.01$<br>$n=26$ groups of 3 |
| 250 | 0.75 | 20.01 | | |

assumed to be 24 $\mu$g, and the equation relating birth weights to parent weights corresponding to that for adult weights and parent weights is:

$$B=24-24.8\,e^{-0.0077P}$$

where

$B=$ actual weight of offspring at birth ($\mu$g)
$P=$ actual weight of parent ($\mu$g)

No direct relationship has yet been demonstrated between weights of lime aphids at birth and at maturity but evidence is beginning to emerge for such an effect in *Aphis fabae* Scop. (Dharma, 1979). For the lime aphid, the expected adult weight in the absence of crowding is about 580 $\mu$g. Given a maximum birth weight of 24 $\mu$g this yields a factor for increase of 24.

Laboratory experiments have shown, therefore, that crowding, temperature and plant quality during development, conditioning of leaves by previous aphid infestation, and parental weight all affect the weight of an adult lime aphid. Having established which factors are involved and before moving on to consider the process of growth, we can quantify in an approximate way their relative importance by a brief analysis of data from the field. The data consist of weekly measurements of adult weights throughout each season, from 1969 to 1973, on the trees sampled for population numbers. Associated with each weight is an estimate of the mean temperature, density and cumulative density experienced during development, assumed to be over the previous 3 weeks, while parent weights are assumed to be those of adults weighed 3 weeks previously. In deriving the growth rate later in this section the data are analyzed by regression methods, but for present purposes a ranking and grouping procedure is used; as Watt (1968) pointed out, this is particularly useful when dealing with intercorrelated variables. Maximum aphid weights in summer are about 600 μg and in spring when temperatures are low and plant quality high maximum weights observed are around 850 μg. By partitioning the records for summer weights according to temperature, a 4°C drop in temperature corresponding to that between summer and spring gives a weight gain of about 50 μg, leaving 200 μg attributable to plant quality. The extent to which the maximum summer weight of 600 μg is reduced by crowding can be assessed in a similar way, by grouping the data according to values of density and cumulative density experienced during development, ignoring the few cases where parental weights are small enough to affect those of the offspring (less than 350 μg). High densities give a maximum weight reduction of 75 μg and high cumulative densities a reduction of 175 μg so that an adult aphid's weight can be partitioned as shown in Fig. 45. Such a scheme is only approximate since several of the factors may interact in practice, but it serves as a fair indication of their relative importance. Plant quality appears to be the most significant of the extrinsic factors, and cumulative density, presumably acting through the plant, the most significant of the aphid-induced ones.

## The growth process

Considering the graphs of weight gain given by Llewellyn (1970), growth in the lime aphid appears to be exponential to a plateau reached at the adult moult. Therefore, knowing the development rate (*DV*) and the ratio of adult weight to weight at birth (*R*) for a set of constant conditions, we can calculate a growth factor as

$$GF = R^{DV}$$

for the conditions prevailing over the given small time interval, and where *DV* refers to this interval. If development is assumed to be independent of growth in size, then the factor GF can be applied to the current weight over each time increment from birth until ac-

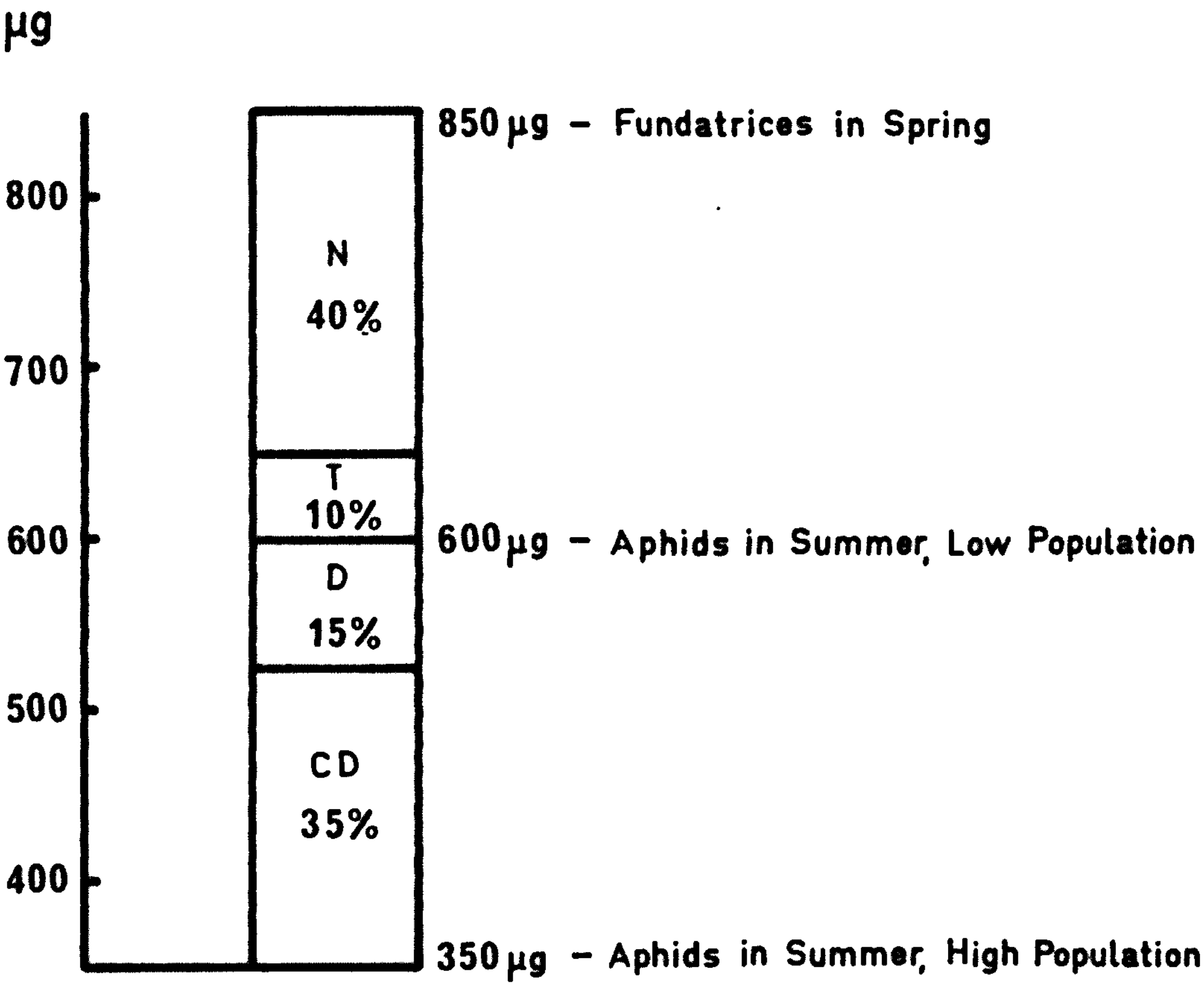


Fig. 45. The components of an adult aphid's weight, estimated from field data (see text). N, the increase associated with the increased concentration of amino-nitrogen in the phloem in spring; T, the increase associated with lower temperatures in spring; D, the decrease associated with crowding; and CD, the decrease associated with cumulative density (aphid-weeks) within a season. Percentages relate to the total range of variation of adult weights.

cumulated development reaches unity and the aphid moults. Although convenient for modelling this assumption is almost certainly a considerable over-simplification, for the time of moulting is likely to depend on weight and perhaps on current growth rates. Wilbur & Collins (1973) suggested that metamorphosis in amphibians is facultative and can occur over a wide range of body weights, depending on the net advantage of remaining in the aquatic environment. Doing so increases the risk of predation but provides opportunity for continued growth which may lead to enhanced future fecundity and an increased probability of survival. So, they suggested, metamorphosis occurs at a low weight if the growth rate is low but at a high weight if it is high. Lime aphids appear to behave in a similar way. Fig. 46 shows the relationship between final weight

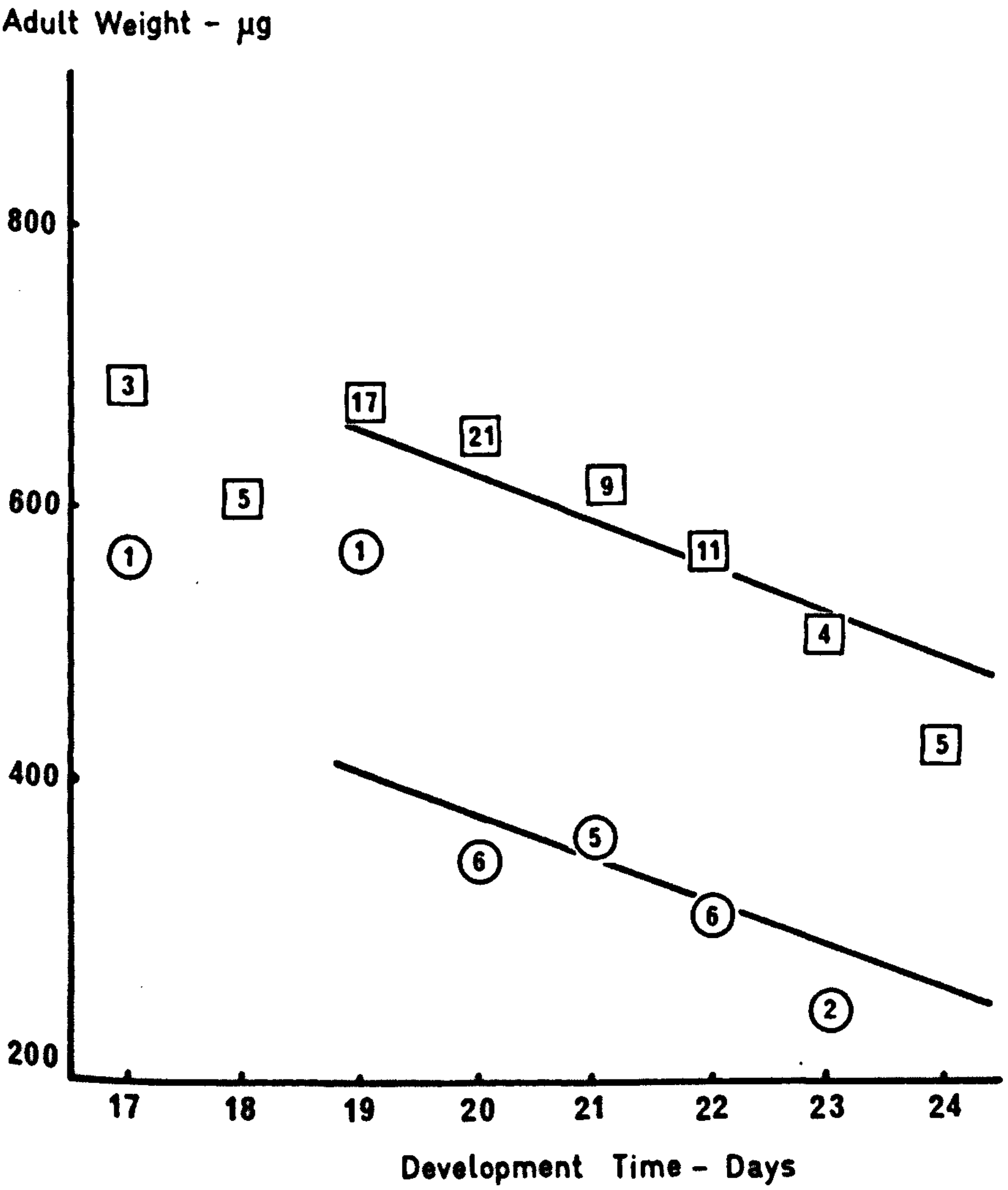


Fig. 46. Relationship between weight attained and development time for aphids reared at a constant temperature of 15°C, isolated (☐), and crowded (○). Points are means of numbers of individual records denoted by figures within them.

attained and the time taken to develop by aphids reared at 15°C on saplings of *Tilia platyphyllos* Scop. The relationships are:

$$W = 1258 - 1.55t \qquad 19 \leqslant t \leqslant 24$$

$$r = 0.43, \text{ d.f.} = 73, P < 0.01$$

for isolated aphids, and

$$W = 996 - 1.4731t \qquad 19 \leqslant t \leqslant 24$$

$$r = 0.70, \text{ d.f.} = 22, P < 0.01$$

for aphids crowded during development. The slopes are not significantly different ($P > 0.25$) though the intercepts are ($P < 0.01$), and in both cases aphids which take longest to develop are also smallest at the moult, implying a smaller exponential or specific growth rate throughout. In other words, as with amphibians, moulting occurs at a low weight if the growth rate is low and at a high weight if it is high. Ecologically, this is reasonable as the intrinsic rate of increase is greatly affected by development time (Lewontin, 1965). On the other hand, moulting early also permits rapid emigration when conditions favour colonisation elsewhere over reproduction and competition in the original environment. It may be that the facility to emigrate rapidly is so important that it explains why the crowded aphids in Fig. 46 moult at similar times to the isolated ones rather than at similar weights which take longer to achieve.

If moulting is in some way linked to growth rates, a mechanism is required to explain this link, and to account for the fact that, although crowded aphids are smaller at the moult than isolated ones, they appear to take no longer to develop (Table 9). There are a variety of known stimuli for the secretion of moulting hormone (Wigglesworth, 1972), but suppose this is related to the quantity of food passing through the pharynx, relative to its size. Such a situation exists in *Locusta migratoria migratorioides* (R. & F.) (described in Wigglesworth). Variations in growth rates will depend both on variations in food quality and in the amount ingested. For crowded aphids the observed reduction in weight at the time of the moult may be due mainly to decrease in the quality of the food while the specific amount ingested, hence the time of moulting, may remain the same. There is still the relationship among crowded aphids between weights achieved and development times which would be assumed to represent variations in quantities ingested. Aphids developing on growing tissue rich in amino-nitrogen are heavier and their development times are shorter. However, perhaps feeding rates are high under these conditions which would, on the above basis, account for the shorter development time. Hence it is possible that the specific feeding rate determines the time of moulting and the food quality, amount ingested and the time of moulting determine the weight achieved. Fig. 47 shows the position of the moulting point in the weight/time plane.

## Derivation of the daily growth factor

As shown above, the growth factor on any day can be obtained from the development rate and the expected ratio of adult weight to

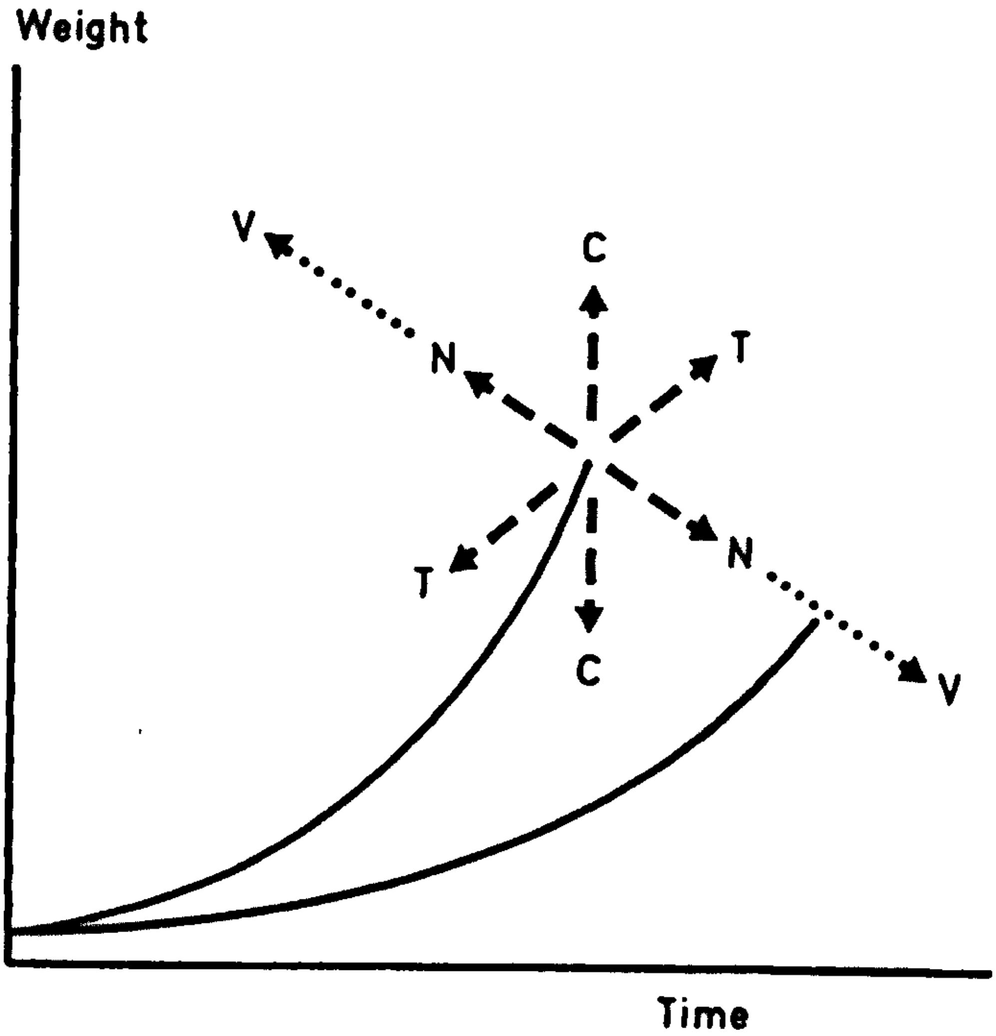


Fig. 47. Diagrammatic representation of growth and of the action of factors determining the time of moulting and weight at the moult. C, changes in degree of crowding during development; T, changes in temperature during development; N, changes in soluble amino-nitrogen concentration during development; V, background variability observed given otherwise constant conditions (e.g. including local variations in food quality).

weight at birth under the conditions prevailing that day. The calculation of development rate has already been described, and given the factors which affect adult weight their quantitative effects on growth were assessed by regression analysis of the field data. The dependent variable was log (adult weight/estimated birth weight) since it gave the best fit and its overall value is approximately equal to the arithmetic mean of the separate values for each day of the aphid's development. Averages of the independent variables, temperature, density and cumulative density, over the development period were also used. Birth weights were calculated from estimated parent weights and although cumulative density and density during development were highly correlated, grouping the data into classes according to the values of these variables showed that their effects on log (weight/estimated birth weight) were approximately additive. The resulting regression equation, for adults of the second and later generations, is:

$$\log\left(\frac{W}{B}\right) = 1.5373 - 0.00064C - 0.00174D - 0.00809T \qquad 50 \leqslant C \leqslant 350$$

$$R^2 = 0.6, \text{d.f.} = 16, P < 0.01$$

where

$W$ = adult weight
$B$ = weight at birth
$C$ = aphid-weeks/100 $\mathrm{cm}^2$, with a minimum of 50 and maximum of 350
$D$ = denisty (aphids/100 $\mathrm{cm}^2$)
$T$ = mean shade temperature (°C)

The plant quality effect involves the addition of the term $0.24(N-0.2)$ for values of $N$, the percentage of amino-nitrogen in the phloem, greater than 0.2. The regression equation indicates that, in the field, a maximum increase in weight of about 10% may be expected from the low temperatures in April and May when fundatrices develop. Given an observed maximum weight for fundatrices 50% greater than for adults of later generations, this leaves 40% of the increase attributable to an increase in mean nitrogen concentrations experienced from 0.2 to 0.8 (Fig. 18). A 40% increase is an increase in log (adult weight/birth weight) of 0.146, giving a coefficient for the nitrogen effect of 0.146/0.6 or 0.24. The effect of temperature appears to be much less in the field than in the laboratory and the reason for this is not entirely clear; given the assumptions about growth and development, a higher final weight would be expected under fluctuating temperatures than under a constant temperature with the same mean, but the effect is too small to account for the discrepancy.

### *3.5.9 Parasitism*

The model (subroutine PARA)

The aphid is parasitized by a species of *Praon* (Brown, 1975). All deaths from parasitism are assumed to occur at the adult moult and the proportion killed is time-dependent but density-independent, thus (Fig. 48):

$$PAR = 0.01\,DAY - 2.06 \qquad 0 \leqslant PAR \leqslant 0.155$$

where

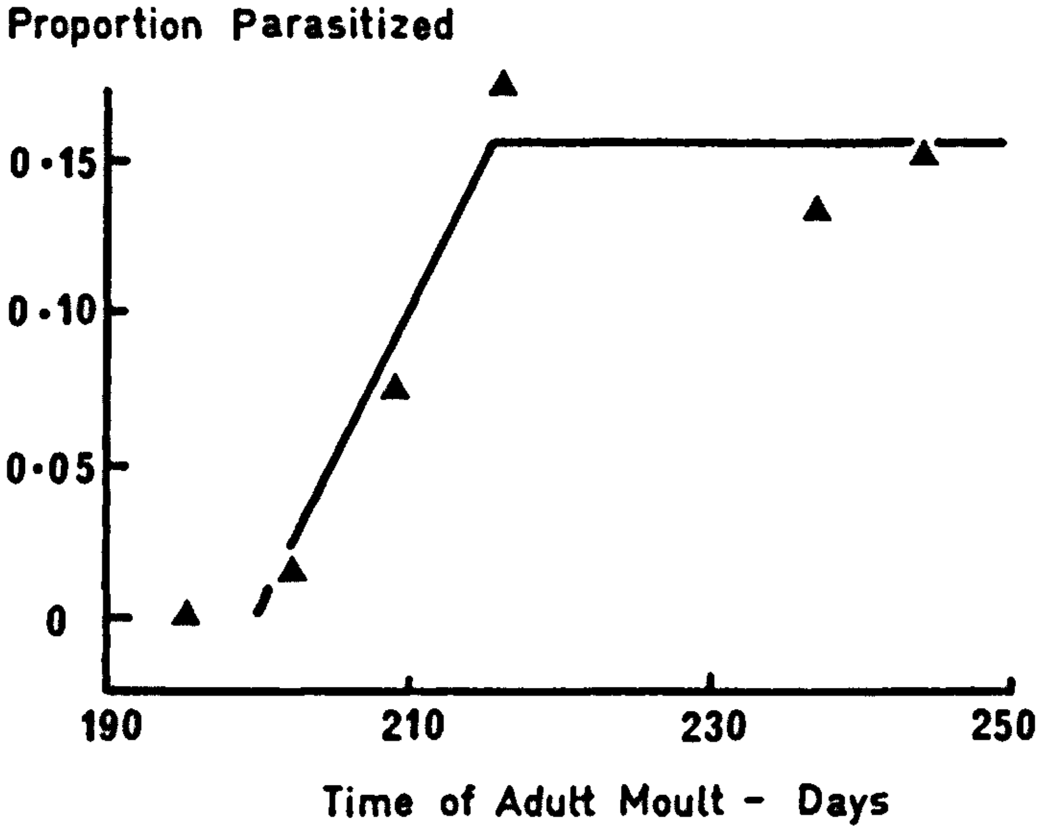


Fig. 48. Effect of time of year on the proportion of adults parasitized.

*PAR* = proportion of moulting adults parasitised
*DAY* = time of year in days.

The data

Fig. 48 was based initially on Brown's (1975) dissections of adult aphids from the field in 1971. The aphids were assumed to have moulted a week before being dissected so 7 days were subtracted from the time of each observation; the line was fitted by eye. The assumption that mortality from parasitism precedes reproduction is probably not unreasonable, since live parasitized adults have a greatly reduced reproductive rate.

In addition, mummified carcasses of parasitized aphids were counted and removed each week as part of the sampling programme. There was no positive relationship between observed proportions of the population parasitized in August and September and the average population density during these months (Table 15). Proportions parsitized were the weighted means of weekly observations which fell in the different density classes. Re-analysis of the data also yielded no evidence for an effect of cumulative density (cf. Barlow, 1977). The weighted mean proportion parasitized in August and September of 1971, when cumulative density was high, was lower than the weighted mean for other years when it was low (0.035 and 0.043, respectively). Brown's figures for 1971 were then multiplied by 0.61, the correction factor of:

Table 15. Proportions of aphids parasitized during August and September, at different population densities in the field.

| density (number/100 cm$^2$) | proportion parasitized |
|---|---|
| <1 | 0.099 |
| 1–3 | 0.022 |
| 3–6 | 0.035 |
| >6 | 0.026 |

$$\frac{\text{mean observed proportion parasitized in all years}}{\text{observed proportion parasitized in 1971}}$$

to give the relationship used in the model.

### *3.5.10 Winter mortality*

The model

The proportion of eggs laid which hatch in the following spring is taken to be constant and equal to 0.172, or approximately 1/6.

The data

All eggs on a 3-m high sapling (*Tilia platyphyllos*) in the field were counted in March. The total included those obviously dead, from their shrivelled and sunken appearance. The 3rd and 4th instar nymphs were counted subsequently on the leaves, in the middle of May. There were 470 eggs and 81 nymphs, giving a survival rate of 0.172. This is obviously a fairly crude estimate, and is likely to omit mortality of eggs which disintegrated to the extent that they were no longer discernible, but includes some mortality of 1st and 2nd instar nymphs. However, in estimating the number of nymphs emerging from the number of eggs laid these errors would tend, if anything, to cancel each other out.

## 3.6 The predator/leafhopper submodel

### 3.6.1 *Introduction*

This subsystem includes three components, the black-kneed capsid population, the 2-spot coccinellid population and the leafhopper population, shown in the relational diagrams of Figs 4, 5 and 6. Representing these components are three population sub-models sharing a common structure, applied weekly in subroutine POP and generating changes in numbers and age-distributions of the populations throughout the year. The populations are stored as vectors, the elements of which correspond to numbers in each stage (Fig. 13), and a modified Leslie matrix (Leslie, 1942; Usher, 1972) is used to model the processes of egg-hatching, development, mortality and reproduction, operating over a time period of 1 week (Fig. 49). F is the weekly reproductive rate and the basic elements T and S

$$\begin{bmatrix}
1-T(1) & - & - & - & - & - & F \\
T(1)S(1) & 1-T(2) & - & - & - & - & - \\
- & T(2)S(2) & 1-T(3) & - & - & - & - \\
- & - & T(3)S(3) & 1-T(4) & - & - & - \\
- & - & - & T(4)S(4) & 1-T(5) & - & - \\
- & - & - & - & T(5)S(5) & 1-T(6) & - \\
- & - & - & - & - & T(6)S(6) & 1-T(7)
\end{bmatrix}$$

Fig. 49. The modified Leslie matrix used to model populations of the leafhopper, the 2-spot coccinellid and the black-kneed capsid. T is the probability of entering the next stage each week, in the absence of mortality, S is the probability of surviving the transition, and F is the weekly reproductive rate.

represent, respectively, the probability of entering the next stage each week in the absence of mortality and the further probability of surviving this transition; the product of T and S, therefore, gives the weekly proportion of each stage actually entering the next. Egg-hatch is included in this framework in the same way as transitions between other stages, and for ease of representation adult mortality is considered as a proportion passing from the adult stage to a further, notional stage corresponding to dead adults or adults which have emigrated. With certain exceptions, described below, the transition probabilities, T, are constant and assumed equal to the reciprocals of the stage-lengths (Usher, 1972). The survival probabilities are constant with all mortality assumed to occur on transition between stages. No account is taken of variable development rates, though the effect could be included by making the transition probabilities dependent on temperature or prey intake over the previous week. The specific submodels for leafhopper, capsid and coccinellid populations are now considered in more detail.

### *3.6.2 The leafhopper population*

The model

Overwintering eggs are assumed to hatch over a 2-week period from 19 May to 2 June (Fig. 50a) and hatching success is 27%. The nymphs pass through 5 instars without further mortality at a rate governed by the instar durations and resulting weekly transition probabilities (Table 16). Most adults emigrate shortly after the adult moult and these are ignored by the model, emigration being treated on a 74% mortality between 5th instar nymphs and adults resident on the tree. Resident adults lay eggs at the end of August and die at the end of September (Fig. 50b). For convenience, egg-laying is assumed to occur in a single pulse (Fig. 51b) and is density-dependent (Flanagan, 1974), related to the number of resident adults thus (Fig. 51a):

$$F_L = 19A^{-0.24}$$

where

$F_L$ = eggs laid per resident adult per 100 cm$^2$

$A$ = resident adults per 100 cm$^2$

The data

The time-dependent pattern of egg-hatch was deduced from field observations and the approximate instar lengths were based on a comparison of times at which observed numbers of each instar had reached half their initial peak values in the field. Flanagan (1974) determined hatching success and obtained the following relationships from observations in the field (his Figs 36, and 37 and 38

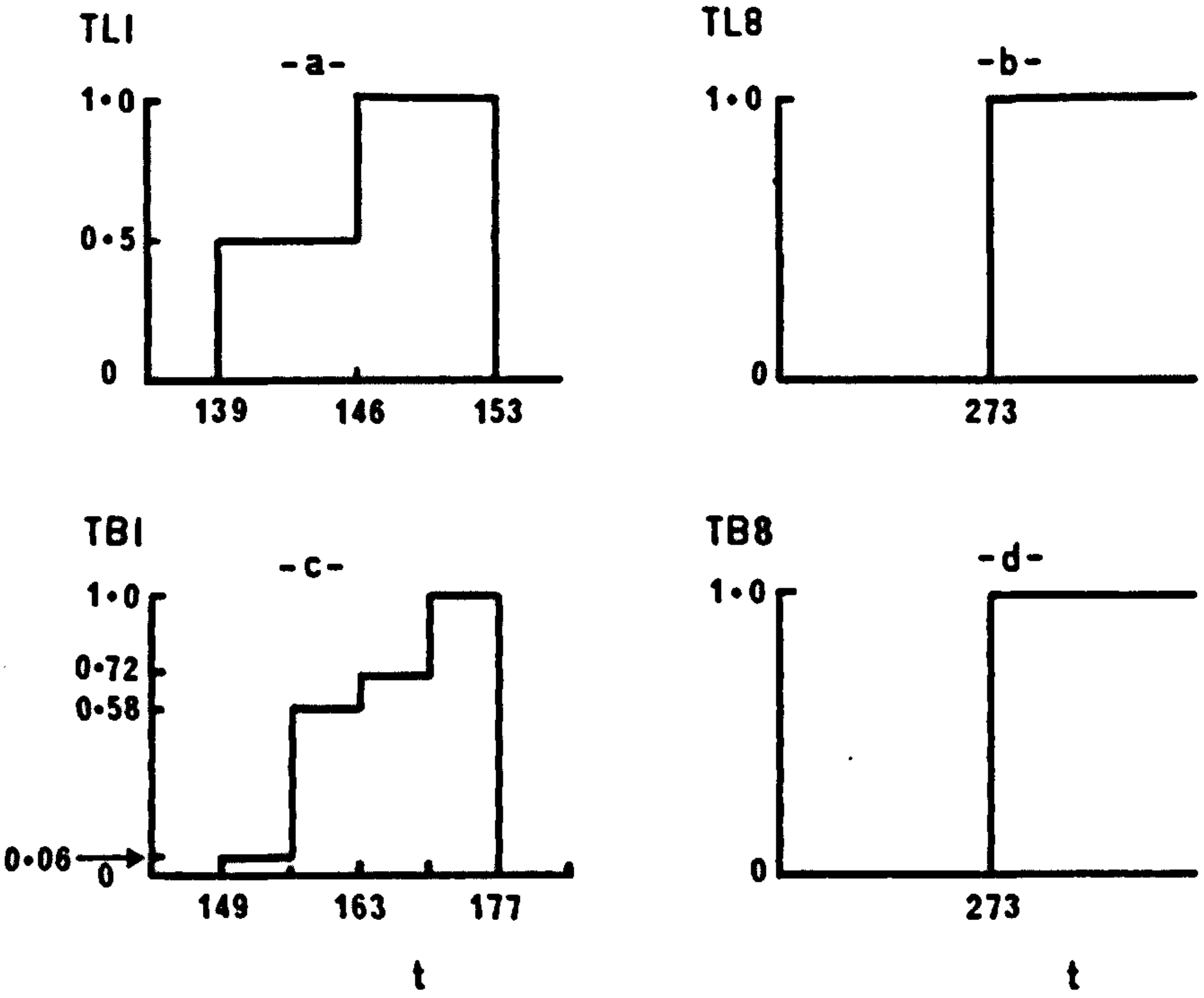


Fig. 50. Time-dependent rates (or transition probabilities) in the predator/leafhopper submodel, namely: a) proportion of leafhopper eggs hatching/week (TL1); b) proportion of leafhopper adults disappearing/week, by emigration or death (TL8); c) proportion of black-kneed capsid eggs hatching/week (TB1); d) proportion of black-kneed capsid adults disappearing/week, by emigration or death (TB8). *t* is the number of days from the start of the year.

Table 16. Duration of stages, transition probilities and survival probabilities for the leafhopper. Transition probabilities are equivalent to the weekly proportions of each stage entering the next in the absence of mortality, and survival probability to the proportions surviving the transitions. TD = time-dependent.

| stage | duration (days) | transition probability (TL) | survival probability (SL) |
|---|---|---|---|
| Egg | — | TD Fig. 50a | 0.27 |
| Instar 1 | 10 | 0.670 | 1.000 |
| Instar 2 | 7 | 1.000 | 1.000 |
| Instar 3 | 7 | 1.000 | 1.000 |
| Instar 4 | 7 | 1.000 | 1.000 |
| Instar 5 | 12 | 0.560 | 1.000 |
| Adult | — | TD Fig. 50b | 1.000 |

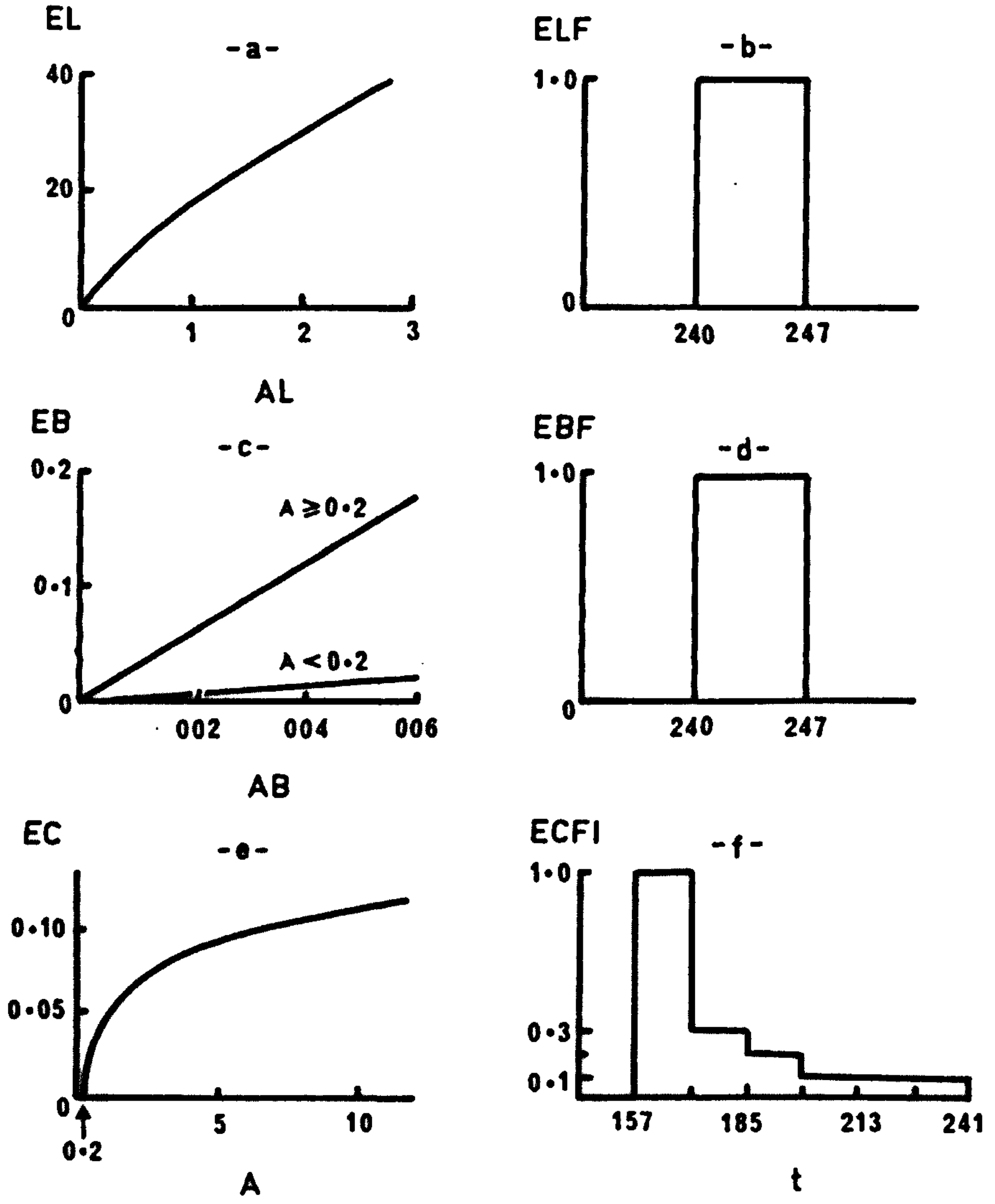


Fig. 51. Variable reproductive rates in the predator/leafhopper submodel. a) Relationship between the number of leafhopper eggs laid per 100 $cm^2$ per week (EL) and adult density (AL). b) The factor (ELF) modifying leafhopper egg-laying, depending on the time of year ($t$). c) Relationship between the number of black-kneed capsid eggs laid per 100 $cm^2$ per week (EB), the density of adult capsids (AB) and the aphid density (A). d) The factor (EBF) modifying capsid egg-laying according to the time of year ($t$). e) Relationship between the number of 2-spot coccinellid eggs laid per 100 $cm^2$ per week (EC) and aphid density (A). f) The factor (ECF1) modifying coccinellid egg-laying according to the time of year ($t$).

combined):

$$E/A = 64.6N^{-0.24}$$

$$A = 0.26N$$

where

$E$ = eggs laid/80 leaves

$A$ = average adults at the time of laying/80 leaves

$N$ = peak nymphs/80 leaves

The second equation gives the survival probability between 5th instars and average adults used in the model and the first, in conjunction with the second, gives density-dependent egg-laying thus:

$$E/A = 64.6\left(\frac{A}{0.26}\right)^{-0.24}$$

$$= 46.7\,A^{-0.24}$$

Hence

$$E_1/A_1 = F_L = 19\,A_1^{-0.24}$$

where

$E_1$ and $A_1$ are numbers per 100 cm².

### 3.6.3 *The black-kneed capsid population*

The model

Overwintering eggs hatch over 4 weeks in June (Fig. 50c) and hatching success is assumed to be 50%. The nymphs pass through 5 instars, with durations and weekly probabilities of transition as in Table 17, and with a 25% mortality between instars 3 and 4. 10% of 5th instars become resident adults on the tree which disappear through death or emigration at the end of September (Fig. 50d); the rest are assumed to emigrate immediately after the moult. As with the leafhopper, egg-laying is considered to take place on a single occasion at the end of August (Fig. 51d), the number laid in this case being (Fig. 51c).

$$F_B = 30; \quad A > 0.2$$

$$F_B = 4; \quad A \leqslant 0.2$$

where

$F_B$ = eggs laid/resident adult/100 cm²

$A$ = aphids/100 cm² at the time

Table 17. Duration of stages, transition probabilities and survival probabilities for the black-kneed capsid. Transition probabilities are equivalent to the weekly proportions of each stage entering the next in the absence of mortality, and survival probabilities to the proportions surviving the transitions. TD = time-dependent.

| stage | duration (days) | transition probability (TB) | survival probability (SB) |
|---|---|---|---|
| Egg | — | TD Fig. 50c | 0.500 |
| Instar 1 | 8 | 0.884 | 1.000 |
| Instar 2 | 8 | 0.884 | 1.000 |
| Instar 3 | 8 | 0.884 | 0.750 |
| Instar 4 | 12 | 0.580 | 1.000 |
| Instar 5 | 14 | 0.494 | 0.100 |
| Adult | — | TD Fig. 50d | 1.000 |

The model thus embodies a numerical response to aphid density (Solomon, 1949) as indicated by field observations and described below.

### The data

The hatching pattern of eggs was again deduced from times of appearance of 1st instar nymphs in the field. Instar lengths were based on the laboratory measurements of Glen (1973), multiplied by $\frac{6}{5}$ since development took 50 days in the laboratory but appears to take 60 days in the field, by comparison of initial appearances of 1st instar nymphs and adults, and medians of 1st instar and 5th instar distributions in time. The hatching success is arbitrary and, as for the leafhopper, is assumed to include all mortality sustained by the eggs. Survival probabilities between instars were derived from the field data, with the number passing through any stage being estimated as the cumulative abundance of the instar (nymph-weeks) divided by the instar length in weeks, since numbers recorded were generally small. In the case of adults field observations showed an initial high number of emigrants, then a rapid decline to a constant population of about 10% of the original total, persisting until the end of September; the emigrants are ignored in the model. The timing of egg-laying is as indicated by Glen (1973) and the equation is based on two pieces of information. First, tracing the fate of one egg and given the above assumptions about survivals and stage-lengths (Table 17), we obtain the following equivalences:

1 egg laid → 3.106 nymph-weeks observed → 0.375 adults → 0.0375 resident adults

Hence

$$E_t = 0.3219\ C_{t+1}$$

and
$$R_t = 0.012\ C_t$$

where

$E_t$ = eggs laid/100 cm$^2$ at the end of year $t$

$R_t$ = resident adults/100 cm$^2$ at the end of year $t$

$C_t$ = nymph-weeks observed in year $t$

$C_{t+1}$ = nymph-weeks observed in year $t+1$

The second piece of information, embodying the numerical response, is the relationship between observed cumulative nymph-weeks in successive years, shown in Fig. 52 and given by:

$$C_{t+1} = 1.1\ C_t; \quad A_t > 0.2/100\ \text{cm}^2\ (r = 0.95,\ \text{d.f.} = 4,\ P < 0.01)$$
$$C_{t+1} = 0.15\ C_t; \quad A_t \leqslant 0.2/100\ \text{cm}^2$$

where

$A_t$ = aphids per 100 cm$^2$ at the end of August in year $t$

The threshold aphid density is arbitrary but consistent with field observations. From these relationships the number of eggs laid per resident adult can be derived thus:

$$E_t/R_t = \frac{0.3219 \times 1.1}{0.012} \simeq 30; \quad A_t > 0.2$$

$$E_t/R_t = \frac{0.3219 \times 0.15}{0.012} \simeq 4; \quad A_t \leqslant 0.2$$

In practice, reduced egg-laying at low aphid densities probably arises rather from increased adult emigration than from reduced egg-laying by the same number of residents, since the observed cumulative abundance of adults in the field, relative to that of nymphs, is lower in years when the aphid populations crash before mid-August than in years when they do not.

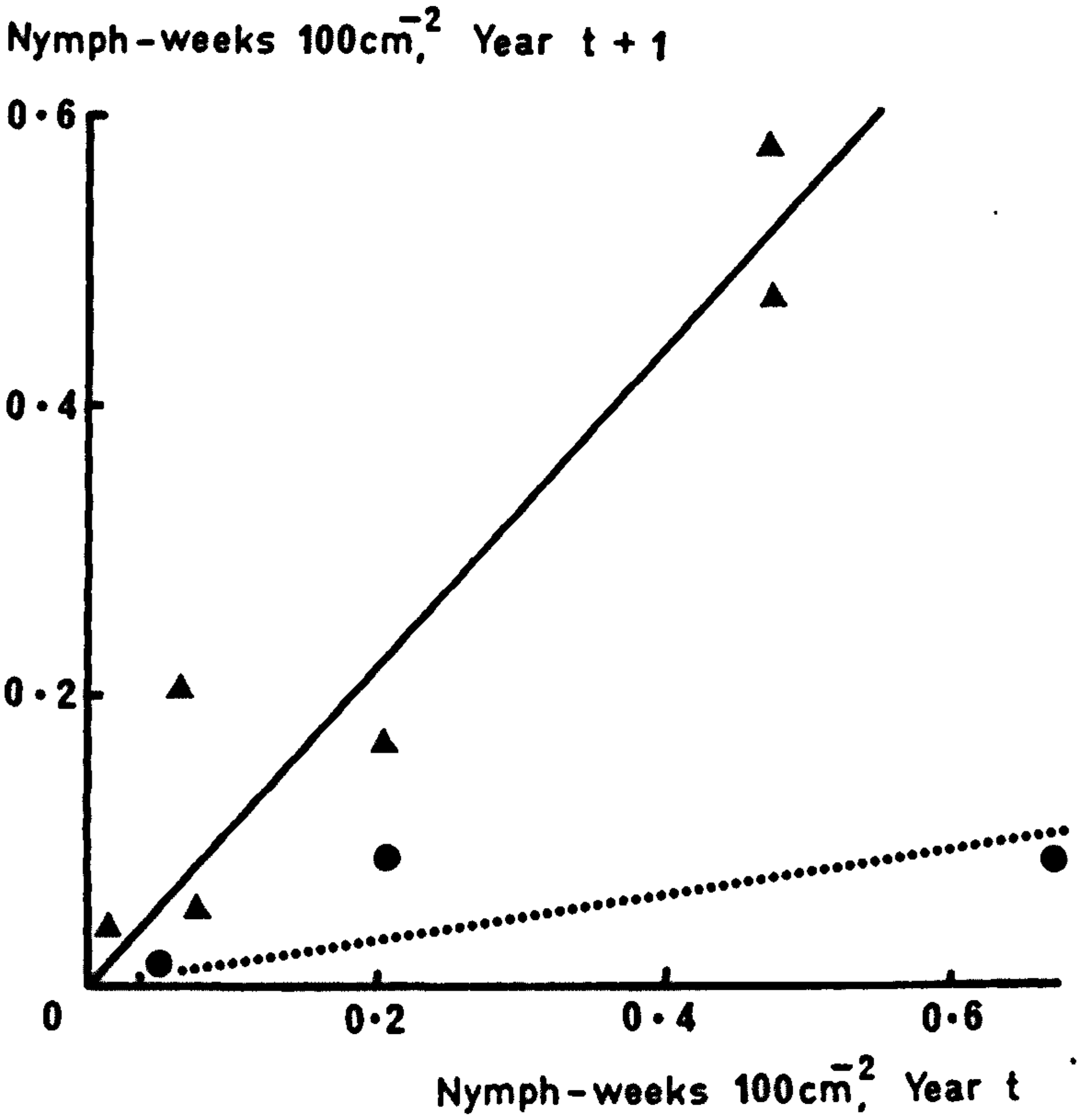


Fig. 52. Relationship between observed cumulative abundance of black-kneed capsid nymphs, in each year, their cumulative abundance in the previous year, and maximum aphid density in August of that year. ▲ ——, aphids in August $\geqslant 0.2/100\ \text{cm}^2$; ● – – –, aphids in August $<0.2/100\ \text{cm}^2$.

### 3.6.4 *The 2-spot coccinellid population*

#### The model

The coccinellid overwinters as an adult and egg-laying is assumed to occur throughout spring and summer at a rate depending on the time of year, aphid density and other factors unrelated to the aphid which may determine the effective abundance of the coccinellid on any given tree in any particular year; these largely unknown factors are represented by a 'coccinellid multiplier' which normally takes the value 1 but in 1971 multiplies expected egg-laying by 0.3. The numerical response to aphid density in the second two weeks of June, when most egg-laying occurs, takes the form (Fig. 51e):

$$EC = 0.066 \log A + 0.046$$

where

$EC$ = total eggs laid per 100 cm$^2$ per week

$A$ = aphids per 100 cm$^2$

inversely density-dependent at high densities but with a lower threshold for laying of 0.2 aphids/100 cm$^2$. This response is modified by the coccinellid multiplier then by a factor varying between 0 and 1 depending on the time of year (Fig. 51f); egg-laying declines rapidly after the peak in mid-June and ceases by the end of August.

The number of immigrant adults present in any week is assumed to be 0.037 times the estimated number of eggs laid that week. Eggs hatch in 10 days and the larvae pass through 4 instars before pupating, with durations and weekly transition probabilities as in Table 18. Adults are assumed to remain for 1 week on the tree and background survival rates of other stages are given in Table 18.

Table 18. Duration of stages, transition probabilities and survival probabilities for the 2-spot coccinellid. Transition probabilities are equivalent to the weekly proportions of each stage entering the next in the absence of mortality and survival probabilities to the proportions surviving the transitions.

| stage | duration (days) | transition probability (TC) | survival probability (SC) |
|---|---|---|---|
| Egg | 10 | 0.700 | 0.500 |
| Instar 1 | 9 | 1.000 | 0.800 |
| Instar 2 | 6 | 1.000 | 0.940 |
| Instar 3 | 6 | 1.000 | 0.940 |
| Instar 4 | 10 | 0.700 | 0.940 |
| Pupa | 17 | 0.410 | 0.850 |
| Adult | 7 | 1.000 | 1.000 |

## The data

Since numbers of eggs recorded in the field were generally small, egg-laying was estimated from observed numbers of 2nd to 4th instar larvae. 1st instars were excluded from the analysis since their distribution on the leaves is highly aggregated, unlike those of later instars. The number of eggs laid in any week $t$ is therefore assumed to be

$$2.66 \times \left( \begin{matrix} \text{2nd instar} & & \text{3rd instar} & & \text{4th instar} \\ \text{larvae in} & + & \text{larvae in} & + & \text{larvae in} \\ \text{week } t+3 & & \text{week } t+4 & & \text{week } t+5 \end{matrix} \right) /3$$

where the time delays are based on instar durations and each larva contributes, on average, 3 times to the estimate. The figure 2.66 corrects for hatching success and 1st instar mortality. Measured in this way the average number of eggs laid in any year during June is related to the mean aphid density, thus (Fig. 53a):

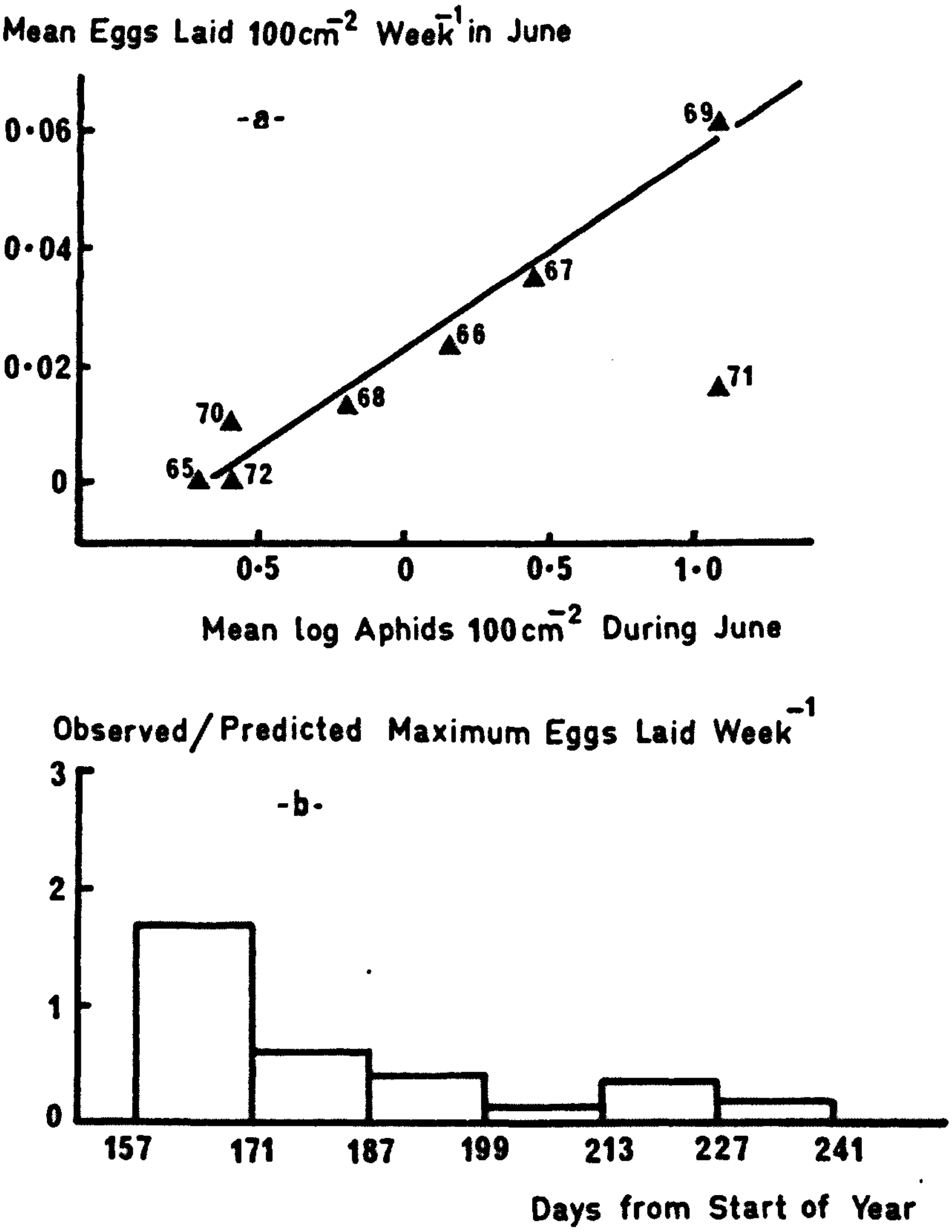


Fig. 53. a) Relationship between coccinellid egg-laying in June, estimated from numbers of larvae (see text), and aphid density at that time. Figures on the graph are years. b) Variation in weekly coccinellid egg-laying with time of year, where predicted values are those given by the above relationship.

$$E = 0.33 \log A + 0.023 \qquad (r = 0.98, \text{d.f.} = 5, P < 0.01)$$

where

$E$ = number of eggs laid/100 cm$^2$ in June

$A$ = mean number of aphids/100 cm$^2$ during June

The point for 1971 was excluded from the regression for reasons given below. From observations of actual egg numbers in 1969, Wratten (1973) presented a somewhat different numerical response, but estimates based on larval numbers suggest that in other years eggs are laid at lower aphid densities than the threshold he quotes. Variation in egg-laying throughout the year is shown in Fig. 53b, in which ratios of numbers of eggs laid to those expected, given the above equation and the aphid density, are plotted against time. Egg-laying and aphid density on each occasion are the maximum values for any year, and the former is estimated, as before, from larval numbers; the yearly pattern is qualitatively similar to that based on the small numbers of eggs actually observed. The coccinellid multiplier was invoked to take account of the one anomalous departure from the relationship between egg-laying and aphid density, namely in 1971. It almost certainly reflects, at least in part, the influence of spring temperatures on coccinellid egg-laying activity. For temperatures were noticeably lower during the middle two weeks of June in 1971 than in any other year except 1972, when aphid densities were in any case too low for significant egg-laying (Fig. 53a).

Since few immigrant adults were observed in spring and early summer, their abundance had to be estimated from the number of eggs laid. Only in 1969 were reasonable numbers of both recorded, when 297 eggs were laid by 11 adults, assuming the latter were each present for 1 week. The adult population in any week was therefore assumed to be at least 0.037 (= 11/297) times the calculated number of eggs laid that week.

Instar lengths in Table 18 are as given by Wratten (1973 and pers. commun.); however, in order to avoid transitions through more than one stage in any week and to keep the model structure simple, transition probabilities were based on durations of 1 week for each of the first 3 instars. Background survival rates are taken from the laboratory data of Ellingsen (1969).

# 4 Results

## 4.1 Comparison of model output with observed results

### *4.1.1* The problem of validation

Caswell (1977) suggested that the problem of validation differs according to the type of model; empirical, predictive models can be validated by statistical methods, while explanatory models can only be corroborated through repeated attempts to refute them. As an example he quoted von Foerster's model of exponential growth in the human population, validated as a predictive model but refuted as an explanatory one since, although agreement with observed data is good up to the present time, it is evident for a number of reasons that it cannot continue to be so. In effect this means that predictive models may be right for the wrong reasons and still serve their purpose, but explanatory models must be right for the right reasons. However, both must give acceptable agreement with what is observed, and this itself raises a problem for it is difficult to see how statistical methods can be used to test such an agreement. Given that sets of observed and predicted data often represent time series, it is not possible to assign significance levels to such indices as $\chi^2$ or the correlation coefficient, although the quantities themselves can readily be computed. Thus, for a given number of points they summarize the extent of agreement between observed and predicated data, and could therefore be used to compare different models, but they cannot serve as absolute measures of any one model's realism. It may prove possible to standardize the testing of ecological or population models but for the moment a model's verisimilitude must lie in the eye of the beholder; there would seem to be no special virtue in representing what is clear to the eye by a correlation coefficient with which no significance level can be associated.

Output of the present model is therefore compared in the usual way with observed data simply by graphing the two, and since it is an explanatory model it is tested under a reasonably wide range of conditions. The comparison is carried out in three stages: first, with the overall within-season (oviparae vs. fundatrices) and between-seasons (fundatrices vs. fundatrices) relationships under average weather conditions in the field; second, with the population trends during each specific year in the field, given the initial conditions and actual weather that year; and finally with the same relationships and population trends in laboratory populations.

### 4.1.2 *Overall changes in numbers within and between years in the field*

The model was run first with average temperatures, a constant daily survival rate for all stages of 0.97, which includes the average effect of wind, and three initial numbers of fundatrices spanning the range observed in the field. (10, 100 and 1000/m$^2$, referred to hereafter as low, medium and high initial numbers). Fig. 54 shows the predicted relationships and the observed points for different years, averaged over trees 1 and 2. Agreement at this level is good; the model re-creates the observed inverse relationships between fundatrices and oviparae and between fundatrices in successive years. Since the line in Fig. 54 has a negative slope close to $-1$, the model predicts stable limit cycles with an amplitude dependent upon the starting density, and a neutral equilibrium point for a fundatrix population of 63/m$^2$ (log value 1.8); superimposed upon this behaviour would be a strong stochastic element representing the action of disturbing factors. Fig. 55 shows the population trends generated by the model for each initial density, and, given that oviparae form a roughly constant proportion of the total at the end of a season, it is clear from this figure how the above inverse relationships arise.

In all except one case, departures of individual points in Fig. 54 from the predicted line are probably due to variation in the disturbing effects of weather on mortality, flight and reproduction. However, although the point for 1971 lies close to the line there is good reason to believe that it is reached through an entirely different mechanism, as described below (p. 120).

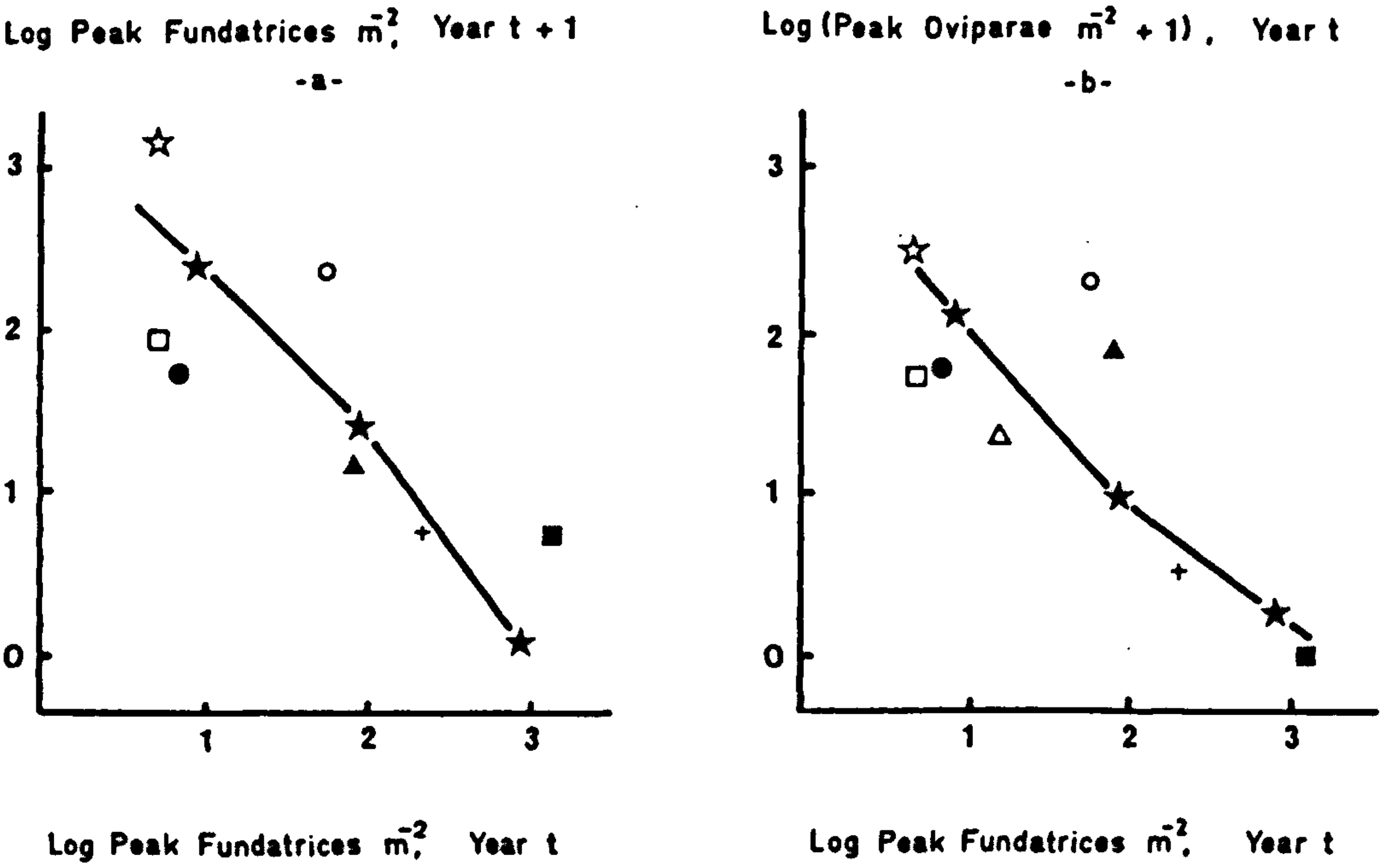


Fig. 54. Comparison of relationships generated by the model (★—★) between a) fundatrix densities in successive years, and b) peak densities of fundatrices and oviparae within each year, and those observed in the field on trees 1 and 2 (● 1965, ○ 1966, + 1967, ☆ 1968, ■ 1969, □ 1970, ▲ 1971, △ 1972; each point is the average for that year over both trees).

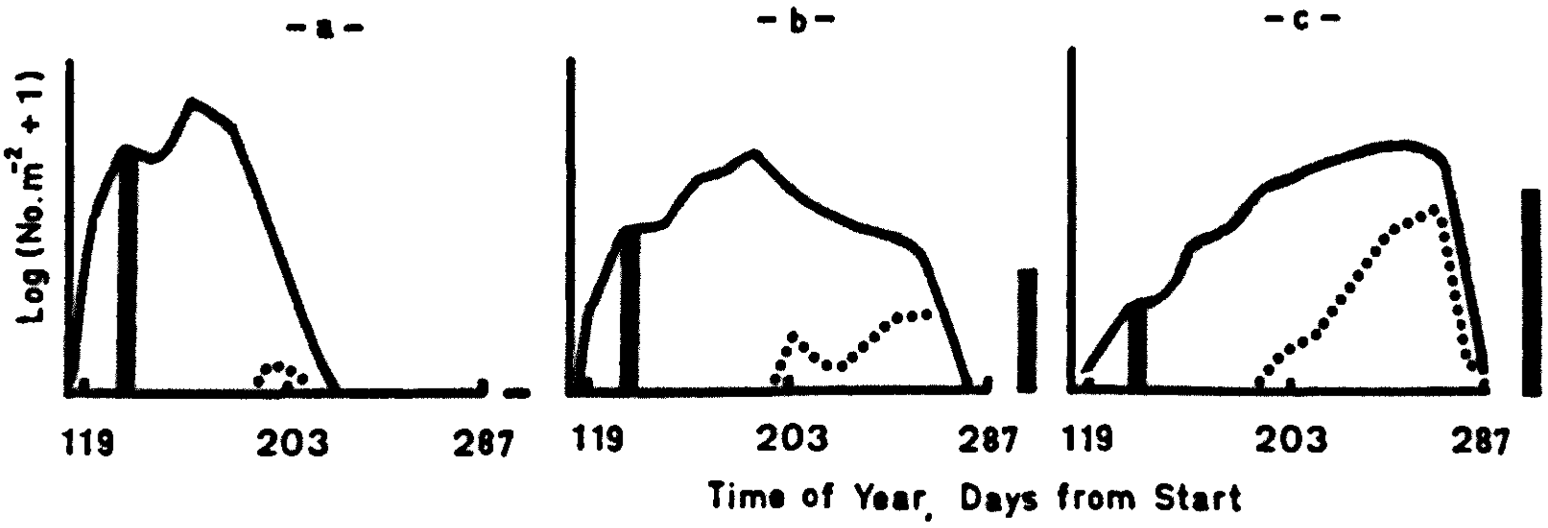


Fig. 55. Population trends throughout the year generated by the model for a) high, b) medium and c) low initial densities, corresponding to the three predicted points in Fig. 54. —— total numbers, ····· ovipara numbers; vertical bars are fundatrix numbers in the current and following years.

Fig. 56 shows the observed and predicted results from 1965 to 1972, given the actual temperatures and winds and the appropriate

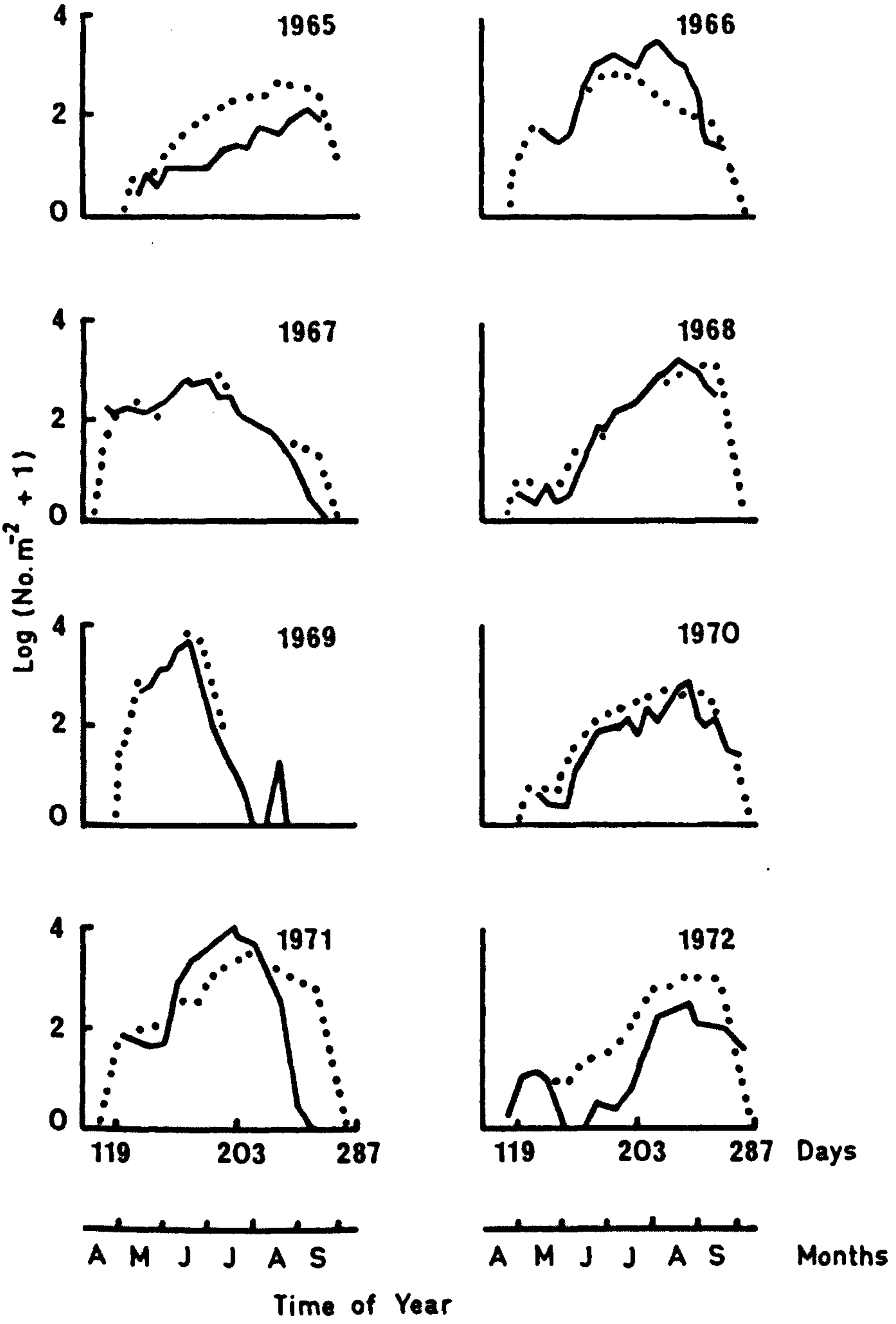


Fig. 56. Comparison of observed population trends on trees 1 and 2 in the field, from 1965 to 1972 (——), and those generated by the model given the same weather and initial conditions each year (· · · · ·).

initial numbers of fundatrices, leafhoppers and black-kneed capsids each year; coccinellid egg-laying is assumed to be only 30% of normal in 1971 (Section 3.6.4). The main disturbing effects now operating are of wind speed on mortality and temperature on egg-hatching, development rate and reproductive rate. Agreement is good in 1967, 1968, 1969 and 1970, and although it is less good in other years the model does express some of the variability observed from year to year in the field, as well as the underlying basic patterns of behaviour; it is the extent of this variability which is lacking. Thus, given similar initial fundatrix populations the model predicts lower numbers in 1965 than in 1968 and lower ones in 1967 than in 1970, but the differences are less than was actually the case. In 1972 the model also predicted a period of retarded growth during June, but not to the extent realised in the field. Looking at the observed and predicted results for 1969 and 1970 in more detail (Fig. 57), there are two main discrepancies. In 1969 the model suggests that more 4th instar nymphs and adults are present immediately before the crash than was actually the case and it fails to re-create the marked decline in numbers of all stages at the end of 1970. Otherwise, predicted instar distributions and adult weights are

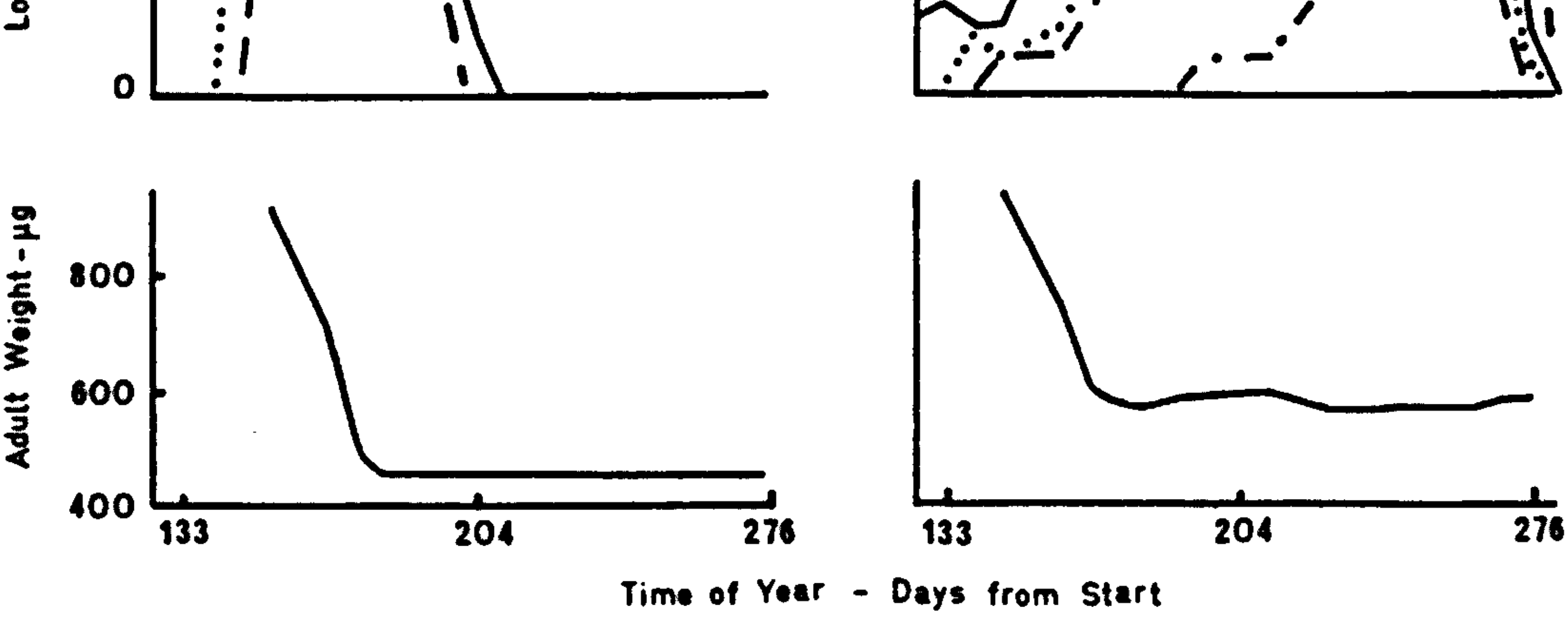


Fig. 57. Detailed population trends and adult weights generated by the model for 1969 and 1970. —— young nymphs (instars 1–3); ····· 4th instar nymphs; – – – viviparae; –·–·– oviparae.

approximately correct, although it must be remembered that the latter are based largely on analysis of field records (c.f. Fig. 12).

In years when there is poor agreement between observed and predicted results, what possible reasons might underly these discrepancies? In 1965 virtually no predators were present and numbers were never high enough for density-dependent flight to become significant, so the reason is almost certainly an omission from the model of one or more effects of weather. Such effects probably act on flight and mortality since reproduction is better understood; actual reproductive rates have been monitored for some years in the field and the variation from week to week is relatively small. As to the actual weather factors which might be involved, temperatures during 1965 were unexceptional (Fig. 16) but wind speeds during June were high (Fig. 17) and the population failed to increase at all during this particular period. Wind speeds were also high during June in 1972 when aphid numbers were extremely low, none being recorded on two sampling occasions; had the model reproduced this effect to the correct extent, agreement during the rest of the season would be good since observed and predicted results differ by a constant amount thereafter (Fig. 56). In general, therefore, where the model overestimates the actual population, as in 1965 and 1972, this may be attributable, at least in part, to underestimation of the effects of high wind speeds on mortality; this is not invariably the case since in 1967, for instance, wind speeds were too low to account for the discrepancy. However, it is less easy to explain why the model should underestimate population growth rates, as in the summers of 1966 and 1971. Wind speeds were not particularly low, and although temperatures during June and July of 1966 were high those up to mid-June in 1971 were extremely low, yet the population was growing rapidly at this time (Fig. 56). Suppression of flight or reduction in mortality would both yield increased rates of population growth and it is not clear as yet which of these is responsible and under what conditions. The lack of agreement at the end of 1971 is because cumulative densities in the model were not high enough to cause a population crash. In the more detailed comparison of population trends in 1969 and 1970 (Fig. 57), the discrepancy at the end of 1970 may also be due to an underestimation of the effects of wind, since it was removed by changing the relationship in the model to one giving a reduced mortality at low wind speeds but a greater one at higher speeds. The model's prediction of too many 4th instar nymphs and adults before the crash in 1969 may be due to the presence of a density-dependent nymphal mortality omitted from the model, or to underestimation of the mortality inflicted by the coccinellid predators; 3rd and 4th instar coccinellids were present earlier in 1969, and were possibly more voracious than the model suggests because of a short period of high temperatures (Fig. 16).

Ideally, the next step would be to run the model continuously from 1965 to 1972 rather than start each year with the correct initial conditions. However, since errors would rapidly accumulate over this period, there is little point in running the model continuously until very good agreement is obtained within individual years. Thus we did not attempt to do this.

### *4.1.4 Population changes in the laboratory*

In applying the model to Brown's (1975) insectary populations certain modifications are necessary. First, since predators and parasites were absent these were omitted from the model. Second, the average daily mortality rate was assumed to be 1% instead of 3%, for all stages. Third, the daily net emigration rate of alates was assumed to be reduced by 50%, since the populations were enclosed in cages and only the roofs and floors of these were sticky, making it possible for alates landing on the sides to return to the plants. Finally, since mortality and flight in the insectary were apparently unaffected by cumulative density and adult weights affected to a lesser extent than in the field, the effect was reduced in the model by dividing the accumulated density by 3. With no predation or parasitism and reduced mortality, flight and effects of cumulative density, the model gives the results shown in Fig. 58. Population trends during the year for low (10/m$^2$) and very high (2000/m$^2$) fundatrix numbers give quite good agreement with those observed in the insectary, though the peak numbers are slightly underestimated (Fig. 58c and d). The predicted relationship between peak fundatrices and peak oviparae (Fig. 58b) is also fairly close to that observed, with a much smaller negative slope than in the field (Fig. 54b) and higher overall fundatrix numbers produced, though these are slightly underestimated by the model. However in the relationship between peak fundatrices one year and the next, the pronounced negative slope observed in the field re-appears among the insectary population but with higher overall numbers. While the model correctly predicts this elevated general level of abundance it does not recreate the inverse relationship (Fig. 58a); rather, it yields one of the same slope as for the oviparae/fundatrices line (Fig. 58b). Why, in the

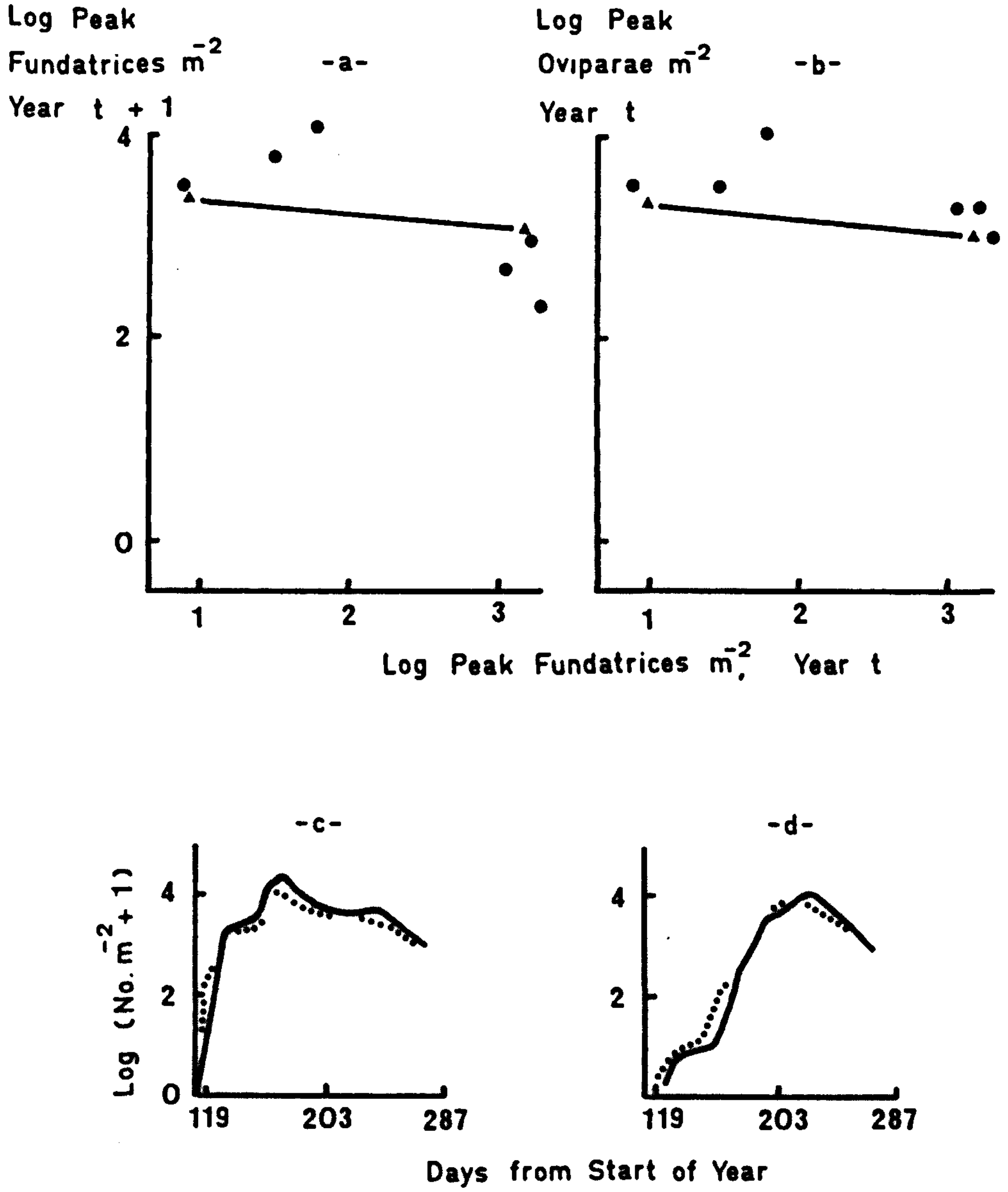
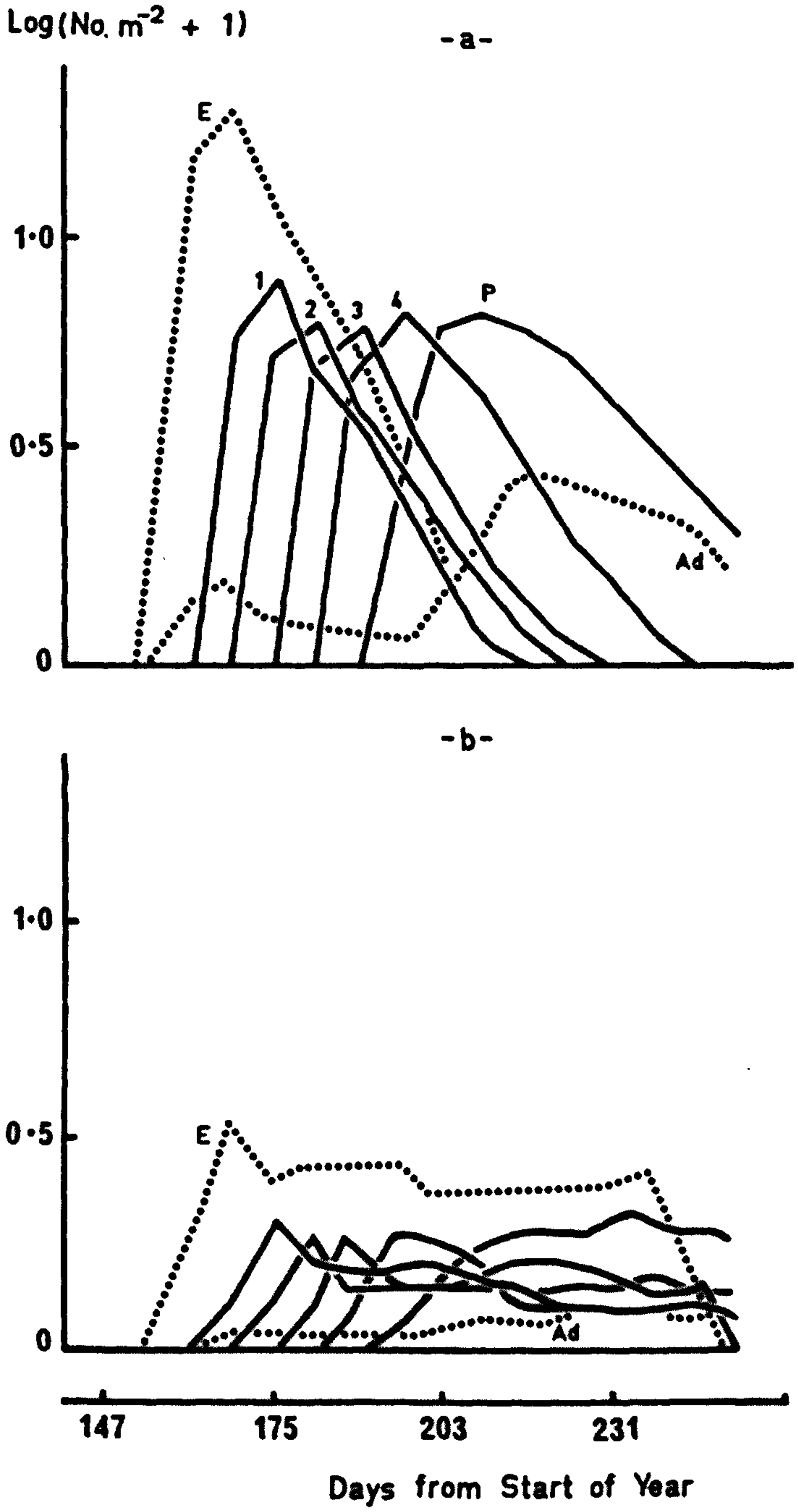


Fig. 58. Comparison of observed population behaviour in an insectary and that generated by the model. a) The relationship between peak fundatrices in successive years (●, observed; ▲—▲, model). b) The relationship between peak oviparae and peak fundatrices in the same year. c) Population trends throughout the year for an initially high-density (2000/m$^2$) population (—— observed; ····· model). d) Population trends throughout the year for an initially low-density (10/m$^2$) population.

insectary populations, should the negative slope in the between-seasons relationship be greater than that in the within-seasons one, and why does the model fail to reproduce the effect? The answer is almost certainly that ovipara weights and hence the number of eggs laid by each were actually much lower (about 200 μg) in the populations initially at a high density than were those in the initially low-density populations (about 400 μg). In the model the weights were 382 μg and 415 μg, respectively at the times of peak ovipara numbers, giving a much smaller difference in egg-laying potential. This in turn must have been due to the underestimation of numbers, hence of cumulative density, in the initially high populations (Fig. 58c), or to an underestimation of its effects on aphid weights in the laboratory.

### *4.1.5 Population changes of predators and leafhoppers*

Fig. 59 shows the predator and leafhopper population trends generated by the model. This is in no sense a validation since the submodel was based to a large extent on field census data, but serves to illustrate the numbers and stages of predators and their alternative prey which affect the aphid population at different times of year. Figs 59a and b show changes in numbers of the 2-spot coccinelid when aphid populations are initially high and low respectively, and average weather conditions are assumed. The main difference is that egg-laying occurs at a lower rate and over a somewhat longer period in the second case than in the first. The population trends for the capsid are given in Figs 59c and d, again for high and low aphid densities, and here the difference lies in the number of eggs produced at the end of the year Figs 59e and f show leafhopper populations developing from two different initial numbers of eggs, 200/m$^2$ and 50/m$^2$ respectively. Since egg-laying is density-dependent (Section 3.6.2) the increase in egg numbers from beginning to end of the year is smaller when the initial density is high than when it is low; the theroretical equilibrium number of eggs is 2400/m$^2$, a very high figure.


Log(No. m⁻² + 1)
-a-
E
1
2
3
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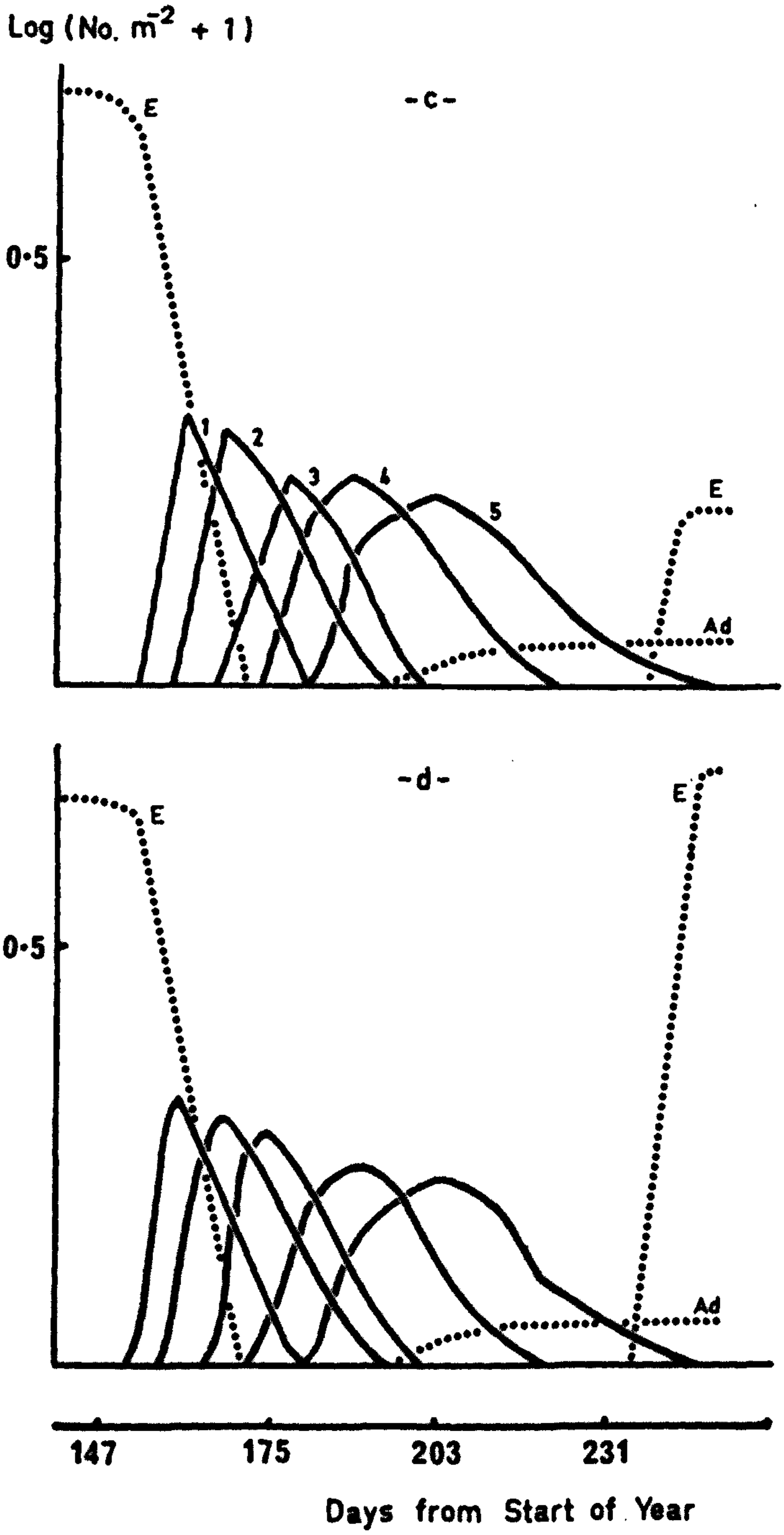
Days from Start of Year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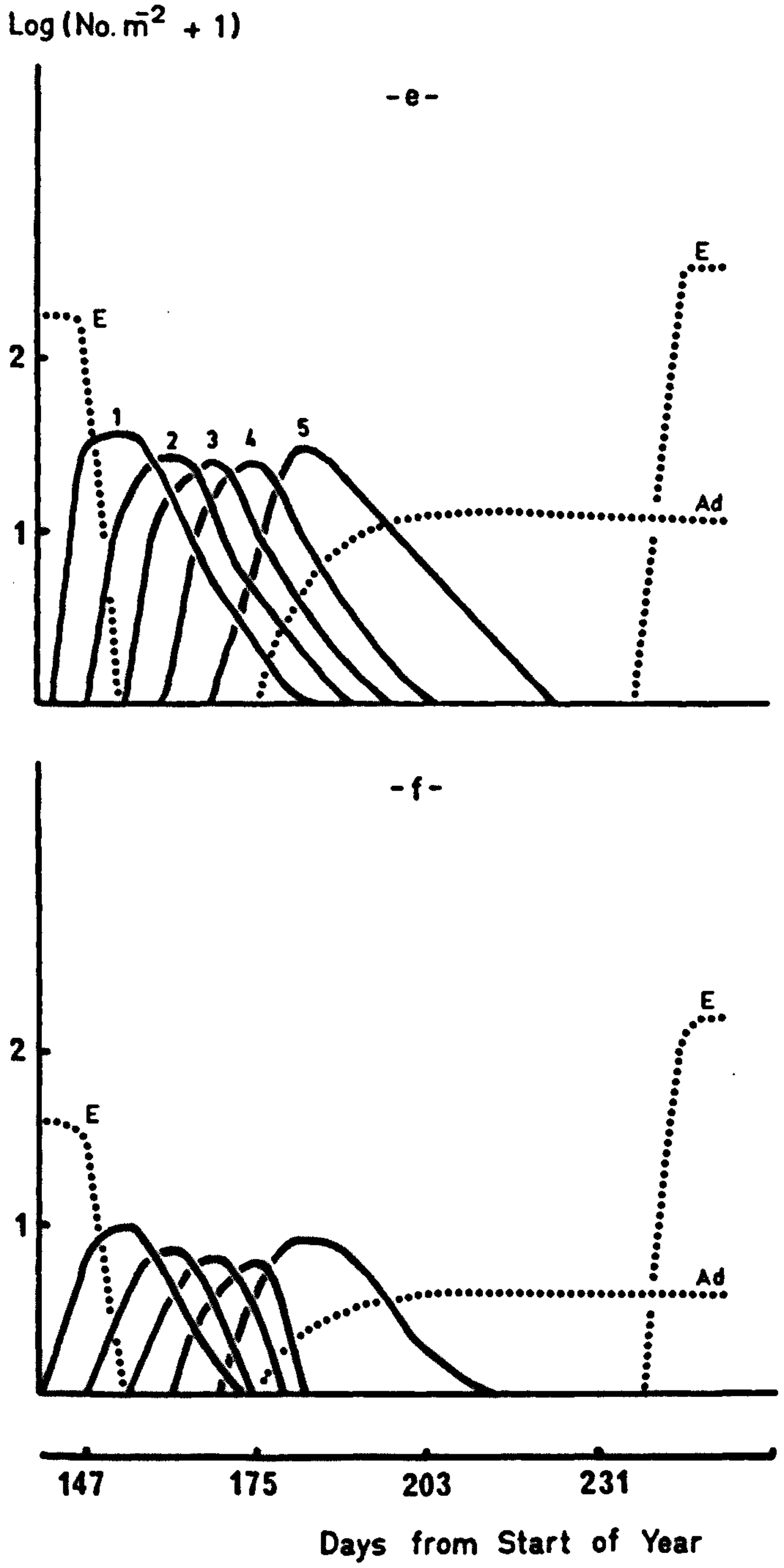

Fig. 59. Population trends of 2-spot coccinellids, black-kneed capsids and leafhoppers throughout the year, generated by the predator/leafhopper submodel. a) Coccinellid with a high initial aphid population (1000/m$^2$). b) Coccinellid with a low initial aphid population (10/m$^2$). c) Capsid with a high initial aphid population which crashes. d) Capsid with a low initial aphid population which increases. e) Leafhopper at a high initial density. f) Leafhopper at a low initial density.

## 4.2 Sensitivity analysis

This section is concerned with the effects of changes in assumptions about the forms of relationships or the values of parameters where these are not well established. The next section deals with changes in the biology as it actually exists, applied to the model in order to gain insight into the functioning of the system.

There is no rigorous approach to sensitivity analysis possible in a model of this kind. In the first place the analysis will rarely be complete, since it is seldom possible to examine all the interactions resulting from simultaneous changes in the values of two or more parameters. Even where parameters are only varied independently, it is difficult to compare the effects in a meaningful way. A common method is to compare the results on a model's output of constant proportional changes in each parameter, assuming that those yielding the greatest effects are most worthy of further study. However, the effect on the model will depend on the absolute value of the parameter. For instance, a 50% decrease in the daily mortality rate of 0.03 will have a much smaller effect than a 50% decrease in the daily survival rate of 0.97, and it is hardly appropriate to conclude that more research should be devoted to survival than mortality. In the present case, therefore, sensitivity analysis involves testing a selected range of specific alternative hypotheses.

The main method adopted for answering the questions in this and the following section is to consider the way in which changes applied to the model affect the relationship between the numbers of fundatrices one year and those the next, expressed as their logarithms (Fig. 54a), and, less frequently, their effects on population trends within a year. Fig. 60 shows the population behaviour through time corresponding to the different relationships, within the ranges shown on the graphs. Where the relationship is linear, it is described empirically by the equation:

$$\log N_{t+1} = a^1 + b^1 \log N_t$$

or

$$N_{t+1} = aN_t^{1-b}$$

where $N_t$ and $N_{t+1}$, are the numbers of fundatrices in successive years. There is an equilibrium point at $N_t = a^{1/b}$ and the population exhibits the following behaviour depending on the values of b and $b^1$:

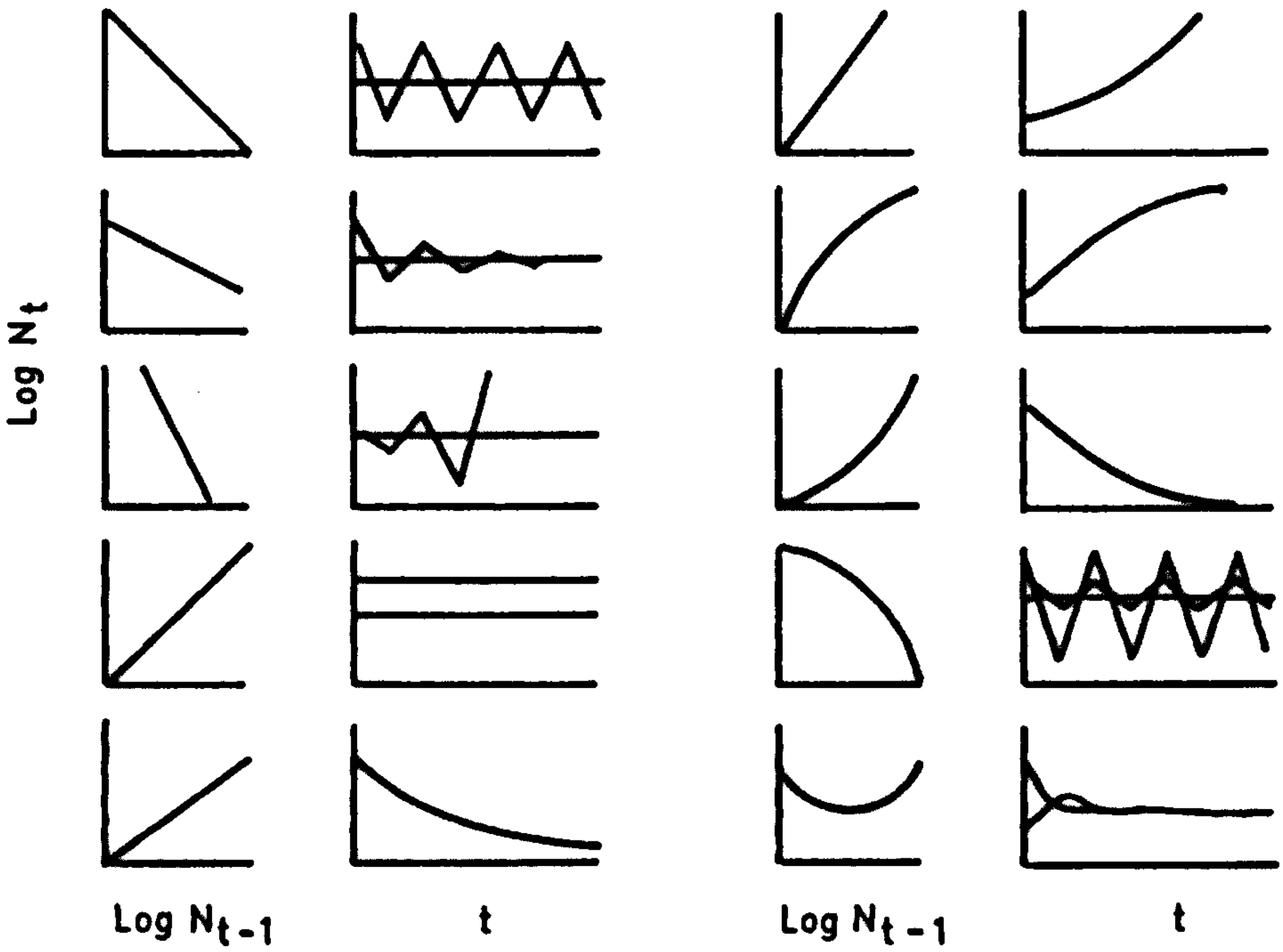

Fig. 60. Effects of different relationships between fundatrices in successive years on population behaviour in time, over the ranges shown in the graphs.

$b \leq 0, b^1 \geq 1$; Continuous increase or decrease
$0<b<1, 0<b^1<1$; decrease or increase towards a stable equilibrium point
$b=1, b^1=0$; perfect regulation—attainment of a stable equilibrium point in the next year
$1<b<2, \quad -1<b^1<0$; converging oscillations
$b=2, b^1=-1$; stable limit cycles
$b>2, b^1<-1$; diverging oscillations and eventual extinction

Where the relationship is curvilinear, it can be considered as a series of straight-line segments and the above conclusion applied to each. For instance, if the relationship at any point has a slope ($b^1$) greater than 1, the population will continue to increase from this point unless at higher numbers the slope changes to become less than 1. The relationship must be distinguished from the usual Ricker curves (Ricker, 1954) and, when linear, from an equation commonly used to describe the dynamics of single-species, discrete-generation populations, since in the present case the relationship operates not from generation to generation but from year to year, covering four or five overlapping generations. It represents the outcome of interactions between competition, predation and various time lags, and the parameters a, $a^1$, b and $b^1$ in the linear form given above are actually complex functions of these different effects. In each figure the normal behaviour of the model is indicated by a dotted line and equilibrium points occur where the solid one, representing the new output, gives $\log N_{t+1}$ equal to $\log N_t$.

The main areas of uncertainty in the model are the forms of the relationships governing alate flight, the maximum adult longevity in the field, the average daily mortality of all stages and the way in which mortality varies with wind speed.

Fig. 61a shows the effects of changing the adult flight component (the proportion of alates flying per day in response to current weighted population density) in two ways: by doubling the slope of the relationship, hence the density-dependence; and by making the response dependent only on densities of adults and 4th instar nymphs, since it may be that younger nymphs do not affect the activity of adults (Kidd, pers. commun.). In neither case is the output significantly changed. Figs 61b and c show the results of alterations to the nymphal component (the proportion of alates flying per day in response to nymphal experience of crowding). These include: removal of the density threshold and two alterations to the slope of the relationship (Fig. 61b); halving of the response; reduction of the maximum response from 0.4 to 0.3 (Fig. 61c). The form of the year-to-year relationship is fairly insensitive to changes in the nymphal component at low or medium initial densities, the only effect being a reduction in its elevation when the threshold is removed, giving more flight at low densities (Fig. 61b). At high initial densities, however, the result depends to a greater extent on the form which the nymphal component takes; different responses tend to give less marked population crashes during summer hence higher numbers of aphids at the end of the year. The behaviour of initially high-density populations during the year, characteristic of different nymphal flight components and different adult ones, are shown in Fig. 62, with no other control processes acting. The adult component yields population peaks in successive generations, while the nymphal one yields peaks in every other generation and more pronounced crashes if it embodies a threshold.

Varying the density-independent background level of flight has a similar effect to changing the background mortality rate of all instars, discussed below (Fig. 61d, compare Fig. 68a). If it is increased, then densities during the year are lowered, the impact of density-related processes reduced, and overcompensation in the

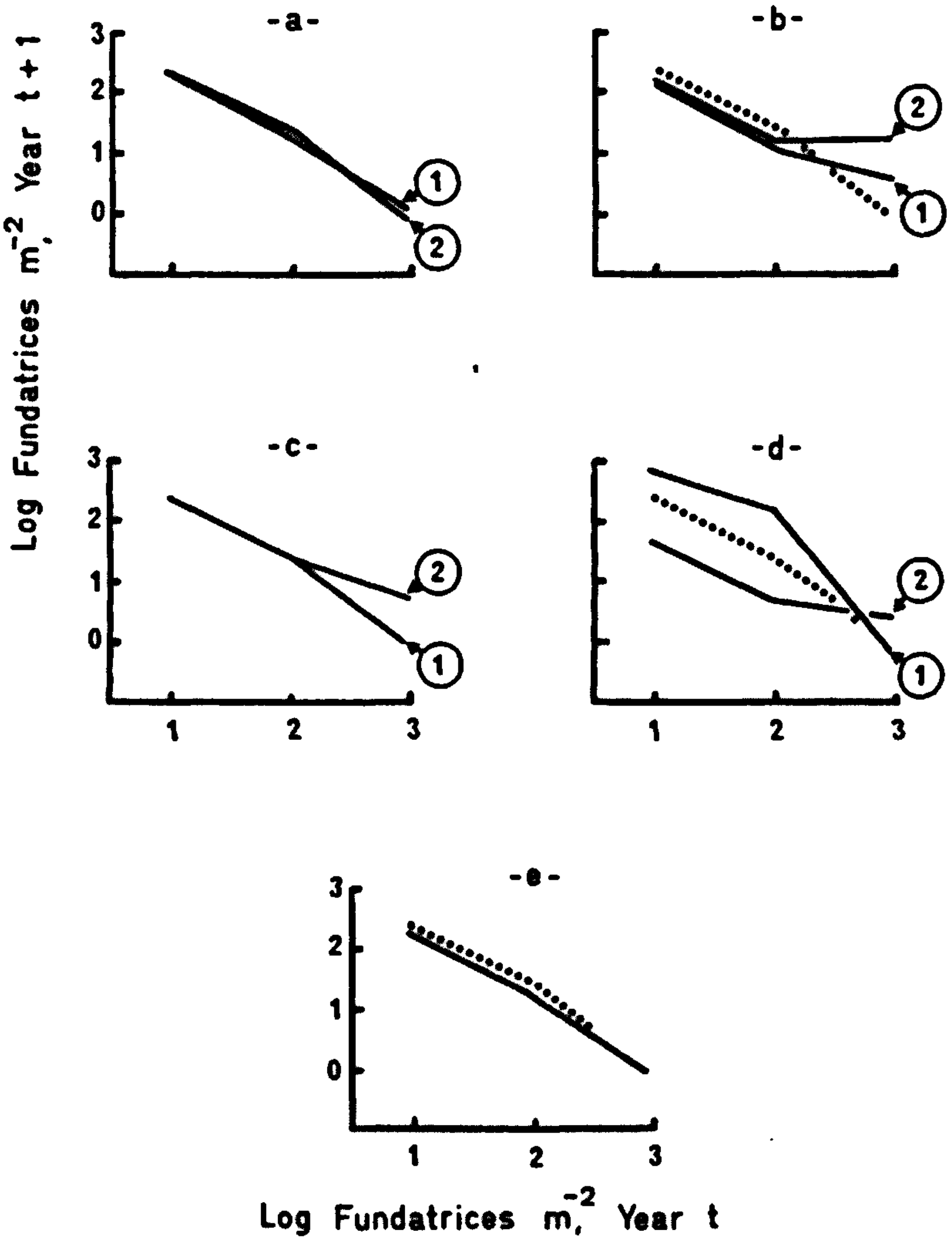

Fig. 61. Effects of changes in the flight equations and the maximum adult longevity on the predicted year-to-year relationship between fundatrix numbers. a) The adult flight component is doubled (FA = 0.01WD, Line 1) or made dependent on densities of adults and 4th instar nymphs only (FA = 0.005(A + N), Line 2); b) the threshold is removed from the nymphal component (FN = 0.01DD, Line 1) or the threshold is removed and the slope halved (FN = 0.005DD, Line2); c) the maximum level of the nymphal component is reduced from 0.4 to 0.3 (Line 1) or the overall response is halved (Line 2); d) the background flight level is halved (Line 1) or doubled (Line 2); e) the maximum adult longevity is halved, from 30 to 15 days. FA and FN are proportions of alates flying per day, A and N densities of adults and 4th instar nymphs, WD weighted density of all stages and DD the mean total density during nymphal development. —— new relationship; ····· original relationship.

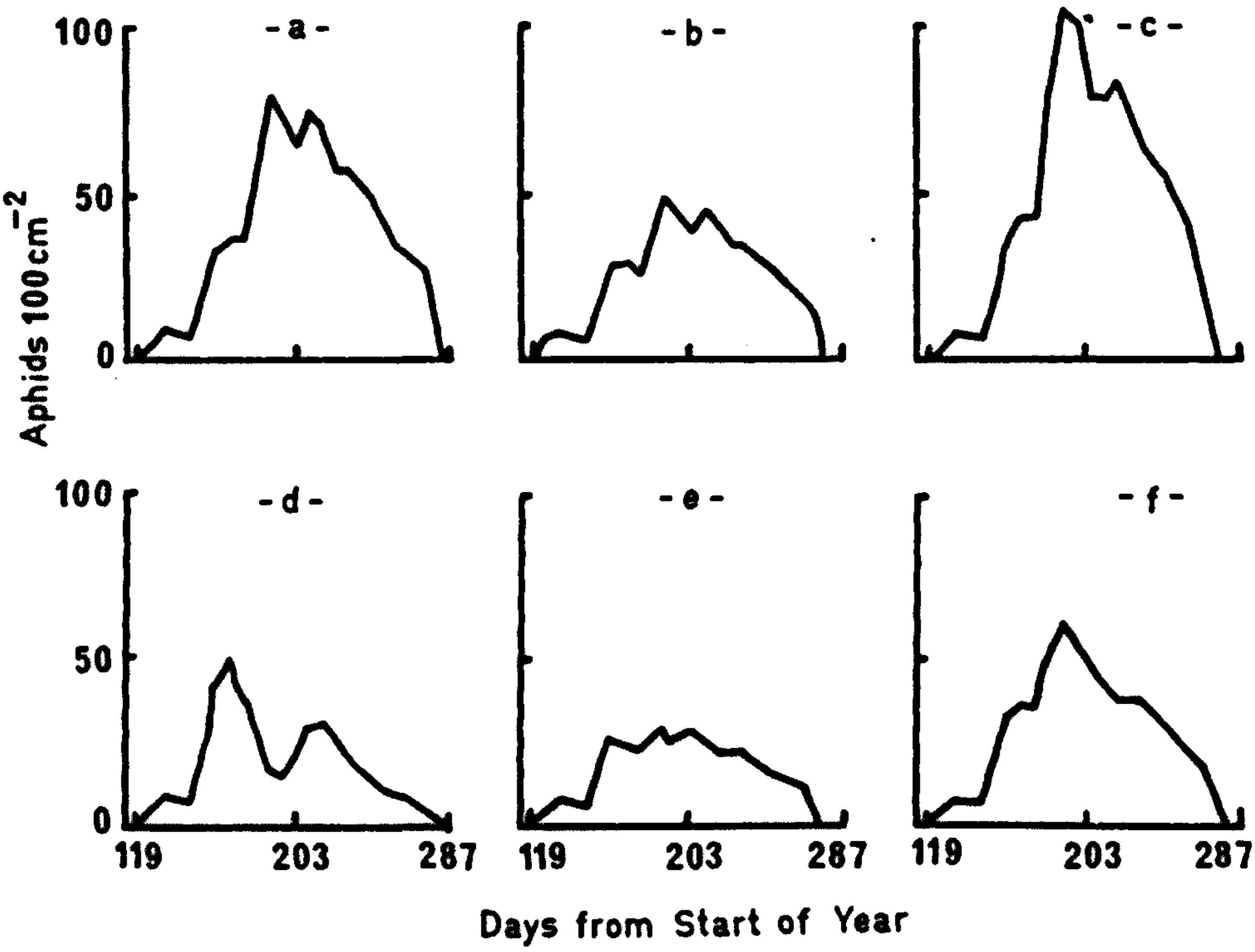

Fig. 62. Effects of different adult (a), b) and c)) and nymphal (d), e) and f)) flight components on population behaviour, generated by the model, when each one is the only control process acting: a) the normal adult component ($FA = 0.005WD$); b) the adult component doubled ($FA = 0.01WD$); c) the adult component dependent only on densities of adults and 4th instar nymphs ($FA = 0.005(A+N)$); d) the normal nymphal component ($FA = 0.01(DD-10)$, $0 \leq FN \leq 0.4$); e) the nymphal component with no threshold ($FN = 0.01DD$, $0 \leq FN \leq 0.4$); f) the nymphal component with no threshold and reduced slope ($FN = 0.005DD$; $FN \leq 0.4$). FA is the proportion of alates flying per day in response to the current weighted density of all instars (WD) or to current density of adults (A) and 4th instar nymphs (N), and FN that are dependent on density during nymphal development (DD); densities are numbers/100 cm$^2$.

year-to-year relationship lessened, first at the high initial density then at the medium density. If it is reduced, higher numbers result at the low and medium initial densities and the theoretical equilibrium level is increased.

Altering the maximum adult longevity from 30 to 15 days has very little effect (Fig. 61e). Changing the relationship between mortality of all instars and wind speed, making it linear or more curvilinear, also has no significant overall effect; rather the fit between modelled and observed population trends tends to be better in some years and poorer in others.

## 4.3 Effects of the different processes

There are two key questions to be asked of the model. First, what are the effects of the various density-related processes on the aphid population: in particular what causes the observed inverse relationship between numbers at the beginning of successive years, and which factors are capable of regulating the populations? Second, what are the effects of disturbing factors on the population's behaviour? These questions are considered first, followed by the effects of varying specific parts of the system or components of the main processes.

### *4.3.1 Density-related processes*

The density-related processes considered are:

1. The adult flight component (dependent on current density)
2. The nymphal flight component (dependent on density during nymphal development)
3. Changes in adult weight (affecting reproductive rate and dependent on density during nymphal development and cumulative density)
4. Predation (a complex function of density)
5. Flight and mortality dependent on cumulative density

The cumulative density effects on flight and mortality remain to be confirmed by experiment but the existence of the other processes is well established. The possibility that aphids are also subject to density-dependent mortality cannot be discounted (Barlow, 1977), though there is little evidence for it and the effect is similar to that of density related flight (Fig. 67). It is difficult to specify the nature of the density-dependence involved in predation; the numerical response of the coccinellids is density-dependent at low densities and inversely density-dependent at high ones (Fig. 53a), but whatever the predators' response the effect on the aphid population depends also upon its own subsequent behaviour and upon the time of year. Of the above list of density-related processes, those involving flight are behavioural while the others are imposed either by the behaviour of other species or by the constraints of the aphids' physiology or environment.

What causes the inverse year-to-year relationship? There are two stages involved in answering this or any similar question which it is important to distinguish; the first involves the factual question as to the basis of the relationship in the model, while the second involves the hypothesis that this also holds in the field. To answer the question in a situation where the processes interact in a complex manner, each in turn was removed from the model (Fig. 63). Removal of an active regulating factor will increase the slope of the relationship, either until it becomes greater than or equal to 1 and the population is no longer controlled, or to another value still less than 1 if a second regulatory process is effective or is activated when

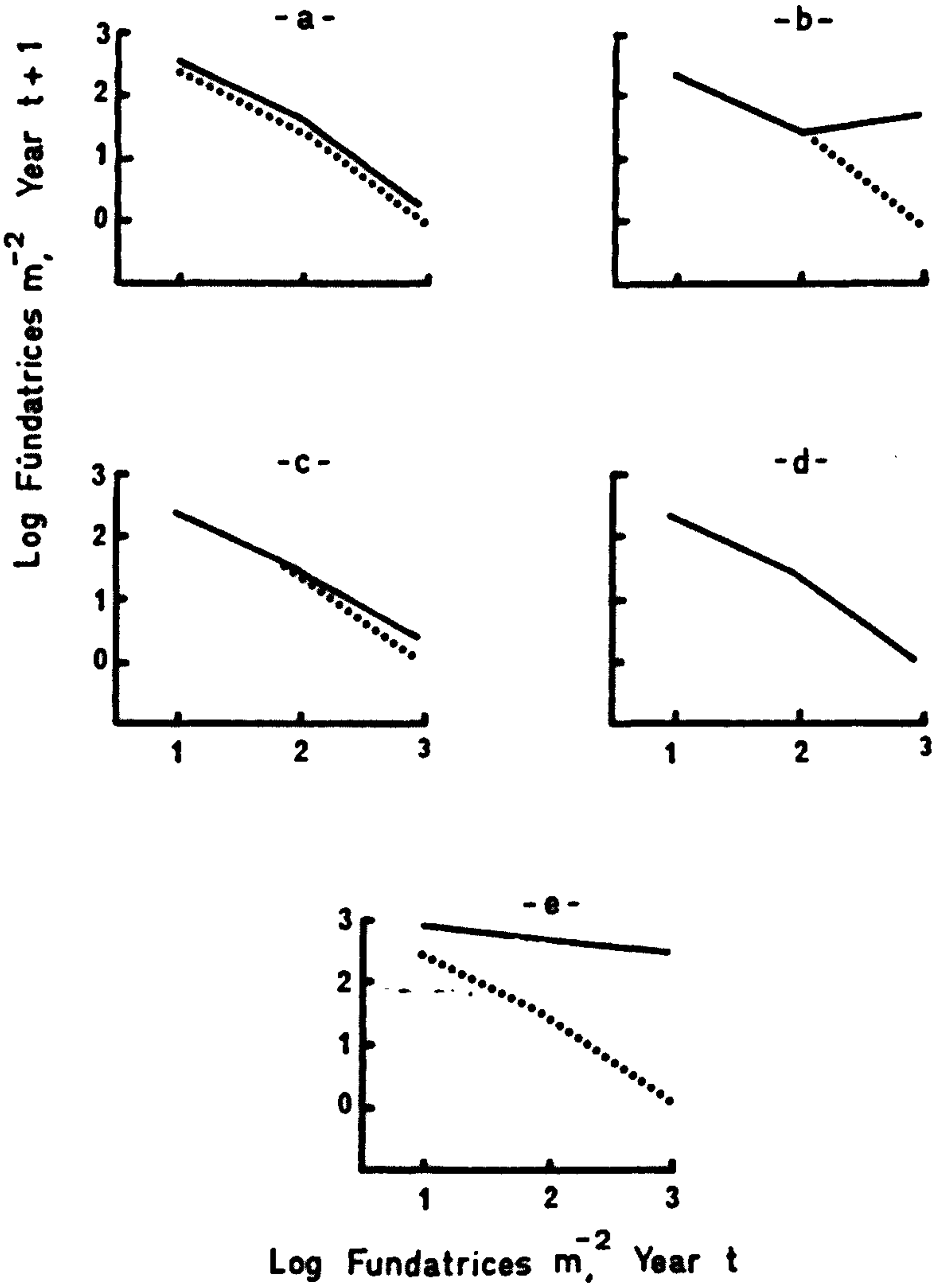

Fig. 63. Effect on the year-to-year relationship between fundatrix numbers of removing each control process in turn from the model, namely: a) the adult flight component; b) the nymphal flight component; c) changes in adult weight; d) cumulative density effects; e) predation. —— new relationship; ····· original relationship.

the first is removed. If there is no change in the relationship this can mean one of two things: either the process removed plays no part in regulating numbers when others are active, though it may be rendered effective in their absence; or a second regulatory process substitutes perfectly for the first. Which of these outcomes is true can usually be assessed by looking more closely at details of the model's output, such as the population trends during the year. The most important regulatory processes may be defined as those whose removal results in the greatest change, and if this is to the extent that the inverse relationship is destroyed, the processes involved must be regarded as necessary, though not necessarily sufficient conditions for its existence. In this case removal of the cumulative density effects yields no change in the output (Fig. 63d) and it is easy to see that this is because they are ineffective at the relatively low cumulative densities resulting from the action of the other processes. Removal of the adult flight component has a small effect at all initial densities (Fig. 63a) and removal of the weight effects produces a slightly greater change at the high density only (Fig. 63c). However, the processes giving the most significant changes are the nymphal flight component at high initial densities and predation at medium and high initial densities (Figs 63b and e). The latter, therefore, are the most important regulatory processes and both are required to give the inverse relationship in the model, since this is largely eliminated when either process is removed. Fig. 64a shows the relationship which results when the two most important processes, predation and the nymphal flight component, act alone. Although these give overcompensation, the precise extent of the response generated by the model at high initial densities is also a result of changes in adult weight and, to a lesser extent, the adult flight component, as shown in Fig. 64a.

Which factors are capable of regulating the population? This is a slightly different question from asking which factors are normally involved, in an interaction with others. Clearly, some processes may not be dependable in the sense that their effect is always the same; predation and flight in particular may be suppressed or enhanced by weather, and in these circumstances other factors like the cumulative density effects may become more important. Although both predation and the nymphal flight component are necessary to give the inverse relationship discussed above, in the absence of either the population is still regulated by one or more of the other processes. There is an enormous potential for increase if no control process acts (Fig. 64b), although in practice the food supply would be

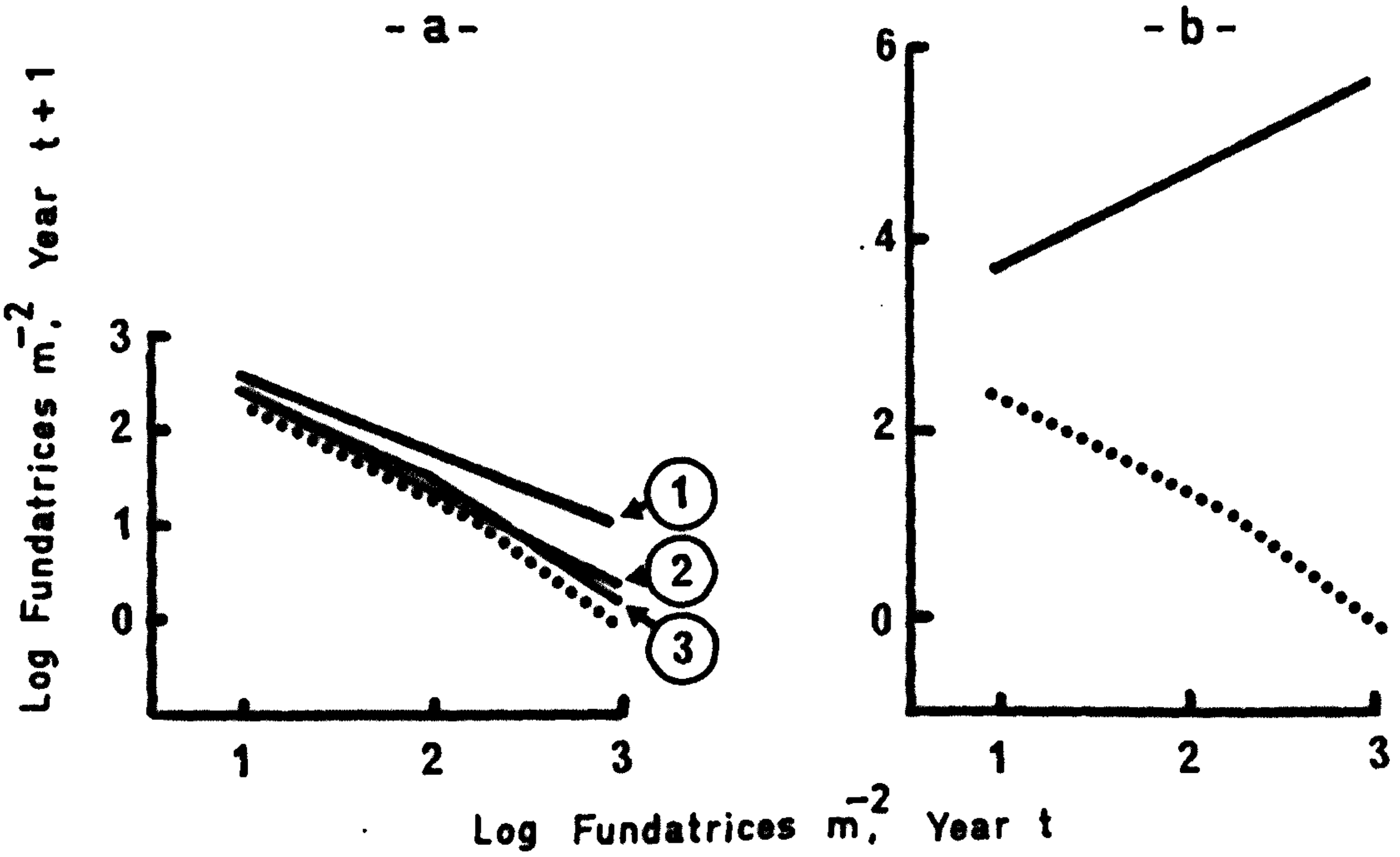

Fig. 64. Effect on the year-to-year relationship between fundatrix numbers of: a) the presence of the key control processes, predation and the nymphal flight component, alone (Line 1), with the adult flight component added (Line 2), or with weight changes added (Line 3); and b) removal of all controls. —— new relationship; ····· original relationship.

exhausted and the population rapidly eliminated were this to occur. Nevertheless this demonstrates the effectiveness of the control processes, for each alone, with the exception of predation, has the potential for regulating fundatrix numbers at levels not much higher than normal (Fig. 65), while cumulative density effects and weight changes can even cause overcompensation (Figs 65c and d). Although predation fails to regulate the population over the whole range of initial densities, it gives results closest of all to normal at low and medium densities, confirming its role as the main factor determining the form of the relationship over this range. In interpreting these figures, showing the year-to-year relationships, it is important to remember that they do not show all the effects of the processes, for numbers during the year may vary more than numbers of fundatrices at the beginning of each; a medium initial density may yield a medium initial density in the following year either if the population stays low or if it rises to high levels and crashes. In addition, any discussion of regulation must relate to the average impact of disturbing factors or to a certain range of population

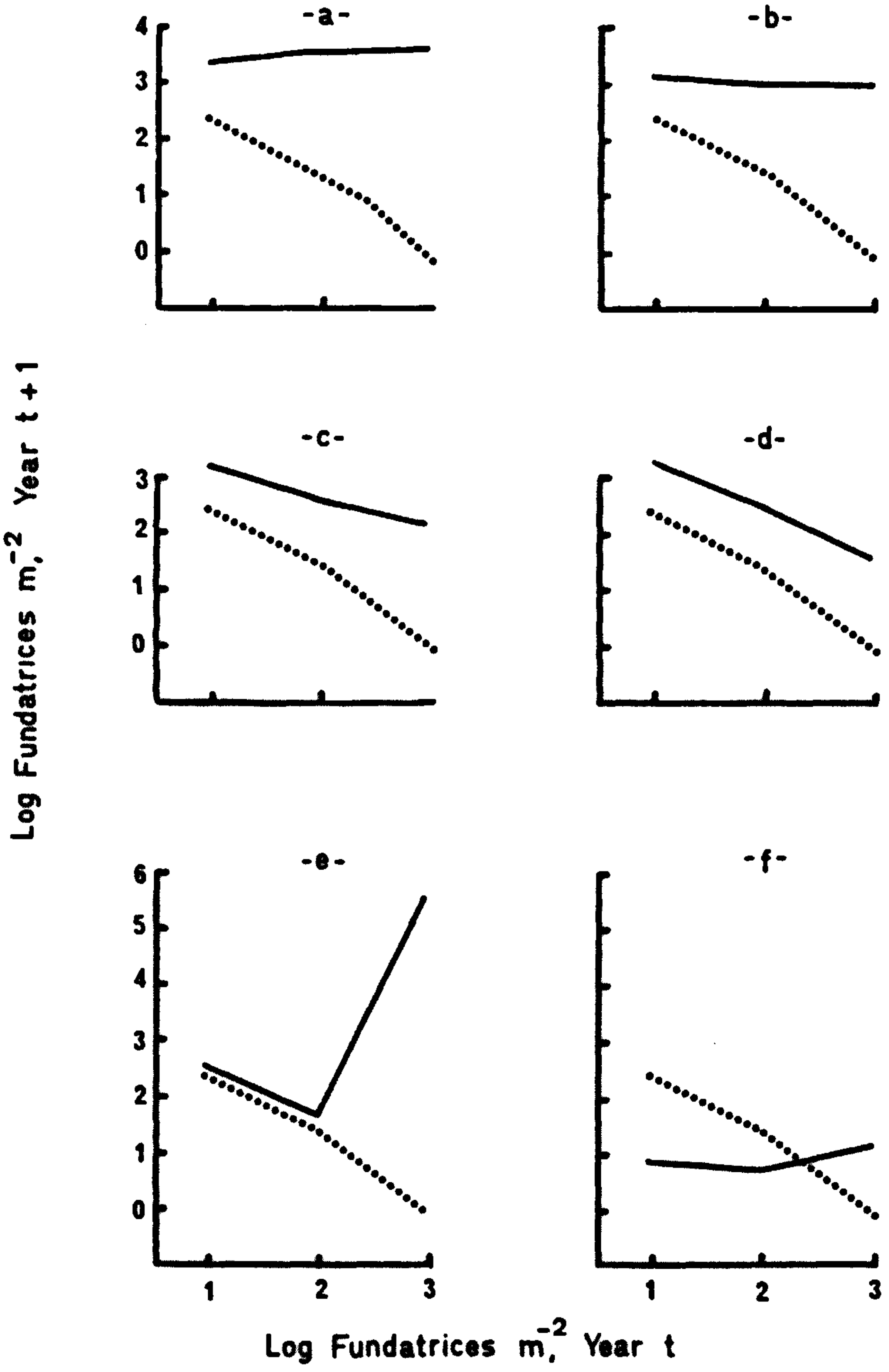

Fig. 65. Effect on the relationship between fundatrix numbers in successive years, of each control process acting in isolation: a) the adult flight component; b) the nymphal flight component; c) changes in adult weight; d) cumulative density effects; e) predation; f) predation with aphid background mortality doubled. —— new relationship; ····· original relationship with all processes included.

densities; there may be a number of local equilibria around which regulation occurs, and it is well known that populations normally controlled by predators and parasites may 'escape' under particularly favourable environmental conditions to reach a much higher though normally temporary equilibrium level. The lime aphid shows the same behaviour, for predation alone can regulate the population and even cause overcompensation within the low to medium range of initial numbers but when the latter are high the aphid population escapes this control (Fig. 65e). If the background mortality rate is increased from 3% to 6% per day, then predators can regulate the population over the whole range of initial densities (Fig. 65f), and the precise effects of the other control processes will likewise change with variations in background flight or mortality rate.

Hence there is no key regulating factor, nor are the effects of the control processes in Fig. 65 additive. Rather, the lime aphid displays a system of hierarchical regulation with each process capable of substituting for another; moreover, the different processes interact and different ones are involved at different initial densities. The model shows that an inverse relationship between fundatrix numbers in successive years, and between fundatrix and ovipara numbers within a year, can be generated in two ways. The first involves predation at medium initial densities and the combination of predation and the nymphal flight component at high ones; at the medium initial density numbers stay fairly low throughout the season but at the high density there is a marked crash (Fig. 55). This mechanism, embodying processes known to exist but with the assumption that their magnitude in the field is comparable with that determined in laboratory experiments, yields results similar to those observed in most years in the field. The second mechanism involves an increase in flight or mortality dependent only on accumulated density during the season. Here population peaks reached during the year are higher and the inverse relationship results from changes in the timing of the crash, which occurs when the cumulative density reaches a threshold; the higher the initial density the sooner the threshold is reached and the crash occurs, and the fewer the sexuals and eggs produced (Figs 66a, b and c). This mechanism has not been verified experimentally but there is independent evidence for its existence (Sections 3.5.3 and 3.5.4) and it would explain the population's behaviour in 1971. In this year, and on tree 6 in 1973, the points in the year-to-year relationship are fairly close to those in 1966 and 1967 (Fig. 54a), yet the population behaviour during the year was quite different; in 1971 much higher numbers were attained, few predators were present, and the population crashed in August (Fig. 11). Clearly, something must have suppressed any density-related flight during the first part of the year, and the model shows that re-activation of flight in late July, combined with preda-

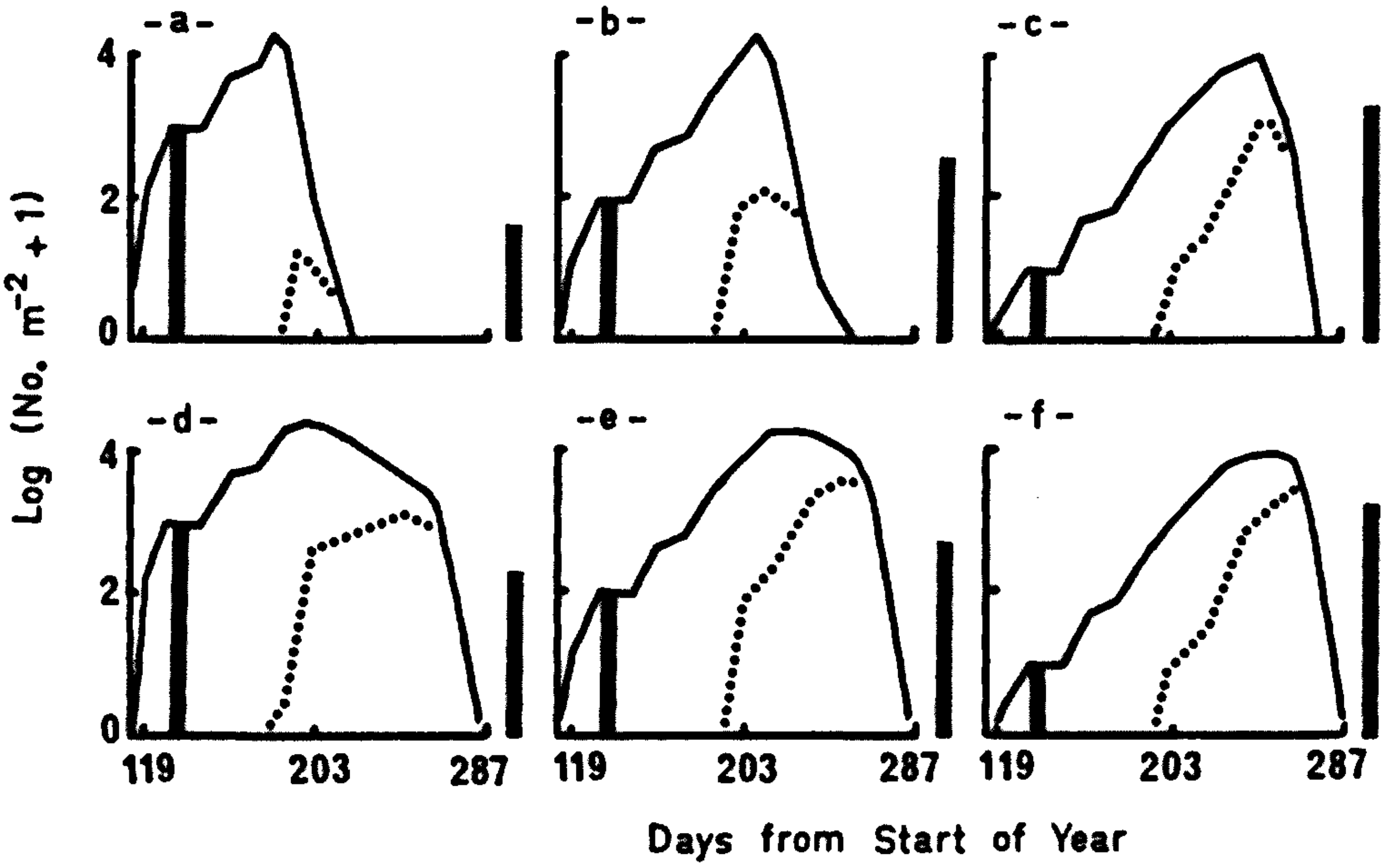

Fig. 66. Effects of cumulative density-dependent processes (a,b and c) and adult weight changes (d, e and f), acting alone, on population trends throughout the year for high, medium and low initial densities. —— total numbers, ····· ovipara numbers; vertical bars are fundatrix numbers in the current and following years.

tion at a reduced level and a decline in adult weight and reproductive rate, both of which were observed in 1971, is not sufficient to give a complete crash (Fig. 67). There is no evidence for increased mortality towards the end of a year, independent of aphid density, which might give a crash when combined with the reduction in reproductive rate. On the contrary when densities are low mortality is constant (Fig. 27) and low-density populations are capable of increasing at the time of the 1971 crash (Fig. 11). Cumulative density effects, therefore, appear necessary to account for its existence. The third mechanism giving an inverse year-to-year relationship, through changes in adult weight alone, yields population behaviour during the year quite unlike any observed, and peak numbers far higher (Figs 66d, e and f). Moreover, here the inverse relationship results not from a reduction in ovipara numbers when initial densities are high, but from a reduction in the number of eggs laid by each because of their lower weight; there is no inverse relationship between fundatrices and oviparae within a year.

Overcompensation between years cannot be the result of density-related processes operating within a generation or from one generation to the next. Effects of such processes simply cancel out over the

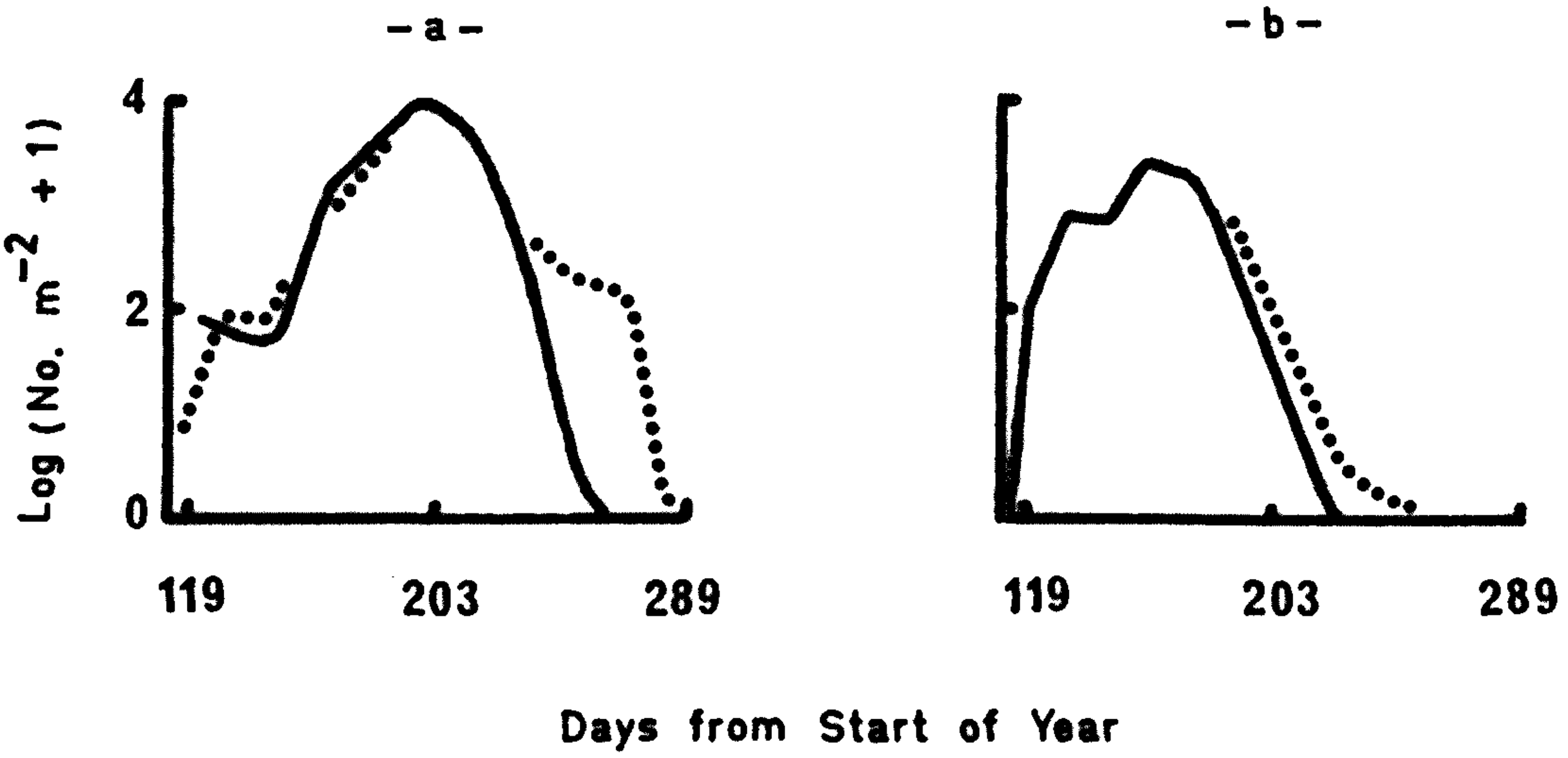

Fig. 67. a) Nature of the decline in numbers resulting when the population is allowed to reach high numbers in early summer, through suppression of flight at this time (see text), but when cumulative density effects are removed (——; ·····, population trends observed in 1971). b) Effect on the population crash from a high initial density (as in 1969) of replacing density-related alate flight (——) by density-dependent mortality of all stages (·····; % daily mortality = 0.001 × numbers/100 $cm^2$).

4 or 5 generations in the year. Rather an effect is required which persists through the season, such as predation, a reduction in adult weight or an increase in flight or mortality related to cumulative density.

Although two mechanisms have been discussed whereby density-related processes can account for the observed inverse year-to-year relationship, the possibility must be considered that the latter is due to chance, and that numbers each year are determined by weather. Under this hypothesis the expected variance would be between years not between trees, and the significance level of the relationship in Fig. 7 is far lower if points for different trees are pooled for each year; clearly, extensive replication in time is highly desirable in population studies in order to take full account of variations in weather, or to test a model's ability to do so. It is unlikely that the inverse relationship is due to chance; there is ample independent evidence for the existence of the density-related processes, and on tree 3 where coccinellids were much scarcer and cumulative density effects absent there was no trace of an inverse relationship.

### *4.3.2 Density-disturbing processes*

Weather may influence population behaviour through its effects on a number of different processes, namely egg-hatching, development rate, growth rate, reproduction, predation, other mortality and flight. Temperature is the most important driving variable affecting the first three processes, but the extent to which these vary in the field has already been shown to be insufficient to give the gross changes evident at the population level (Fig. 56). The same is probably true for the effect of temperature on predation, though this is not included in the model. Good and bad years, favourable and unfavourable for population growth, must therefore be determined largely by the effects of weather on flight, mortality or both. The nature of these effects is not fully understood. So to represent favourable and unfavourable environmental conditions the model was simply run with different background mortality rates and flight components.

The effect of progressive increases in mortality (Fig. 68a) is to reduce the mean level of abundance and the theoretical equilibrium population, but also to change the slope of the year-to-year relationship from negative through zero to positive, first removing the overcompensation and then decreasing the degree of regulation. This is because the increasing mortality exerts a greater effect at low densities than at high ones, being counterbalanced in the second case by a relaxation of control by density-related processes. The lines in Fig. 68a corresponding to mortalities of 1.5% and 6% per day encompass most of the variation observed in the field (see Fig. 54). At the higher level of 6%, the population is almost perfectly regulated but at extremely low numbers (8 fundatrices/m$^2$), and if the background mortality is increased to 9% it becomes extinct. If the environment is extremely favourable for population growth, such that both mortality and flight are only half the normal values, there is still an inverse relationship but with higher fundatrix numbers at low and medium initial densities (Fig. 68b); in this case, however, it results from the action of cumulative density effects and the population peaks reached during the season are much higher. In all these changes it is assumed that the mortality of predators remains the same. In the absence of predation the population is much less sensitive to variations in the mortality rate between 1.5% and 6% per day and the equilibrium point remains unchanged; at the slightly higher mortality of 9%, however, the population still becomes extinct (Fig. 68c).

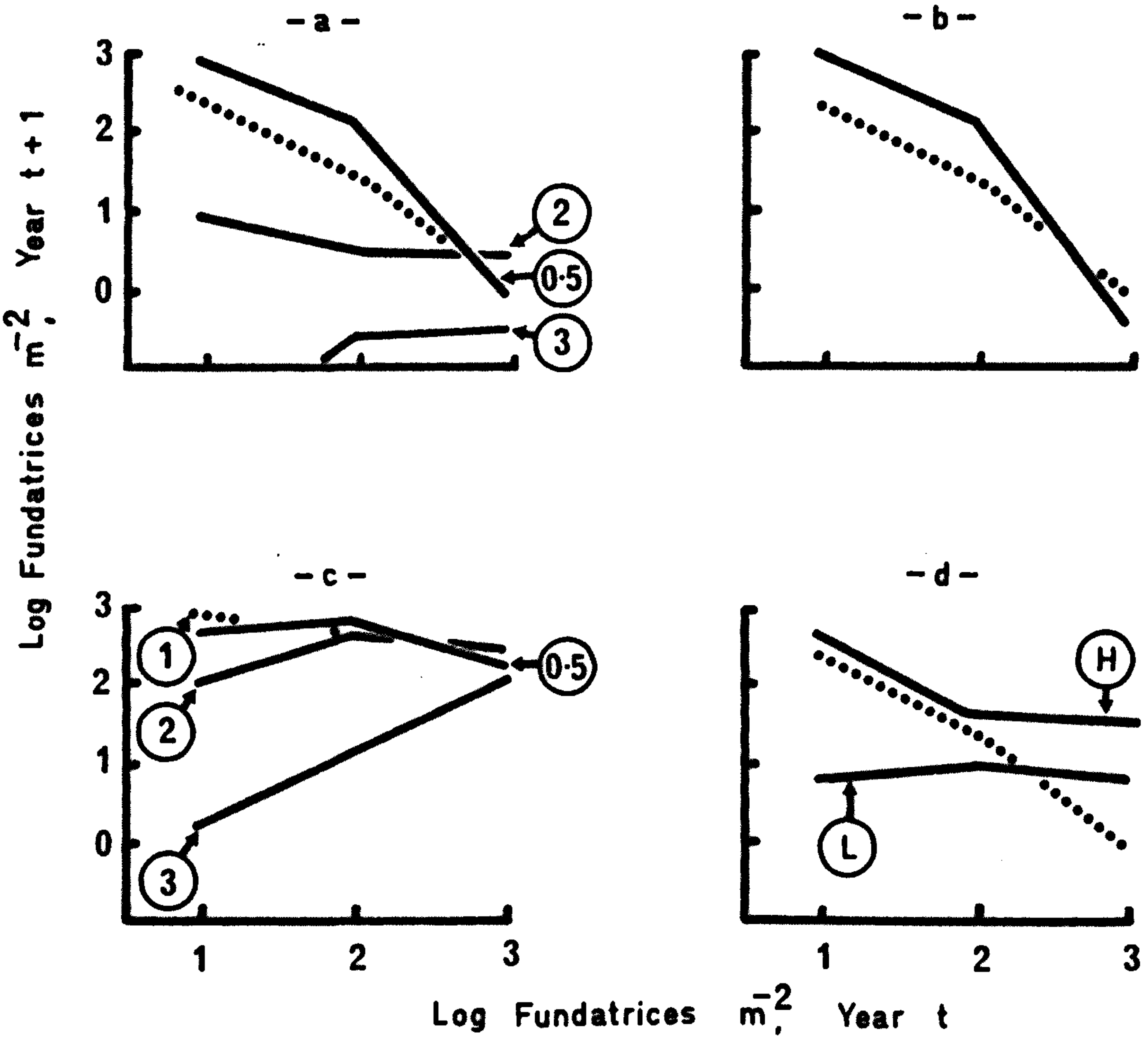

Fig. 68. Effects on the relationship between fundatrix numbers in successive years of variations in background mortality, flight and temperature (--- normal relationship): a) background mortality rate 0.5, 2 and 3 times normal; b) background mortality and all flight 0.5 times normal; c) as a) but with predation removed ((1), normal relationship in absence of predation); d) temperatures 2°C higher (H,——) and lower (L,——) than normal.

Normal variations in temperature appear to have relatively little effect but Fig. 68d shows the results of a 2°C increase and reduction in average temperatures throughout the year, assuming that predation is unaffected. Reducing the temperature has a greater effect than increasing it, particularly at the lowest density where it gives a 35-fold decrease in fundatrix numbers, showing the significance of even a modest temperature change if this is sustained over a whole season. At high initial densities, increasing the temperature effectively allows the population to escape the overcompensating action of predation.

### 4.3.3 *Components of predation*

Having shown that predation has a significant effect on population behaviour of the lime aphid, we then assess the relative importance of the two main predators and the alternative prey. Fig. 69a shows that removal of the leafhopper or increasing its numbers does not affect the aphid population. Similarly, removing the black-kneed capsid has little effect, but here doubling the average number present does reduce aphid densities slightly over the whole range of

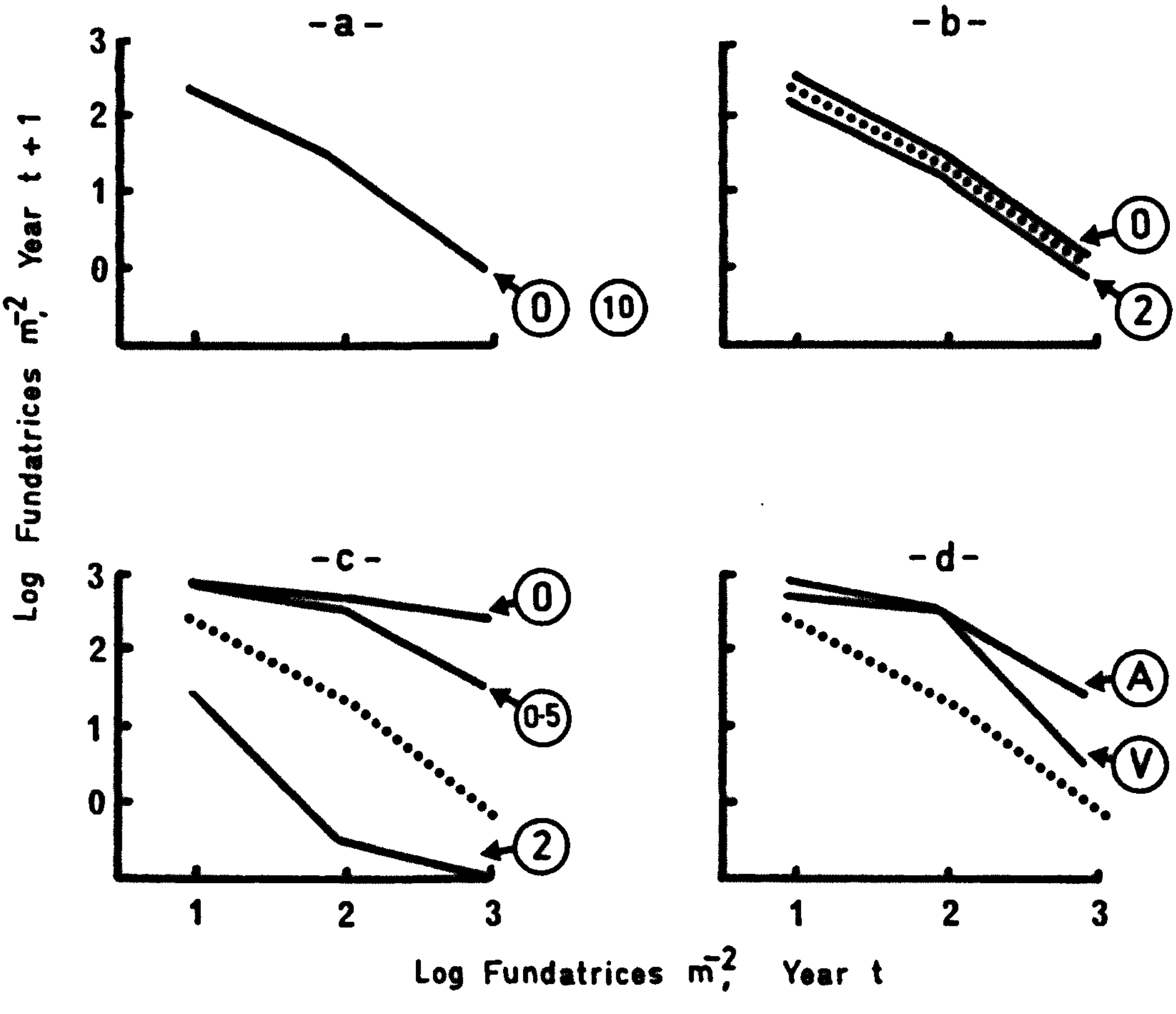

Fig. 69. Effects on the relationship between fundatrix numbers in successive years of changes in the components of predation (---- original relationship): a) removal of the leafhopper or a 10-fold increase in its numbers; b) removal of the black-kneed capsid and a 2-fold increase in its numbers; c) removal of the 2-spot coccinellid, a halving and a doubling of its numbers; d) a halving of the coccinellid attack coefficient (A) and maximum rate of eating prey (V).

initial population sizes (Fig. 69b). Removing the coccinellids gives a result similar to removal of all predation (Fig. 69c, compare Fig. 63e), suggesting that they are almost entirely responsible for its effects, described above. Doubling coccinellid numbers markedly reduces mean aphid abundance (Fig. 69c), bringing the theoretical equilibrium population down to 14 fundatrices/m$^2$ (log value of 1.15).

Given the importance of the coccinellids, Fig. 69d shows the significance of the components of their functional response. At low initial aphid densities, halving attack coefficients or the maximum amount of prey which the coccinellids can eat both have relatively little effect because few coccinellids are present. At medium initial densities either alteration greatly increases the fundatrix numbers in the next year, being virtually equivalent to complete removal of the coccinellids (compare Fig. 69c). In other words a proportional change in the attack coefficient or the amount required for satiation has a greater effect on the aphid population when its value is large than when it is small, and the same is also true for the actual number of coccinellids present. This is the reverse of what would be expected from the functional response equation (p. 38), but arises because a decreasing mortality from predation is eventually compensated for by the resulting increased effect of the aphid's intraspecific control processes. At high initial aphid densities the population crashes to low levels in the presence of large numbers of coccinellids and under these circumstances the coccinellids are unlikely to be satiated. Attack coefficients are therefore of greater significance than the maximum amount each predator can eat per day, so reducing the attack coefficient has the greater effect on aphid numbers (Fig. 69d).

It is interesting to consider why the predators do not appear in larger numbers. For the coccinellid it has already been shown that a numerical response which doubles the number present gives an extremely low equilibrium population of aphids. At this level the risk of extinction of the prey is high and it is unlikely in any case that the first instar coccinellids would obtain sufficient food for survival (Dixon, 1959 Wratten, 1973). Since the black-kneed capsid has a smaller effect, however, slightly higher numbers can be sustained here. Using the model, it is possible to calculate the rate of increase of the capsids, over 1 generation, for different initial numbers of capsids and aphids. There are three basic values for this rate of increase: 1.1 if aphid numbers are fairly high throughout the year; 0.15 if they fall below a threshold of 20/m$^2$ at the time of capsid egg-laying, as may occur at the high initial aphid density; and 0 if the aphid population is driven to extinction during summer or to the very low level at which capsid nymphs starve (Glen, 1973), as may be the case at the low initial aphid density. Fig. 70 shows that the capsid population can only increase if the initial number of eggs

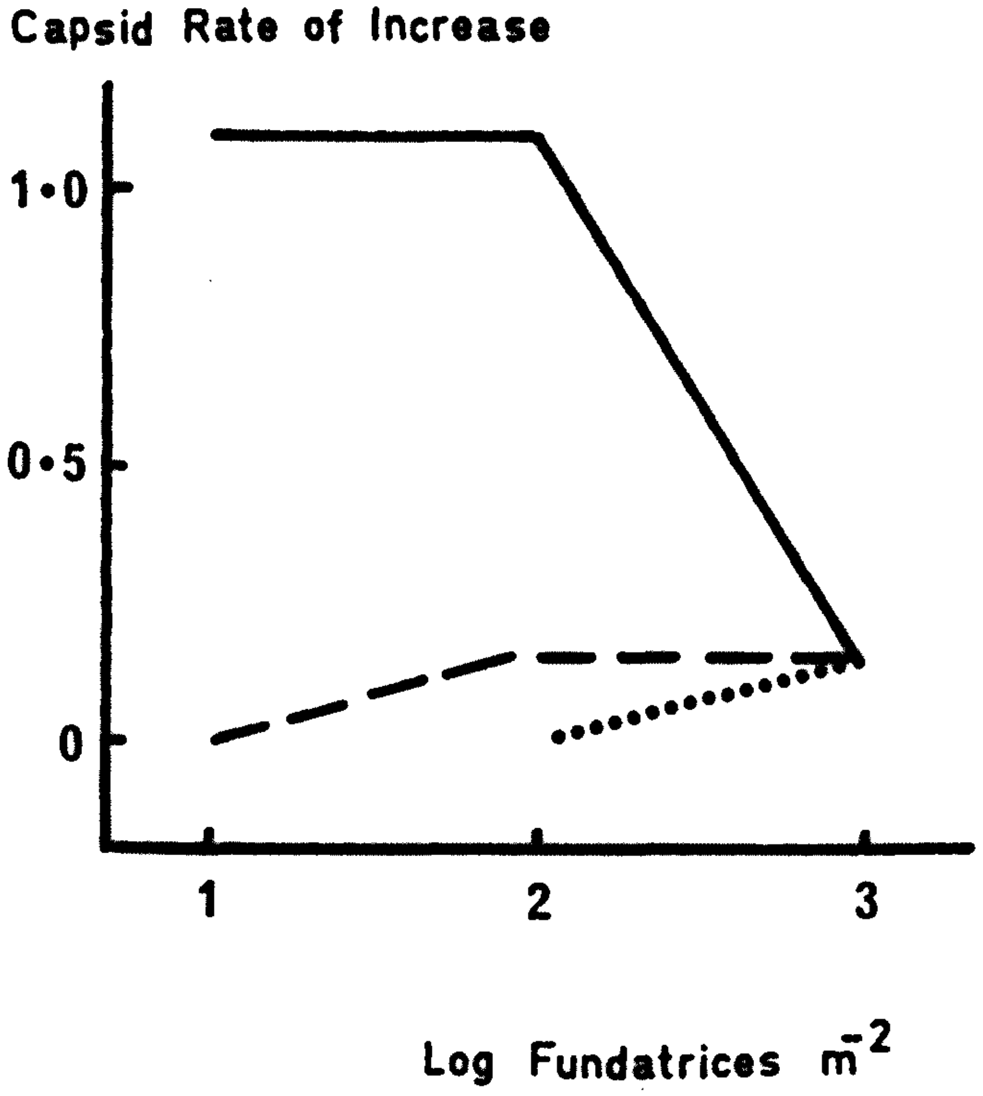

Fig. 70. Effects on the rate of increase of the resident black-kneed capsid population of different initial numbers of 1st instar nymphs (—— ≤ 5/$m^2$, - - - 10/$m^2$, ····· 50/$m^2$) at different initial aphid densities. Average capsid numbers observed are 2/$m^2$ and the rate of increase is taken as the ratio of 1st instar numbers in successive years.

is less than or equal to about 3 times the average observed abundance (about 2/$m^2$), and only then at the low or medium aphid densities. The model suggests, therefore, that both predators are present at the highest average abundance consistent with the long-term survival of their prey. Moreover, for most purposes the 2-predator/2-prey system can be considered as a 1-predator/1-prey one, comprising only the aphid and the coccinellid.

It has already been shown how changes in adult weights affect the year-to-year relationship (Figs 63c and 65c). Weight depends on density and cumulative density and exerts its effect on the population through the adult's pre-reproductive delay and reproductive rate. Figs 71a and b shows the results of direct changes made to these two factors, involving a halving and a doubling of their values. Averaged over the whole range of initial population densities, and the two changes in parameter values in each case, the effects of both

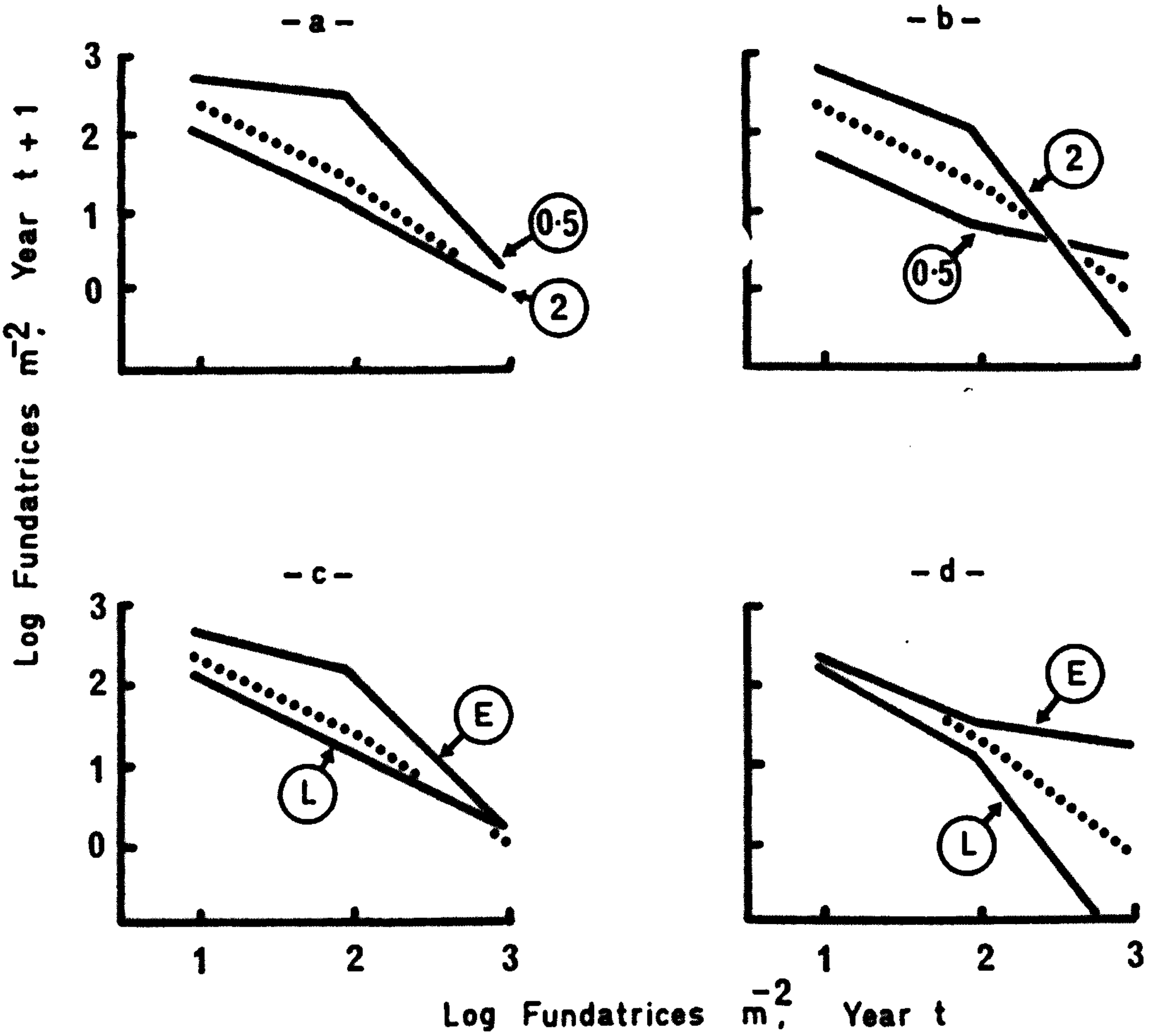

Fig. 71. Effects on the relationship between fundatrix numbers in successive years of: a) halving or doubling the pre-reproductive delay; b) halving or doubling the reproductive rate; c) causing aphids to moult early (E, 0.8 times normal development time) or late (L, 1.2 times normal development time); d) causing sexuals to be produced 2 weeks earlier (E) or later (L) than normal.

alterations are similar. Thus, the pre-reproductive delay and the reproductive rate are equally significant in their effects on the population's behaviour, though these effects take slightly different forms in the two cases. Decreases in the reproductive rate have smaller effects than similar proportional increases in the background mortality rate (compare Fig. 68a), though the results are qualitatively similar.

### 4.3.5 *Effect of parasitism*

Removal of parasitism from the model causes a slight increase in numbers of fundatrices produced at low and medium initial densities but the overall effect of parasites is small.

### 4.3.6 *Significance of development time*

What would be the effect if aphids moulted earlier to become adults of lower weight; would the increased pre-reproductive delay and reduced reproductive rate be compensated for by the decreased development time, in terms of the numbers of fundatrices produced in the following year? In fact, the positive effect of the decreased development time on population growth is greater than the negative one of reduced reproduction; moulting earlier gives a greater rate of increase in the short term. Taken over the whole year, however, the effect is somewhat more complex because of interactions with the intra-specific control processes and particularly with predation; it is small at initially high densities, for instance, because the effect of the population crash is far more significant. Nevertheless a decreased development time does give higher numbers in the next year (Fig. 71c) and the model shows that it also yields more colonising emigrant alates. It is not immediately obvious, therefore, why the lime aphid does not have a shorter development time though there are many constraints not considered here; for instance, while the effects of a shorter growth period on weight gain have been incorporated, physiological maturation may be a different process requiring a certain time at a given temperature for its completion. Small adult aphids are also more vulnerable to natural enemies. It is also interesting to note that in the absence of predation and as a consequence of the intra-specific control processes, these changes in development time have much less effect on numbers of fundatrices, though the effect on numbers of emigrants is actually greater.

### *4.3.7 Significance of the time at which sexuals are produced*

Since the transition to sexual production occurs only gradually, parthenogenetic reproduction and population growth is possible for a long time after this has started. At low initial densities, with a population increasing during the year, bringing forward the time of sexual production reduces peak numbers attained but gives a longer period over which sexuals are present. The net result is little change in their cumulative abundance and in the number of eggs produced (Fig. 71d). If the transition to sexual production occurred more suddenly, the outcome would be different. Then their cumulative abundance in any year and the number of eggs laid would be directly related to the size of the population at the time of transition, which in turn depends on the period available for parthenogenetic reproduction. The latter would thus be the most important factor, yielding fewer sexuals when it is short and the sexuals are produced early, than when it is long.

At high initial densities when the population is decreasing rapidly in summer, changing the time of sexual production has a much greater effect. If it is later in the year, as occurs in the sycamore aphid for example, there is a dramatic decline in the number of fundatrices produced and if the sexuals appear earlier there is a corresponding increase (Fig. 71d). At medium initial densities the effect is similar but much smaller.

Since producing many sexuals early appears to give a greater average increase in numbers over the year, it is not clear why such a strategy has not been developed further in the lime aphid.

## 4.4 Discussion

Other tree-dwelling aphids also exhibit the 'see-saw' effect (the inverse relationship between numbers of fundatrices and oviparae) notably the sycamore aphid and the walnut aphid, although in the latter case it is less well established (Dixon, 1977). A decline in reproductive rate following initial high numbers contributes to the effect in both cases; in the sycamore aphid migration appears to be the other main factor involved and in the walnut aphid the additional factor is probably predation (Dixon, 1977). Interestingly, a host-alternating species, *Aphis fabae*, exhibits the same inverse relationship, in this case due to the delayed action of predators attracted by an initial high density and exerting their main effect later in the year (Way, 1967). So, while such population behaviour is not unique among aphids the mechanisms causing it may differ.

Why should the lime aphid behave in such a way? At the lower densities and as in *Aphis fabae*, the effect is imposed by the action of predators and is the outcome of a time lag and a threshold; a population initially too small to attract many predators becomes larger after a time than one initially higher but subject to predation. However, at the highest initial densities predation alone cannot check population growth and it is the additional presence of a strong density-related flight component which gives the rapid decline in numbers observed. Why then has this kind of flight behaviour evolved? In its absence the population would be controlled by a decline in the weight and reproductive output of adults, or at an even lower level by cumulative density effects setting an effective limit on cumulative abundance of the aphid in any one year, below the level at which a host tree is seriously damaged. Nevertheless, in either of these cases the densities reached are extremely high, and if such infestations were sustained or occurred too frequently over a period of years it is possible that the tree could be damaged or killed. Thus, Llewellyn (1970) showed that about 8000 aphids/m$^2$ during the season will drain completely the annual net production of the tree, assuming no compensatory growth, and Dixon (1971b) suggested that the figure may be even lower, around 5000/m$^2$. As shown above, these values may be reached (log numbers of 3.9 and 3.7) in the absence of population regulation. In addition, Dixon (1971b) found that the roots of infested saplings do not grow. While death of a host tree has not been shown to result from aphid infestation, a prevention of growth of this kind could lead to extinction of an aphid population through suppression of recruitment to the population of its host, under conditions where the trees grow naturally from seed. Density-related flight behaviour may therefore avoid damage to the host. While a gene causing an aphid to refrain from such behaviour may be selected for in the short term, it seems reasonable to suppose that it would be eliminated in the long term, were the host to be destroyed. If the density-related response were replaced by a greater constant proportion flying, this would eliminate the risk of over-exploiting the host but reduce the theoretical equilibrium number of aphids, the mean density from year to year, and the ability of the aphid to recover rapidly from catastrophic mortalities at low densities. Clearly some flight is necessary, since colonisation must occur and must be selected for, however small the probability may be for any one aphid of encountering an alternative host. For although the life-span of the host is long relative to that of the aphid, and tree-dwelling aphids depart in this respect from what might be expected of animals considered to be r-selected (Southwood, 1976), nevertheless the tree lives for a finite time and any resident population incapable of movement is doomed.

Emigration by flight is therefore necessary, and a density-related response rather than a density-independent one not only fulfills the need for colonisation but also distributes flight according to the resident population's ability to sustain the loss and may play a part in preventing over-exploitation of the host. It could be asked why the density-dependence is so marked as to bring about a population crash; a nymphal flight component reduced by a half (Fig. 61) would appear to satisfy the main criteria for the aphid's success without the possible risks of extinction associated with dramatic population crashes. There is no answer to this, save that such speculations are not necessarily fruitful for they tend to involve extrapolations which the available data do not justify. For instance, it may be that a potential density-dependent mortality does exist in the lime aphid, as a simple consequence of the increased movement known to occur at high densities and possibly associated with a deterioration in overall food quality and the increasing difficulty of finding individual feeding sites which are suitable. The flight response may then be a desirable alternative to such a mortality, in the sense of substituting a small probability of successful colonisation for a certainty of death. A second possibility is that any change in the aphid population's behaviour, particularly in the direction of increasing stability, may qualitatively change the response of the natural enemy complex, again a situation which it is impossible to predict. Any prediction of an organism's optimum strategy would appear risky, since it is difficult to be certain that all relevant factors are considered and not all strategies which are conceivable may be physiologically possible. It may also be difficult to identify the criterion for optimality as measurements of fitness are time-dependent; a gene which causes a greater rate of increase over one or a few generations may become extinct through over-exploitation of the resources upon which the local population depends. Finally, even if the true optimum strategy could be identified, it is not necessarily reasonable to expect the organism to exhibit it; if evolution is occurring, then by definition at least some organisms are imperfectly adapted to their current environment.

# 5 Conclusions

## 5.1 Suggestions for further work

Modelling the lime aphid has shown that there is a need for more experimental work in several areas and there is considerable scope, too, for developments in the model itself. The experimental work involves, in order of importance:

1. The effects of weather on mortality and flight in the field. The significance of weather and the importance of understanding its effects are highlighted, first, by the discrepancies between observed population trends in specific years and those predicted by the model, second, by the fact that on tree 3, numbers of fundatrices do not relate to those in the previous year but vary widely from year-to-year, presumably owing to weather, and finally, by the fact that the inverse relationship between numbers of fundatrices in successive years on all trees (Fig. 7), while highly significant, nevertheless accounts for only 44% of the variance. Clearly, some of the remainder may be random 'noise' but there is every reason to believe that a significant proportion can still be explained.

Experiments already carried out suggest that wind is an important factor affecting mortality and that temperature affects flight (Barlow, 1977), but it seems that other factors are involved particularly in the second case. Mortality must be assessed in the field by monitoring experiments similar to the one described in Section 3.5.3, and although the effect of temperature on flight could be studied in the laboratory it would seem best that this too be investigated in the field. The aim in both cases is to derive predictive equations relating daily mortality and flight to weather so that the model is able to mimic more accurately the behaviour of the population in any one year.

2. The effect of cumulative density on flight and mortality in the field. Laboratory experiments have so far failed to confirm the existence of such an effect on young saplings, but the model suggests that it exists to an extent sufficient to cause a population crash, and the next step is to test this hypothesis on mature trees in the field. This would involve monitoring flight and mortality in late July on

trees which have been subjected to high cumulative densities and on those which have not. It may be that mature trees must commit reserves to fruit production which in some way diminishes their ability to compensate for aphid damage.

3. The extent of density-related flight and predation by coccinellids in the field. The magnitude of these effects indicated by laboratory experiments needs to be confirmed in the field. Only estimates of the maximum and minimum extents of flight and predation are required, at high and low densities respectively.
4. The existence and magnitude of any density-dependent nymphal mortality in the field.

These represent the main areas of uncertainty in the model, and are mostly associated with the need to study flight and mortality, as opposed to reproduction, in the field. Demonstrating the existence of an effect through laboratory experiments is of great value, but quantifying its magnitude and role in the field is altogether a different problem. Moreover, since numbers change so rapidly monitoring carried out in the field must be done on a daily basis, and it would be particularly profitable to analyse a population crash in this way.

So far as developments in the model are concerned, these should be in the direction of increased simplicity, for the aim of building complex models should be to learn how to build simple ones which capture the essence of the system's behaviour. The best approach for a simple model would be to partition the within-year relationship (Fig. 8a) into two or three equations relating logarithms of peak numbers at intermediate times. This would enable the interactions to be properly modelled which result from the sequential action of different processes, while density-dependence would be included in the equations along with terms representing the effects of weather and predation; the detailed model can be used where necessary to show the forms of these relationships.

## 5.2 Population change in the lime aphid

Given a knowledge of the separate component processes, a simulation model of their combined action yields the following hypothesis which accounts for the observed behaviour of lime aphid populations in Scotland.

First, the 2 predator/2 prey system can effectively be considered as a 1 predator/1 prey one, comprising the lime aphid and the 2-spot coccinellid. Second, weather is important as a disturbing factor and as a major determinant of peak numbers or numbers of fundatrices in any one year. Finally, the population is regulated by a hierarchy of different processes controlling population growth at different densities and capable of substituting one for another. The ultimate limit to growth in any one season appears to be not available space, nor death of the host through over-exploitation, but rather a decline in its quality to a level at which aphid survival is greatly reduced. Below this level numbers are regulated through a combination of the numerical response of the coccinellid to aphid densities early in the year and, at higher densities, increased flight dependent on densities experienced during nymphal development of the alates; the effect of flight in response to current density appears to be less significant than previously supposed (Barlow, 1977; Dixon & Barlow, 1979).

Specifically:

a) At low initial densities (about 10/m$^2$) intra-specific processes are insignificant, few coccinellids lay eggs and the population builds up to a peak late in the year the size of which depends on weather. Large numbers of sexuals and eggs are therefore produced, giving a high initial density in the following year.

b) At medium initial densities (100/m$^2$) many more coccinellid eggs are laid and the proportional mortality inflicted later in the summer by the voracious 3rd and 4th instar larvae is much greater than in the previous case. Intra-specific controls, mainly the flight response to nymphal experience of crowding, are only significant if the weather permits rapid population growth and a consequent reduction in the impact of the coccinellids. Peak numbers are reached earlier in the year and fewer sexuals and eggs are produced, giving a medium initial density in the next year.

c) At high initial densities (1000/m$^2$) still more coccinellids are present but the proportional mortality they inflict is lower. However, in this case the density-related flight has a greater impact, causing an early population crash at the end of June. Predation accentuates this crash and keeps numbers low thereafter, giving few sexuals, few eggs and a low initial population in the following year.

At medium or high initial densities, and if conditions are exceptionally favourable for population growth with both mortality and flight reduced, then very high densities are attained and a late population crash occurs at the end of July. Here the crash appears to be caused by greatly increased flight and mortality, occurring when the cumulative density in any season exceeds a threshold.

This hypothesis, summarized in Fig. 72, accounts for the inverse

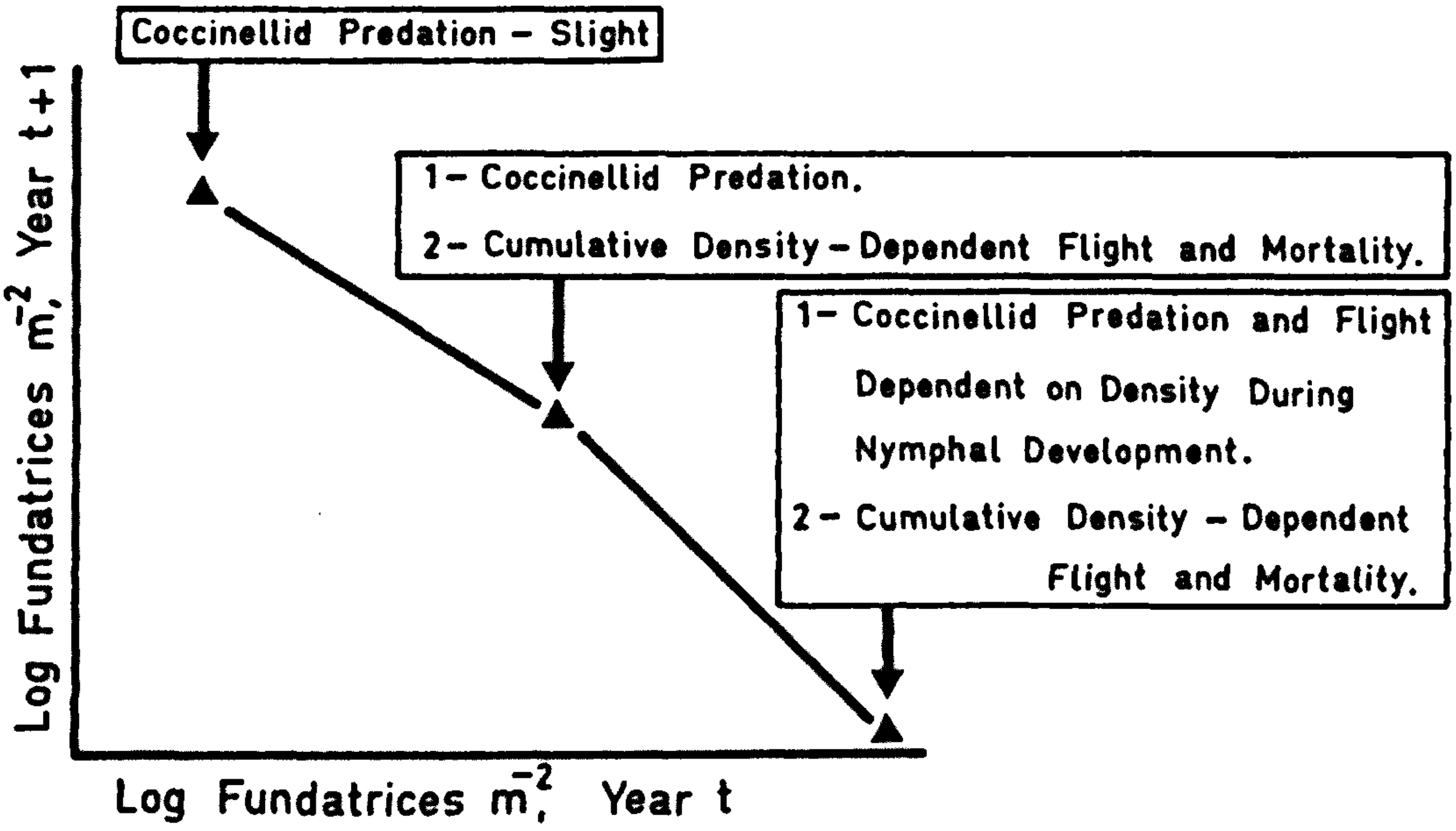

Fig. 72. A summary of the main factors which the model suggests regulate aphid numbers at different initial densities (▲—▲ relationship generated by the model).

relationship observed between fundatrix numbers in successive years, for the presence of a single population peak and the inverse relationship between fundatrix numbers and the time of year at which this peak occurs, and for the two kinds of dramatic population crash which can result from high numbers. The rates of population growth generated by the model are also realistic, and it shows that regulation by changes in quality of the aphids and by alate flight in response to current density is relatively unimportant.

The model has also raised some important questions which might otherwise have been overlooked. It indicates the likely importance of weather and the need for complementing laboratory studies with measurements of flight and mortality in the field. It also suggests the existence of cumulative or integrated density-dependent effects. Raising questions is an important function of the model but the answers will depend on additional experimental work. The form of the model is deliberately contrived so that these answers can readily be incorporated; variables like the proportion of alates flying each day are those which are actually measured.

A model of this kind calls the bluff of an optimistic ecologist; no-one would wish or expect to be able to recreate population trends exactly, but on the other hand there is a challenge which, in its entirety, does not appear to have yet been met. Can a set of ecological processes, derived totally independently, be assembled to recreate population behaviour which shows no major and consistent departures from that observed in the field, over a realistically wide range of conditions? This study was intended as a significant step towards such a goal and the model gives very encouraging results.

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# References

Barlow, N. D., 1977. A simulation study of lime aphid populations. PhD thesis, University of East Anglia.

Behrendt, K., 1963. Uber die Eidiapause von *Aphis fabae* Scop. (Homoptera: Aphididae). Zool. Jahrb. Physiol. 70: 309–398.

Bos, J. van den & Rabbinge, R. 1976. Simulation of the fluctuations of the grey larch bud moth. Pudoc, Wageningen (Simulation Monographs).

Brown, M. I., 1975. Intra-specific mechanisms regulating the numbers of the lime aphid. PhD thesis, University of Glasgow.

Calow, P., 1973. On the regulatory nature of individual growth; some observations on freshwater snails. J. Zool. 170: 415–428.

Carter, N., Aikman, D. P. & Dixon, A. F. G., 1978. An appraisal of Hughes' time-specific life table analysis for determining aphid reproductive and mortality rates. J. Anim. Ecol. 47: 677–688.

Caswell, H., 1977. The validation problem. In: B. C. Batten (ed.) Systems analysis and simulation in ecology. Vol. 4. Academic Press, New York.

Chambers, R. J., 1979. Simulation modelling of a sycamore aphid population. PhD thesis, University of East Anglia.

Conway, G. R. & Murdie, G., 1972. Population models as a basis for pest control. In: J. N. R. Jeffers (ed.) Mathematical models in ecology. Blackwell Scientific Publications, Oxford.

Crawley, M. J., 1973. Simulation studies of the biological control of *Aphis fabae*. PhD thesis, University of London.

Davis, C. S., 1957. The biology of the walnut aphid, *Chromaphis juglandicola* Kalt. (Homoptera: Aphididae). PhD thesis, University of California, Berkeley.

Dharma, T. R., 1979. Fecundity and size in the black bean aphid *Aphis fabae*. PhD thesis, University of East Anglia.

Dixon, A. F. G., 1959. An experimental study of the searching behaviour of the predatory coccinellid betle *Adalia decempunctata* L. J. Anim. Ecol. 28: 259–281.

Dixon, A. F. G., 1970. Quality and availability of food for a sycamore aphid population. In: Adam Watson (ed.) Animal populations in relation to their food resources. Blackwell Scientific Publications, Oxford.

Dixon, A. F. G., 1971a. The role of intra-specific mechanisms and predation in regulating the numbers of the lime aphid, *Eucallipterus tiliae* L. Oecologia (Berl.) 8: 179–193.

Dixon, A. F. G., 1971b. The role of aphids in wood formation. II. The effect of the lime aphid, *Eucallipterus tilia* L. (Aphididae), on the growth of lime, *Tilia* × *vulgaris* Hayne. J. appl. Ecol. 8: 393–399.

Dixon, A. F. G., 1972. The 'interval timer', photoperiod and temperature in the seasonal development of parthenogenetic and sexual morphs in the lime aphid, *Eucallipterus tiliae* L. Oecologia (Berl.) 9: 301–310.

Dixon, A. F. G., 1976. Timing of egg-hatch and viability of the sycamore aphid, *Drepanosiphum platanoides* Schr., at bud-burst of sycamore, *Acer pseudoplatanus* L. J. Anim. Ecol. 45: 593–604.

Dixon, A. F. G., 1977. Aphid ecology: life cycles, polymorphism and population regulation. Ann. Rev. Ecol. Syst. 8: 329–353.

Dixon, A. F. G. & Barlow, N. D. 1979. Population regulation in the lime aphid. J. Linn. Soc. (Zool.) 67:

Ellingsen, Inger-Johanne, 1969. Fecundity, aphid consumption and survival of the aphid predator *Adalia bipunctata* L. (Col., Coccinellidae). Norsk. ent. Tidsskr. 16: 91–95.

Flanagan, J. T., 1974. Population dynamics of the leafhopper *Alnetoidea alneti* Dahlbom and its effect on tree growth. PhD thesis, University of Glasgow.

Fransz, H. G., 1974. The functional response to prey density in an acarine system. Pudoc, Wageningen (Simulation Monographs).

Frazer, B. D. & Gilbert, N., 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). J. Entomol. Soc. Brit. Columbia 73: 33–55.

Gilbert, N. & Gutierrez, A. P., 1973. A plant-aphid-parasite relationship. J. Anim. Ecol. 42: 323–340.

Gilbert, N., Gutierrez, A. P., Frazer, B. D. and Jones, R. E., 1976. Ecological relationships. Freeman, Reading.

Gilbert, N. & Hughes, R. D., 1971. A model of an aphid population—three adventures. J. Anim. Ecol. 40: 525–534.

Glen, D. M., 1971. The role of the black-kneed capsid, *Blepharidopterus angulatus* Fall., in regulating the numbers of the lime aphid, *Eucallipterus tiliae* L. PhD thesis, University of Glasgow.

Glen, D. M., 1973. The food requirements of *Blepharidopterus angulatus* (Heteroptera: Miridae) as a predator of the lime aphid *Eucallipterus tiliae* L. Entomologia exp. appl. 16: 255–267.

Glen, D. M., 1975. Searching behaviour and prey-density requirements of *Blepharidopterus angulatus* Fall. (Heteroptera: Miridae) as a predator of the lime aphid *Eucallipterus tiliae* L. and leafhopper *Alnetoidea alneti* Dahlbom. J. Anim. Ecol. 44: 116–134.

Glen, D. M. & Barlow, N. D., 1980. Interaction of a population of *Blepharidopterus angulatus* Fall. (Heteroptera: Miridae) and its prey, the lime aphid *Eucallipterus tiliae* L.

Gutierrez, A. P., Havenstein, D. E., Nix, H. A. & Moore, P. A., 1974. The ecology of *Aphis craccivora* Koch. and subterranean clover stunt virus in South East Australia. II, A model of cowpea aphid populations in temperate pastures. J. appl. Ecol. 11: 1–20.

Holling, C. S., 1966. The functional response of invertebrate predators to prey density. Mem. entomol. Soc. Can. 48: 1–86.

Howe, R. W., 1967. Temperature effects on embryonic development in insects. Ann. Rev. Ent. 12: 15–42.

Hubbell, S. P., 1971. Of sowbugs and systems: the ecological bioenergetics of a terrestrial isopod. In: B. C. Patten (ed.) Systems analysis and simulation in ecology. Vol. 1. Academic Press, New York.

Hughes, R. D., 1962. A method for estimating the effects of mortality on aphid populations. J. Anim. Ecol. 31: 389–396.

Hughes, R. D., 1963. Population dynamics of the cabbage aphid *Brevicoryne brassicae* L. J. Anim. Ecol. 32: 393–424.

Hughes, R. D. & Gilbert, N., 1968. A model of an aphid population—a general statement. J. Anim. Ecol. 37: 553–563.

Ives, W. G. H., 1973. Heat units and outbreaks of the forest tent caterpillar *Malacosoma disstria* (Lepidoptera: Lasiocampidae). Can. Ent. 105: 529–543.

Kidd, N. A. C., 1975. The behavioural interactions of the lime aphid (*Eucallipterus tiliae* L.) and their role in regulating population numbers. PhD thesis, University of Glasgow.

Kidd, N. A. C., 1976a. Aggregation in the lime aphid (*Eucallipterus tiliae* L.) 1. Leaf vein selection and its effect on distribution on the leaf. Oecologia (Berl.) 22: 299–304.

Kidd, N. A. C., 1976b. Factors influencing leaf vein selection in the lime aphid (*Eucallipterus tiliae* L.) Oecologia (Berl.) 23: 247–254.

Kidd, N. A. C., 1977. The influence of population density on the flight behaviour of the lime aphid, *Eucallipterus tiliae*. Ent. exp. appl. 22: 251–261.

Lees, A. D., 1966. The control of polymorphism in aphids. Adv. Insect Physiol. 3: 207–277.

Leslie, P. H., 1945. On the use of matrices in certain population mathematics. Biometrika 35: 183–212.

Lewontin, R. C., 1965. Selection for colonising ability. In: H. G. Baker and G. L. Stebbins (eds.) The genetics of colonising species. Academic Press, New York.

Llewellyn, M., 1970. The ecological energetics of the lime aphid, *Eucallipterus tiliae* L. and its effect on tree growth. PhD thesis, University of Glasgow.

Llewellyn, M., 1972. The effects of the lime aphid, *Eucallipterus tiliae* L. (Aphididae) on the growth of the lime *Tilia* × *vulgaris* Hayne. 1. Energy requirements of the aphid population. J. appl. Ecol. 9: 261–282.

Lloyd, M., 1967. Mean crowding. J. Anim. Ecol. 26: 1–30.

Messenger, P. 1964. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid *Therioaphis maculata*. J. Econ. Entomol. 57: 71–76.

Milne, W. 1971. Factors affecting aphid populations on broad beans. PhD thesis, University of London.

Perrin, R. M., 1974. The ecology of nettle aphids with particular reference to their role as prey for beneficial natural enemies. PhD thesis, University of London.

Ricker, W. E., 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11: 559–623.

Rogers, D., 1972. Random search and insect population models. J. Anim. Ecol. 41: 369–384.

Solomon, M. E., 1949. The natural control of animal population. J. Anim. Ecol. 18: 1–35.

Southwood, T. R. E., 1976. Bionomic strategies and population parameters. In: Robert M. May (ed.) Theoretical Ecology. Blackwell Scientific Publications, Oxford.

Thompson, W. R., 1924. La theorie mathématique de l'action des parasites entomophages et le facteur du hasard. Annls. Fac. Sci. Marseille, Ser. 11, 2: 1–89.

Usher, M. B., 1972. Developments in the Leslie matrix model. In: J. N. R. Jeffers (ed.) Mathematical models in ecology. Blackwell Scientific Publications, Oxford.

Watt, K. E. F., 1968. Ecology and resource management. McGraw-Hill, New York.

Way, M. J., 1967. The nature and causes of annual fluctuations in numbers of *Aphis fabae* Scop. on field beans *Vicia faba*. Ann. appl. Biol. 59: 175–188.

Way, M. J. & Banks, C. J., 1968. Population studies on the active stages of the black bean aphid *Aphis fabae* Scop. on its winter host *Euonymus europaeus* L. Ann. appl. Biol. 62: 177–197.

White, P. L., 1970. The effects of aphids on tree growth. PhD thesis, University of Glasgow.

Wigglesworth, V. B., 1972. The principles of insect physiology. 7th edition. Chapman and Hall, London.

Wilbur, H. M. & Collins, J. P. 1973. Ecological aspects of amphibian metamorphosis. Science 182: 1305–1314.

Wit, C. T. de & Goudriaan, J., 1974. Simulation of ecological processes. Pudoc, Wageningen (Simulation monographs).

Wratten, S. D., 1971. The role of the predatory coccinellid beetle, *Adalia bipunctata* L., in regulating numbers of the lime aphid, *Eucallipterus tiliae* L. PhD thesis, University of Glasgow.

Wratten, S. D., 1973. The effectiveness of the coccinellid beetle *Adalia bipunctata* L. as a predator of the lime aphid *Eucallipterus tiliae* L. J. Anim. Ecol. 42: 785–802.

# Appendix A Glossary of FORTRAN symbols

| | |
|---|---|
| A | Predator/prey attack coefficients |
| AA | Aphid adults in detail (see Fig. 13) |
| AGE | Subroutine updating population age structure |
| AI | Immigrating coccinellid adults |
| AM | Intermediate variable used in linear interpolation (function F1) |
| AM | Daily mortality of adult viviparae and oviparae |
| AN | Aphid nymphs in detail (see Fig. 13) |
| AS | Aphid population summarized by instars, adult morphs and their weights (see Fig. 13) |
| AO | Initial density of aphid eggs |
| BS | Black-kneed capsid population by instars |
| BUD | Date of bud burst (0 if this has not occurred) |
| BO | Initial density of capsid eggs |
| C | Cumulative density (in subroutine GROWTH) |
| C | Intermediate variable used in linear interpolation (function F1) |
| CPH | Cumulative proportion of eggs hatched |
| CPHE | Expected cumulative proportion of eggs hatched by the end of the current day |
| CS | 2-spot coccinellid population by instars |
| CUM | Cumulative density |
| CO | Initial density of coccinellid eggs |
| D | Pre-reproductive delay |
| DATE | Date in days and months |
| DAY | Time counter-days from start of year |
| DD5 | Summed day-degrees above 5°C from 1st March |
| DEVA | Expected cumulative development achieved at each moult (= 1 at the adult moult) |
| DN | The difference between current plant nitrogen level and the average level during summer |
| DT | Temperature component of the pre-reproductive delay |
| DUM | Dummy variables for input of unwanted records |
| DUM1 | |
| DUM2 | |
| DVA | Proportion of development achieved in 1 day |
| E | Accumulated flight during a week (in subroutines FLIGHT and OUTPUT) |
| E | Eggs laid (in subroutine EPROD) per ovipara |
| EB | Total capsid eggs laid per week |

| | |
|---|---|
| EC | Total coccinellid eggs laid per week |
| ECF1 | Factor modifying coccinellid egg-laying depending on time of year |
| ECF2 | Factor modifying coccinellid egg-laying depending on the year ('coccinellid multiplier') |
| EG1 | Eggs at the beginning of the current year |
| EG2 | Eggs at the beginning of the next year |
| EL | Total leafhopper eggs laid per week |
| EPROD | Subroutine for egg-laying |
| F | Background daily proportion of alates flying |
| FA | Proportion of alates flying in response to current weighted density |
| FC | Proportion of alates flying in response to cumulative density |
| FLIGHT | Subroutine for alate emigration by flight |
| FLT | Total proportion of alates flying each day |
| FMT | Total number of males flying per day |
| FN | Proportion of alates flying in response to density during nymphal development |
| FVT | Total number of viviparae flying per day |
| F1 | Function carrying out linear interpolation |
| F3 | Function converting a day number to a date |
| GF | Daily growth factor, multiplying aphid weights |
| GFL | Log (Expected aphid weight as an adult/weight at birth) |
| GROWTH | Subroutine updating aphid weights |
| HATCH | Subroutine causing eggs to hatch |
| I,II | Counters |
| ID | Days of month |
| IDUM | Integer dummy variable |
| IM | Counter |
| IMAX | Maximum adult longevity |
| J,JJ | Counters |
| JD | Month |
| K | Counter |
| L | Counter |
| L | Leafhopper population by instars and weights |
| L0 | Initial density of leafhopper eggs |
| M | Counter denoting instar (in subroutine SUMP) |
| M | Weekley counter for input of observed predator/leafhopper numbers |
| MA | Counter denoting instar |
| MAXY | Year on which model is to cease running (1 = 1965) |
| MINY | Year on which model is to begin running |
| MM | Counter for the number of model runs required |
| MO | Numbers of days in each month |
| MORTY | Subroutine for daily mortality (other than from predation, parasitism and ageing) |

| | |
|---|---|
| MY | Year counter (from MINY to MAXY) |
| N | Prey densities, by instars |
| NA | Uncorrected proportion of each prey killed by each predator |
| NAC | Corrected proportion of each prey killed by all predators |
| NAT | Uncorrected proportion of each prey killed by all predators |
| ND | Counter incremented each week for operation of predator/leafhopper submodel |
| NDIM | Number of values between which linear interpolation is carried out (in function F1) |
| NIT | Tree amino-nitrogen levels each day of the season |
| NUMB | Subroutine interpolating daily numbers of predators and leafhoppers, if required, from those observed on weekly sampling occasions |
| O | Array containing dates on which output is required (col. 1), aphid numbers generated by the model (cols. 2–7) and actual numbers of predators and leafhoppers or those generated by the model (cols. 10–29) |
| OBS | Subroutine assigning dates on which output is required |
| OUTPUT | Subroutine printing out dates and computed aphid numbers |
| P | Predator densities, by instars |
| PAR | Proportion of moulting adults parasitised |
| PARA | Subroutine applying parasitism |
| PH | Daily proportion of eggs hatching |
| PM | Proportion of new-born aphids which are males |
| PO | Proportion of new-born aphids which are oviparae |
| POP | Subroutine updating predator and leafhopper populations |
| PRED | Subroutine applying predation |
| PV | Proportion of new-born aphids which are viviparae |
| R | Daily reproductive rate (in subroutine REPROD) |
| R | Day number (in subroutine TEMPS) |
| RD | Factor modifying reproductive rate to take account of pre-reproductive delays involving fractions of days |
| RDAY | Day number |
| REPROD | Subroutine carrying out parthenogenetic reproduction |
| RF | Factor modifying reproductive rate according to accumulated temperature experience of adults |
| RI | Number of days since bud-burst |
| RO | Proportion of female offspring which are oviparae |
| S | Correction factor for satiation of each predator instar (in subroutine PRED) |
| S | Daily survival rate (in subroutine MORTY) |
| S | Syrphid numbers (in subroutine OBS) |
| SB | Survival rates for capsid instars |
| SC | Survival rates for coccinellid instars |
| SC | Proportion of alates surviving per day dependent on cumulative density (in subroutine MORTY) |

|  |  |  |
|---|---|---|
| SL | Proportion of alates surviving per day dependent on time of year (in subroutine MORTY) |  |
| SL | Survival rates for leafhopper instars |  |
| STORE | Subroutine storing values for output |  |
| SUMP | Subroutine summarizing the aphid population by instars |  |
| SW | Proportion of alates surviving per day dependent on wind speed |  |
| T | Temperature |  |
| TB | Weekly transition probabilities for capsid instars |  |
| TC | Weekly transition probabilities for coccinellid instars |  |
| TDAY | Day number |  |
| TEMP | Maximum and minimum temperatures throughout the season |  |
| TEMPS | Subroutine assigning temperatures throughout the year |  |
| TL | Weekly transition probabilities for leafhopper instars |  |
| TM | Mean temperature |  |
| TN | Minimum temperature |  |
| TOT | Total aphid density |  |
| TOTLG1 | Log (aphids/100 $cm^2+1$) |  |
| TOTLG2 | Log (aphids/$m^2+1$) |  |
| TREE | Subroutine updating amino-nitrogen levels and cumulative aphid density |  |
| TX | Maximum temperature |  |
| VOR | Maximum rates of prey ingestion by predator instar |  |
| W | Weights of prey instars |  |
| WIN | Mean daily wind speeds throughout the season |  |
| WIND | Subroutine assigning wind speeds throughout the season |  |
| WMORT | Subroutine applying overwintering mortality to eggs |  |
| X | x-value for which corresponding y-value is required through linear interpolation (in function F1) |  |
| XVAL | Set of x-values (see YVAL, NDIM) | used for linear interpolat |
| XV1 | temperature values |  |
| XV2 | day-degrees above 5°C from 1st March |  |
| XV3 | times of year since bud burst |  |
| XV4 | times of year |  |
| XV6 | times of year |  |
| XV7 | times of year |  |
| YVAL | Set of y-values (see XVAL, NDIM) |  |
| YV1 | development rates |  |
| YV2 | cumulative proportions of eggs hatching |  |
| YV3 | soluble nitrogen concentrations |  |
| YV4 | average minimum temperatures |  |
| YV5 | average maximum temperatures |  |
| YV6 | proportions of males among new-born offspring |  |
| YV7 | proportions of oviparae among new-born female offspring |  |

# Appendix B Program listing

```
PROGRAM LAM (INPUT, OUTPUT, NUMB F1, TEMPF, WINDF,
TAPE 1 = NUMB F1, TAPE 2 = OUTPUT. TAPE 4 = TEMP F,
TAPE 5 = WIND F,).
REAL WIN (366), TEMP (2,366), NIT (366), O(30,31)
REAL AO(9), LO(9), BO(9), A(11,11), H(11,11), VOR(11),
       DEVA(4)
REAL TB(7). TL(7), TC(7), SB(7), SL(7), SC(7)
REAL AS(9,2), LS(7,2), CS(7), BS(7), AA(30,6), AN(50,6),
       AM(30,2)
REAL XV1(15), YV1(15), XV2(11), YV2(11), XV3(9), YV3(9),
        XV4(12), YV4(12)
REAL YV5(12), XV6(6), YV6(6), XV7(6), YV7(6)
REAL ECF2(9)
INTEGER MO(12), BUD, DAY.
DATA WIN, NIT, O, CS, BS, AA, AN, AM/2216*0./
CUMULATIVE PROPORTIONS OF DEVELOPMENT ACHIEVED IN INSTARS.
DATA DEVA/0.23, 0.53, 0.685, 1./
MAXIMUM ADULT LIFE-SPAN.
DATA IMAX/30/
DAYS IN MONTHS
DATA MO/31, 28, 31, 30, 31, 30, 31, 31, 30, 31, 30, 31/
INITIAL APHID WEIGHTS
DATA AS/10*0., 70., 170., 330., 700., 1000., 1000., 700.,
        0./
LEAFHOPPER WEIGHTS
DATA LS/8*0., 40., 110., 200., 360., 650., 700./
MAXIMUM DAILY INTAKE OF PREDATORS.
DATA VOR/160., 550., 1300., 3470., 4125., 22., 44., 75.,
         124., 196., 448./
ATTACK COEFFICIENTS FOR PREDATORS.
DATA A/.33, 1.81, 2.76, 4.51, 4.51, 1.27, 6.00, 12.58,
       14.43, 15.16, 11.38, 1.32, .45, 2.44, 6.58, 6.58,
       .47, 2.5, 6.98, 15.39, 25.65, 23.55, 1.04, .21, .65,
       3.2, 3.2, .16, 1.7, 8.73, 15.32, 39.79, 40.64, 1.06,
       .36, 1.71, 2.74, 2.74, 0., 0.58, 1.68, 7.70, 28.76,
       34.25, 10., .19, .85, 2.88, 2.88, 0., 0.41, 1.65,
       7.77, 19.38, 39.25, 10., .09, .23, .28, .28, .43,
       11.74, 0., 0., 0., 10., 0., 0., .17, .17, .14, 4.31,
       13.59, 23.59, 0., 0., 10., 0., 0., 0., 0., 0., 1.9,
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4.82, 15.69, 0., 0., 10., 0., 0., 0., 0., 0., .81, 2.59,
10.32, 28.91, 0., 10., 0., 0., 0., 0., 0., .28, 0., 4.16,
10.93, 0., 10., 0., 0., 0., 0., 0., 0., 0., 0., 0., 3./
TEMPERATURES AND DEVELOPMENT RATES.
DATA XVI/3., 5., 7., 9., 11., 13., 16., 18., 19., 20.,
         21.5, 23., 25., 26., 28./
DATA YVI/.000, .002, .006, .013, .023, .038, .065, .082,
         .088, .091, .094, 1.095, .093, .091, .080/
DAY-DEGREES ABOVE 5 AND CUMULATIVE PROPORTIONS OF EGGS
HATCHED.
DATA XV2/105., 120., 129., 135., 141., 147., 153., 160.,
         168., 181., 225./
DATA YV2/0., 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9,
         1.0/
TIMES AND SOLUBLE NITROGEN CONCENTRATIONS.
DATA XV3/2.0, 17.0, 31.0, 50.0, 66.0, 108.0, 122.0, 135.0,
         156.0/
DATA YV3/1.55, 0.52, 0.19, 0.17, 0.15, 0.13, 0.15, 0.18,
         0.28/
TIMES AND AVERAGE MAX AND MIN TEMPERATURES.
DATA XV4/15.0, 49.0, 74.0, 105.0, 135.0, 166.0, 196.0,
         227.0, 258.0, 288.0, 1319.0, 349.0/
DATA YV4/2.5, 2.5, 3.0, 4.0, 6.0, 9.0, 10.5, 10.0, 8.0,
         5.5, 3.0, 2.5/
DATA YV5/6.0, 7.0, 8.5, 11.0, 15.0, 17.0, 18.0, 17.5, 15.5,
         12.5, 8.0, 6.5/
TIMES AND PROPORTIONS OF MALES AT BIRTH.
DATA XV6/170., 190., 210., 230., 250., 270./
DATA YV6/0., 0.11, 0.14, 0.12, 0.05, 0./
TIMES AND PROPORTIONS OF OVIPARAE AT BIRTH.
DATA XV7/170., 180., 200., 215., 240., 250./
DATA YV7/0., .050., .050, .300, .900, 1.0/
WEEKLY TRANSITION PROBABILITIES FOR CAPSIDS, COCCINELLIDS
AND LEAFHOPPERS.
DATA TB/0., .884., .884, .884, .58, .494, 0./
DATA TC/.7, 1., 1., 1., .7, .41, 1./
DATA TL/0., .67, 1., 1., 1., .56, 0./
SURVIVAL PROBABILITIES FOR CAPSIDS, COCCINELLIDS AND
LEAFHOPPERS.
DATA SB/.5, 1., 1., .75, 1., 0.1, 1./
DATA SC/.5, .8, .94, .94, .94, .85, 1./
DATA SL/.27, 4*1., .26, 1./
NUMBERS OF APHID EGGS AT THE BEGINNING OF THE YEARS.
DATA A0/0.05, 0.45, 1.83, 0.03, 14., 0.074, 2., 0.17, 2.05/
NUMBERS OF LEAFHOPPER EGGS AT HE BEGINNING OF THE YEARS.
DATA L0/4*1., 2.14, 0.54, 0.27, 1./
NUMBER OF CAPSID EGGS AT THE BEGINNING OF THE YEARS.
```

```
  DATA B0/0.03, .063, .067, .118, .118, 0., 0., 0., 0./
  COCCINELLID MULTIPLIER FOR EACH YEAR.
  DATA ECF2/6*1., 0.3, 2*1./

  MINY = 1
  MAXY = 8
  MM = 0
  DO 1 MY = MINY, MAXY
  MM = 1
  INITIALISING OF SEASON-SPECIFIC VARIABLES
  DAY = 59
  DD5 = 0.
  CPH = 0.
  BUD = 0.
  M = 1
  ND = 0
  CUM = 0.
  E = 0.
  DO 6 J = 1, 6
  DO 7 I = 1, 50
7 AN (I,J) = 0.
  DO 6 K = 1, 30.
6 AA (K, J) = 0.
  DO 2 J = 1, 2
  DO 2 K = 1, 30
2 AM (K, J) = 0
  DO 3 K = 2, 7
  BS (K) = 0.
  CS (K) = 0.
3 LS (K,1) = 0.
  DO 4 K = 2, 9
4 AS (K, 1) = 0.
  AS (1, 1) = A0 (MY)
  LS (1, 1) = L0 (MY)
  BS (1) = B0 (MY)
  INPUT OF TEMPERATURES.
  CALL TEMPS    (TEMP, XV4, YV4, YV5, MINY, MM, MY)
  INPUT OF WIND SPEEDS.
  CALL WIND     (WIND, MINY, MM, MY)
  INPUT OF DATES FOR OUTPUT (AND OBSERVED NUMBERS OF LEAF-
  HOPPERS AND PREDATORS IF REQUIRED).
  CALL OBS      (0, MINY, MM, MY)
  DAILY ITERATIONS CARRIED OUT.
  5 DAY = DAY + 1
  INTERPOLATION OF OBSERVED PREDATOR AND LEAFHOPPERS NUMBERS.
  CALL NUMB     (0, LS, BS, CS, DAY, M)
  EGG-HATCHING.
```

```
  CALL HATCH    (DAY, DD5, XV2, YV2, CPH, AN, TEMP, AS, MM)

  CALCULATION OF BUD-BURST TIME, NITROGEN LEVEL AND
  CUMULATIVE APHID INFESTATION OF TREE
  CALL TREE     (BUD, DAY, NIT, DD5, XV3, YV3, CUM, AS)
  SUMMARISING OF POPULATION(S) BY INSTARS/STAGES
  CALL SUMP     (AN, AA, AS, DEVA, IMAX)
  IF (CPH.LT.1E-6) GOTO 8
  PREDATION
  CALL PRED     (AA, AN, AS, AM, LS, CS, BS, TEMP, A, H, MM,
                 VOR, DEVA, IMAX, M, O, DAY)
  MORTALITY OTHER THAN PREDATION AND PARASITISM.
  CALL MORTY    (AN, AA, AM, AS, CUM, TEMP, WIN, DAY, IMAX,
                 MM)
  FLIGHT.
  CALL FLIGHT   (AA, AS, AM, TEMP, WIN, DAY, CUM, MM, IMAX,
                 E)
  SEXUAL REPRODUCTION (EGG PRODUCTION)
  CALL EPROD    (AA, AM, AS)
  PARTHENOGENETIC REPRODUCTION
  CALL REPROD   (AA, AN, AM, AS, TEMP, DAY, XV6, YV6, XV7,
                 YV7, MM, IMAX, DVA)
  GROWTH AND DEVELOPMENT
  CALL GROWTH   (AN, AA, TEMP, DAY, NIT, CUM, DVA, XV1, YV1,
                 AS, MM)
  STORING OF VARIABLES FOR OUTPUT
8 CONTINUE
  IF (DAY.EQ.O(M,1))  CALL STORE (O, AS, LS, BS, CS, M)
  AGEING OF POPULATION
  CALL AGE      (AN, AA, AM, IMAX, MM)
  PARASITISM
  CALL PARA     (AA, DAY, MM)
  UPDATING OF PREDATOR AND LEAFHOPPER POPULATIONS
  ND = ND + 1
  IF (ND.EQ.7)  CALL POP  (AS, LS, CS, BS, TB, TL, TC, SB,
                  SL, SC, ECF2, DAY, MM, ND, MY)
  IF (DAY.LT.305) GOTO 5
  M = M - 1
  WINTER EGG MORTALITY COMPUTED
  CALL WMORT    (AS, O)
  OUTPUT
  CALL OUTPUT   (O, MO, E, CUM)
1 CONTINUE
  STOP
  END

  SUBROUTINE OBS   (O, MINY, MM, MY)
```

```
    REAL O(30, 31), S(3)
    IF (MM.GT.1) GOTO 4
    IF (MY.GT.MINY.OR.MINY.EQ.1) GOTO 2
    IM = (MINY - 1) * 25
    DO 1 I = 1, IM
  1 READ (1, 100) IDUM
100 FORMAT (13, 69X/72X)
  2 CONTINUE
    DO 3 I = 1,25
    READ (1, 101) O(I, 1), (O(I,J), J = 10, 15), (S(K),
          K = 1,3), (O(I,L), L = 24, 29), 1(O(I,M), M = 17, 22)
101 FORMAT (3X, F4.0,6F6.2,3F5.3/7X,12F5.3)
    DO 3 J=1,3
  3 O(I,J+24)=O(I,J+24)+S(J)
  4 CONTINUE
    RETURN
    END

    SUBROUTINE TEMPS  (TEMP, XV4, YV4, YV5, MINY, MM, MY)
    REAL XV4(12), YV4(12), YV5(12)
    REAL TEMP (2,366)
    IF (MM.GT.1) GOTO 6
    IF (MY.GT.MINY.OR.MINY.EQ.1)  GOTO 2
    IM = (MINY-1)*245
    DO 3 I = 1, IM
  3 READ (4, 100) DUM 1, DUM 2
100 FORMAT (26 X, 2F7.1)
  2 CONTINUE
    DO 4 I = 1, 245
  4 READ (4, 100) TEMP (1, 1 + 59), TEMP (2, I + 59)
    DO 5 I = 1, 59
    TEMP (1, I) = 7.0
  5 TEMP (2, I) = 2.5
  6 CONTINUE
    RETURN
    END

    SUBROUTINE TEMPS  (TEMP, XV4, YV4, YV5, MINY, MM)
    REAL XV4 (12), YV4 (12), YV5 (12)
    REAL TEMP (2, 366)
    IF (MM.GT.1) GOTO 2
    DO 1 I = 50, 305
    R = I
    TEMP (1, I) = F1 (R, XV4, YV5, 12)
    TEMP (2, I) = F1 (R, XV4, YV4, 12)
  1 CONTINUE
  2 CONTINUE
```

```
      RETURN
      END

      SUBROUTINE WIND   (WIN, MINY, MM, MY)
      REAL WIN (366)
      IF (MM.GT.1) GOTO 6
      IF (MY.GT. MINY. OR. MINY. EQ.1) GOTO 2
      IM = (MINY-1)*214
      DO 3 I = 1, IM
    3 READ (5, 100) DUM
  100 FORMAT (14X, F5.1, 9X)
    2 CONTINUE
      DO 4 I = 1, 214
      READ (5, 100) WIN (I + 90)
      IF (WIN(I +90). LT. 1E-4) WIN (I + 90) = 7.74
    4 CONTINUE
      DO 5 I = 1, 90
    5 WIN (I) = 7.74
    6 CONTINUE
      RETURN
      END

      SUBROUTINE WIND   (WIN, MINY, MM)
      REAL WIN (366)
      IF (MM. GT. 1) GOTO 2
      DO 1 I = 50, 305
    1 WIN (I) = 8.0
    2 CONTINUE
      RETURN
      END

      SUBROUTINE NUMB         (O,LS,BS,CS,DAY,M)
      REAL O(30,31),LS(7,2),BS(7),CS(7)
      INTEGER DAY
      IF(M.LT.2) RETURN
      F=(DAY.O(M-1,1))/(O(M,1)-O(M-1,1))
      DO 1 I=10,15
    1 LS(I-8,1)=F*(O(M,I)-O(M-1,I))+O(M-1,I)
      DO 2 I=17,22
    2 BS(I-15)=F*(O(M,I)-O(M-1,I))+O(M-1,I)
      DO 3 I=24,29
    3 CS(I-22)=F*(O(M,I)-O(M-1,I))+O(M-1,I)
      RETURN
      END

      SUBROUTINE TREE         (BUD,DAY,NIT,DD5,XV3,YV3,CUM,AS)
      INTEGER BUD,DAY
      REAL XV3(9), YV3(9),NIT(366),AS(9,2)
```

```
  IF(BUD.GT.0) GOTO 1
  IF(DD5.GE.122) BUD=DAY
1 R1=DAY-BUD+1
  IF(BUD.LE.1E-6) RI=1.
  NIT(DAY)=F1(RI,XV3,YV3,9)
  CUM=CUM+AS(9,1)/7.
  RETURN
  END

  SUBROUTINE HATCH       (DAY,DD5,XV2,YV2,CPH,AN,TEMP,AS,MM)
  REAL AN(50,6),TEMP(2,366),AS(9,2),XV2(11),YV2(11)
  INTEGER DAY
  THE SUBROUTINE IS SKIPPED IF ALL EGGS HAVE ALREADY HATCHED
  OR THE DATE IS EARLIER THAN MARCH 1ST.
  IF(DAY.LT.60.OR.CPH.EG.1.0) RETURN
  DAY-DEGREES UPDATED
  TX=TEMP(1,DAY)
  TN=TEMP(2,DAY)
  TM=(TX+TN)/2.0
  IF(TN.GE.5.0) DD5=DD5+TM-5.0
  IF(TN.GE.5.0) GOTO 2
  IF(TX.GT.5.0.AND.TN.LT.5.0) DD5=DD5+(TX-5.)**2/(2.*(TX-TM))
  EXPECTED CUMULATIVE PROPORTION HATCHING IS CALCULATED
2 CPHE=F1(DD5,XV2,YV2,11)
  DAILY PROPORTION HATCHING OF THOSE REMAINING COMPUTED
  PH=(CPHE-CPH)/(1.-CPH)
  CUMULATIVE PROPORTION ALREADY HATCHED IS UPDATED
  CPH=CPHE
  NYMPHAL POPULATION AND EGG POPULATION UPDATED
  AS(2,1)=AS(2,1)+AS(1.1)*PH
  AN(1,1)=AS(1,1)*PH
  AN(1,4)=0.
  AN(1,5)=0.
  AN(1,6)=24.
  AS(1,1)=AS(1,1)*(1.-PH)
  RETURN
  END

  SUBROUTINE SUMP        (AN,AA,AS,DEVA,IMAX)
  REAL AN(50,6),AA(30,6),AS(9,2),DEVA(4)
  DO 5 J=1,2
  DO 5 I=2,9
5 AS(I,J)=0.
  NYMPHS
  M=2
  DO 1 I=1,50
  IF(M.GT.5) M=5
```

```
  IF(AN(I,4).GT.DEVA(M-1)) M=M+1
  DO 1 J=1,3
  AS(M,2)=AS(M,2)+AN(I,J)*AN(I,6)
1 AS(M,1)=AS(M,L)+AN(I,J)
  DO 2 M=2,5
  IF(AS(M,1).GT.0.) AS(M,2)=AS(M,2)/AS(M,1)
2 CONTINUE
  ADULTS
  DO 3 I=1,IMAX
  DO 3 M=6,8
  AS(M,2)=AS(M,2)+AA(1,M-5)*AA(I,6)
3 AS(M,1)=AS(M,1)+AA(I,M-5)
  DO 4 M=6,8
  IF(AS(M,1).GT.0.) AS(M,2)=AS(M,2)/AS(M,1)
  IF(M.EQ.8) AS(M,2)=AS(M,2)*0.7
4 CONTINUE
  DO 6 I=2,8
6 AS(9,1)=AS(9,1)+AS(I,1)
  RETURN
  END

  SUBROUTINE PRED        (AA,AN,AS,AM,LS,CS,BS,TEMP,A,H,MM,
                          VOR,DEVA,IMAX,M,O,DAY)
  INTEGER DAY
  REAL AA(30,6),AN(50,6),AM(30,2),AS(9,2)
  REAL LS(7,2),CS(7),BS(7),TEMP(2,366),A(11,11),H(11,11),
          VOR(11)
  REAL N(11),P(11),NA(11,11),W(11),NAC(11),NAT(11),S(11),
         0,(30,31)
  REAL DEVA(4)
  PREY ENTERED TO ARRAY N, WEIGHTS TO W AND PREDS TO P.
  DO 1 J=1,4
  P(J)=CS(J+1)
  W(J)=AS(J+1,2)
1 N(J)=AS(J+1,1)
  P(5)=CS(7)
  W(5)=AS(6,2)
  N(5)=AS(6,1)+AS(7,1)+AS(8,1)
  DO 2 J=6,11
  P(J)=BS(J-4)
  W(J)=LS(J-4,2)
2 N(J)=LS(J-4,1)
  UNCORRECTED PROPNS OF EACH PREY KILLED BY EACH PRED.
  DO 3 K=1,11
  NAT(K)=0.
  DO 3 JJ=1,11
  J=12-JJ
```

```
  3 NA(K,J)=A(K,J)*P(K)
    UNCORRECTED PROPNS OF EACH PREY KILLED BY ALL PREDS.
    DO 16 K=1,11
    S(K)=0.
    DO 15 J=1,11
    IF(P(K).GT.0.) S(K)=S(K)+NA(K,J)*W(J)*N(J)/P(K)
 15 CONTINUE
    IF(S(K).GT.0.) S(K)=VOR(K)/S(K)
    IF(S(K).GT.1.) S(K)=1.
    DO 16 J=1,11
    NA(K,J)=NA(K,J)*S(K)
 16 NAT(J)=NAT(J)+NA(K,J)
    CORRECTED PROPNS OF EACH PREY KILLED BY ALL PREDS.
    DO 6 J=1,11
  6 NAC(J)=1.-EXP(-NAT(J))
    UPDATING OF APHIDS, LEAFHOPPERS AND MORTALITY FROM
    PREDATION
    MA=1
    DO 9 I=1,50
    IF(AN(I,4).GT.DEVA(MA)) MA=MA+1
    DO 9 J=1,3
  9 AN(I,J)=AN(I,J)*(1.-NAC(MA))
    DO 12 I=1,IMAX
    DO 12 J=1,3
    IF(J.LT.3) AM(I,J)=AM(I,J)+AA(I,J)*NAC(5)
 12 AA(I,J)=AA(I,J)*(1.-NAC(5))
    TOT=AS(9,1)
    AS(9,1)=0.
    DO 10 I=2,6
    AS(I,1)=AS(I,1)*(1.-NAC(I-1)
 10 AS(9,1)=AS(9,1)+AS(I,1)
    DO 13 I=7,8
    AS(I,1)=AS(I,1)*(1.-NAC(5))
 13 AS(9,1)=AS(9,1)+AS(I,1)
    O(M,31)=O(M,31)+TOT-AS(9,1)
    DO 11 I=2,7
 11 LS(I,1)=LS(I,1)*(1.-NAC(I+4))
    RETURN
    END

    SUBROUTINE MORTY          (AN,AA,AM,AS,CUM,TEMP,WIN,DAY,IMAX,
                               MM)
    REAL AN(50,6),AA(30,6),AM(30,2),AS(9,2),TEMP(2,366),
            WIN(366)
    INTEGER DAY
    BACKGROUND MORTALITY AND EFFECT OF WIND SPEED.
    SW=0.99(1.-0.0003*WIN(DAY)**2)
```

```
  IF(SW.LT.0.2) SW=0.2
  EFFECT OF LEAF FALL
  SL=(277-DAY)/10.
  IF(SL.LT.0.) SL=0.
  IF(SL.GT.1.) SL=1.
  EFFECT OF CUMULATIVE DENSITY
  SC=1.-0.001*(CUM-250.)
  IF(SC,LT.0.) SC=0.
  IF(SC.GT.1.) SC=1.
  COMBINED EFFECT
  S=SW*SL*SC
  POPULATION UPDATED
  DO 1 I=1,50
  DO 1 J=1,3
1 AN(I,J)=AN(I,J)*S
  DO 2 I=1, IMAX
  AM(I,1)=AM(I,1)+AA(I,1)*(1,-S)
  DO 2 J=1,3
2 AA(I,J)=AA(I,J)*S
  AM(1,2)=AM(1,2)+AA(1,2)*(1.-S)
  DO 3 I=2,8
3 AS(I,1)=AS(I,1)*S
  AS(9,1)=0.
  DO 5 I=2,8
5 AS(9,1)=AS(9,1)+AS(I,1)
  RETURN
  END

  SUBROUTINE FLIGHT      (AA,AS,AM,TEMP,WIN,DAY,CUM,MM,IMAX,
                          E)
  REAL AA(30,6),AS(9,2),AM(30,2),TEMP(2,366),WIN(366)
  INTEGER DAY
  FMT=0.
  FVT=0.
  DO 1 I=1,IMAX
  AGE-CLASS SKIPPED IF NO ALATES PRESENT
  IF((AA(I,1)+AA(I,3)).LE.1E-6) GOTO1
  ADULT COMPONENT
  FA=0.005*((AS(2,1)+AS(3,1)+AS(4,1))/4.+AS(5,1"+AS(6,1)+
             AS(7,1)+AS(8,1))
  NYMPHAL COMPONENT
  FN=0.02*(AA(I,5)-10.)
  IF(FN.LT.0.) FN=0.
  IF(FN.GT.0.4) FN=0.4
  CUMULATIVE DENSITY COMPONENT
  FC=0.005*(CUM-250.)
  IF(FC.LT.0.) FC=0.
```

```
IF(FC.GT.0.55) FC=0.55
AGE COMPONENT
F=0.1
EFFECT OF TEMPERATURE
COMBINED EFFECT
FLT=FA+FN+F+FC
IF(FLT.LT.0.) FLT=0.
IF(FLT.GT.1.) FLT=1.
ALATE POPULATION UPDATED
AM(I,1)=AM(I,1)+AA(I,1)*FLT
AA(I,1)=AA(I,1)*(1.-FLT)
AA(I,3)=AA(I,3)*(1.-FLT)
FMT=FMT+AA(I,3)*FLT
FVT=FVT+AA(I,1)*FLT
CONTINUE
AS(6,1)=AS(6,1)-FVT
AS(8,1)=AS(8,1)-FMT
AS(9,1)=AS(9,1)-FVT-FMT
E=E+FVT
RETURN
END

SUBROUTINE EPROD       (AA,AM,AS)
REAL AA(30,6),AM(30,2),AS(9,2)
E=0.0162*AA(1,6)-2.736
IF(E.LT.0.) E=0.
AS(1,1)=AS(1,1)+E*(AA(1,2)+(AM(1,2)/2.))
RETURN
END

SUBROUTINE REPROD      (AA,AN,AM,AS,TEMP,DAY,XV6,YV6,XV7,
                        YV7,MM,IMAX,DVA)
REAL AA(30,6),AN(50,6)AM(30,2),AS(9,2)
REAL TEMP(2,366), XV6(6),YV6(6),XV7(6),YV7(6)
INTEGER DAY
IF(AS(6,1).LE.1E-6) GOTO 3
MORPH DETERMINATION
RDAY=DAY
PM=F1(RDAY,XV6,YV6,6)
RO=F1(RDAY,XV7,YV7,6)
PO=RO*(1.-PM)
PV=(1.-RO)*(1.-PM)
PRE-REPRODUCTIVE DEVELOPMENT
T=(TEMP(1,DAY)+TEMP(2,DAY))/2.+1.5
DT=1652000./T**2.68
DO 2 I=1,IMAX
RD=1.
```

```
  IF(AA(I,4).LT.1E-6) GOTO 2
  IF(AA(I,4).GE.2-) GOTO 1
  D=DI/(AA(I,6)-100.)
  AA(I,4)=AA(I,4)+1./n
  RD=(AA(I,4)-2.)*D
  IF(RD.GT.1.) RD=1.
  IF(RD.LT.0.) RD=0.
  IF(AA(I,4).GT.2.) AA(I,4)=A.
  REPRODUCTION
  IF(AA(I,4).LT.2.) GOTO 2
1 AA(I,4)=AA(I,4)+0.0011*T**1.5
  RF=2.578-0.526*AA(I,4)
  IF(RF.LT.0.) RF=0.
  IF(RF.GT.1.) RF=1.
  R=T**1.5*AA(I,6)*RF*RD*(AA(I,1)+AM(I,1)/2.)/14817.
  AS(2,1)=AS(2,1)+R
  AN(1,1)=AN(1,1)+R*PV
  AN(1,2)=AN(1,2)+R*PO
  AN(1,3)=AN(1,3)+R*PM
2 CONTINUE
  IF((AN(1,1)+AN(1,2)+AN(1,3)).LE.1E-6) GOTO 3
  IF(AN(1,6).LE.1E-6) AN(1,6)=24.-24.8*EXP(-0.0077*AS(6,2))
3 CONTINUE
  RETURN
  END

  SUBROUTINE GROWTH      (AN,AA,TEMP,DAY,NIT,CUM,DVA,XV1,
                          YV1,AS,MM)
  REAL AN(50,6),AA(30,6),NIT(366),TEMP(2,366),XV1(15),YV1(15)
  REAL AS(9,2)
  INTEGER DAY
  DN=NIT(DAY)-0.2
  IF(DN.LT.0.) DN=0.
  TX=TEMP(1,DAY)+1.5
  TN=TEMP(2,DAY)+1.5
  TM=(TEMP(1,DAY)+TEMP(2,DAY))/2.+1.5
  DEVELOPMENT INCREMENT CALCULATED
  DVA=(F1(TX,XV1,YV1,15)+F1(TN,XV1,YV1,15)+F1(TM,XV1,YV1,
       15))/3.
  DVA=DVA*(1,+0.27*DN)
  LOG(EXPECTED FINAL WT/BIRTH WT) CALCULATED
  C=CUM
  IF(C.LT.50.) C=50
  IF(C.GT.350.)C=350
  GFL=1.5373-0.00064*C-0.00174*AS(9.1)-0.00809*(TM-1.5)+
      0.24*DN
  GF=10**(DVA*GFL)
```

```
  NYMPHAL WEIGHTS, DEVELOPMENT AND CROWDING EXPERIENCE UP-
  DATED.
  DO 1 I=1,50
  IF((AN(I,1)+AN(I,2)+AN(I,3)).LT(1E-6) GOTO 1
  AN(I,4)=AN(I,4)+DVA
  AN(I,5)=AN(I,5)+AS(9,1)
  AN(I,6)=AN(I,6)*GF
  IF(AN(I,4).LE.1.) GOTO 1
  AN(I,6)=AN(I,6)*10**(GF*(1.-AN(I,4)))
  AN(I,4)=1.
1 CONTINUE
  RETURN
  END

  SUBROUTINE STORE       (O,AS,LS,BS,CS,M)
  REAL O(30,31),AS(9,2),LS(7,2),BS(7),CS(7)
  O(M,2)=AS(2,1)+AS(3,1)+AS(4,1)
  DO 1 I=3,6
1 O(M,I)=AS(I+2,1)
  O(M,7)=AS(1,1)
  O(M,8)=AS(6,2)
  O(M,9)=0.
  O(M+1,31)=0.
  DO 2 I=2,8
2 O(M,9)=O(M,9)+AS(I,1)*AS(I,2)
  GOTO 6
  DO 3 I=10,15
3 O(M,I)=LS(I-8,1)
  O(M,16)=LS(1,1)
  DO 4 I=17,22
4 O(M,I)=BS(I-15)
  O(M,23)=BS(1)
  DO 5 I=24,29
5 O(M,I)=CS(I-22)
  O(M,30)=CS(1)
6 CONTINUE
  M=M+1
  RETURN
  END

  SUBROUTINE AGE         (NA,AA,AM,IMAX,MM)
  REAL AN(50,6),AA(30,6),AM(30,2)
  NYMPHS UPDATED
  DO 1 I=1,49
  II=51-I
  DO 1 J=1,6
1 AN(II,J)=AN(II-1,J)
```

```
  DO 2 J=1,6
2 AN(1,J)=0.
  ADULTS UPDATED
  IM=IMAX-1
  DO 3 I=1,IM
  II=(IMAX+1)-I
  DO 3 J=1,6
3 AA(II,J)=AA(II-1,J)
  DO 4 J=1,6
4 AA(1,J)=0.
  ADULT DAILY MORTALITY ZEROED
  DO 5 I=1,IMAX
  DO 5 J=1,2
5 AM(I,J)=0.
  NYMPHS MOULT IF SUFFICIENT DEVELOPMENT ATTAINED
  DO 6 I-1,49
  II-51-I
  IF(AN(II,4).LT.1.) GOTO 6
  DO 7 J=1,3
  AA(1,J+3)=AN(II,J+3)
  AN(II,J+3)=0.
  IF(AA(1,4).GT.1.) AA(1,4)=1.
  AA(1,J)=AA(1,J)+AN(II,J)
7 AN(II,J)=0.
  AA(1,5)=AA(1,5)/II
6 CONTINUE
  RETURN
  END

  SUBROUTINE PARA        (AA,DAY,MM)
  REAL AA (30,6)
  INTEGER DAY
  PAR=0.01*(DAY-206)
  IF(PAR.GT.0.155) PAR=0.155
  IF(PAR.LT.0.) PAR=0.
  DO 1 J=1,3
1 AA(1,J)=AA(1,J)*(1.-PAR)
  RETURN
  END

  SUBROUTINE POP         (AS,LS,CS,BS,TB,TL,TC,SB,SL,SC,
                          ECF2,DAY,MM,ND,MY)
  REAL AS(9,2),LS(7,2),CS(7),BS(7),ECF2(9)
  REAL TB(7),TC(7),TL(7),SB(7),SC(7),SL(7)
  INTEGER DAY
  COCCINELLID POPULATION
  REPRODUCTION
```

```
  ECF1=0.
  IF(DAY.GE.157.AND.DAY.LE.170) ECF1=1.
  IF(DAY.GE.171.AND.DAY.LE.184) ECF1=0.3
  IF(DAY.GE.185.AND.DAY.LE.198) ECF1=0.2
  IF(DAY.GE.199.AND.DAY.LE.240) ECF1=0.1
  EC=0.
  IF(AS(9,1).GT.0.2) EC=0.066*ALOG10(9,1))+0.046
  EC=EC*ECF1*ECF2(MY)
  DEVELOPMENT AND SURVIVAL
  DO 8 II=2,7
  I=9-II
8 CS(I)=CS(I)*(1.-TC(I))+CS(I-1)*TC(I-1)*SC(I-1)
  CS(1)=CS(1)*(1.-TC(1))+EC
  AI=0.037*CS(1)
  IF(CS(7).LT.AI) CS(7)=AI
  BLACK-KNEED CAPSID POPULATION
  REPRODUCTION
  EB=0.
  IF(DAY.GE.240.AND.DAY.LE.246) EB=30.*BS(7)
  IF(EB.GT.0.AND.AS(9,1).LT.0.2) EB=4.*BS(7)
  DEVELOPMENT AND SURVIVAL
  TB(1)=0.0
  IF(DAY.GE.149.AND.DAY.LE.155) TB(1)=0.063
  IF(DAY.GE.156.AND.DAY.LE.162) TB(1)=0.583
  IF(DAY.GE.163.AND.DAY.LE.169) TB(1)=0.719
  IF(DAY.GE.170.AND.DAY.LE.176) TB(1)=1.0
  TB(7)=0.
  IF(DAY.GT.273) TB(7)=1.
  DO 4 II=2,7
  I=9-II
4 BS(I)=BS(I)*(1.-TB(I))+BS(I-1)*TB(I-1)*SB(I-1)
  BS(1)=BS(1)*(1.-TB(1))+EB
  LEAFHOPPER POPULATION
  REPRODUCTION
  EL=0.
  IF(DAY.GE.240.AND.DAY.LE.246) EL=19.*LS(7,1)**0.76
  DEVELOPMENT AND SURVIVAL
  TL(1)=0.0
  IF(DAY.GE.139.AND.DAY.LE.145) TL(1)=0.5
  IF(DAY.GE.146.AND.DAY.LE.152) TL(1)=1.0
  TL(7)=0.
  IF(DAY.GET.273) TL(7)=1.
  DO 9 II=2,7
  I=9-II
9 LS(I,1)=LS(I,1)*(1.-TL(I))+LS(I-1,1)*TL(I-1)*SL(I-1)
  LS(1,1)=LS(1,1)*(1.-TL(1))+EL
  DAY COUNTER ZEROED
```

```
      ND=0
      RETURN
      END

      SUBROUTINE WMORT      (AS,O)
      REAL AS(9,2),O(30,31)
      AS(1,1)=AS(1,1)/5.75
      RETURN
      END

      SUBROUTINE OUTPUT     (O,MO,E,CUM)
      REAL O(30,31)
      INTEGER MO(12),ID(30),JD(30)
      DO 1 J=1,25
      DATE=F3(O(J,1),MO)
      ID(J)=DATE/100
    1 JD(J)=DATE-ID(J)*100
      WRITE(2,100)
  100 FORMAT(1H1,31X,17HNUMBERS/100 SQ CM////)
      WRITE(2,101)
  101 FORMAT(1H0,3X,3HDAY,30X,7HJASSIDS/1H, 2X, 9HNUMBER,
             4HDATE,7X
             137H1     2     3     4     5    AD        EGGS)
      WRITE(2,102)
  102 FORMAT(1H0,100X)
      DO 2 J=1,25
    2 WRITE(2,103) O(J,1),ID(J),(O(J,I),I=10,16)
  103 FORMAT(1H,2X,F4.0,4X,12,1H/,12,2X,7F6.2)
      WRITE(2,100)
      WRITE(2,104)
  104 FORMAT(1H0,2X,3HDAY,20X,19HBLACK-KNEED/CAPSIDS,22X,
             12HCOCCINELLIDS 1/1H, 14HNUMBER DATE,8X,1H1,5X,1H2,
             5X,1H3,5X,1H4,5X,1H5,5X,12HAD,4X,1HE,6X,1H1,5X,1H2,
             5X,1H3,5X,1H4,5X,1HP,4X,2HAD,5X,1HE)
      WRITE(2,102)
      DO 3 J=1,25
    3 WRITE(2,105) O(J,1),ID(J),JD(J),(O(J,I),I=17,30)
  105 FORMAT(1H, 1X,F4.0,3X,I3,1H/,I2,3X,7F6.3,2X,7F6.3)
      WRITE(2,106)
  106 FORMAT(1H1,59X,3HLOG,3X,3HLOG,10X,5HTOTAL/1H, 24X,
             12HNUMBERS PER 9H100 SQ CM,12X,6HTOT/SQ,1X,6HTOT/SQ,
             1X,5HADULT,1X,7HLIVE/WT/1H,14H DAY,3X,4HDATE,5X,
             3H1-3,4X,1H4,5X,1HV,5X,2HOV,5X,1HM,3X,4HEGGS,2X,
             5HTOTAL,2X,4HDM+1,3X,3HM+1,4X,2HWT,1X,10H(MG/SQ DM),
             6H PREDN)
      WRITE(2,102)
      DO 4 J=1,25
```

```
    TOT=0.
    DO 5 K=2,6
  5 TOT=TOT+O(J,K)
    TOTLG1=ALOG10(TOT+1.)
    TOTLG2=ALOG10(TOT*100.+1.)
  4 WRITE(2,107) O(J,1),ID(J),JD(J),(O(J,I),I=2,7),TOT,
          TOTLG1,TOTLG2, 1O(J,8),O(J,9),O(J,31)
107 FORMAT(1H, F5.0,1X,I2,1H/,I2,2X,6F6.2,F8.2,F6.3,F7.3,F6.0,
           F8.2,F8.2)
    EG1=-99.
    EG2=-99.
    IF(O(1,7).GT.O.) EG1=ALOG10(O(1,7))+2.
    IF(O(25,7).GT.O.) EG2=ALOG10(O(25,7))+2.-0.76
    WRITE(2,108) EG1,EG2,E,CUM
108 FORMAT(1HO,24HLOG INITIAL EGGS/SQ M =,F6.3,5X,
           124HLOG FINAL EGGS/SQ M =,F6.3,5X,
           12HEMIGRATION =,F6.2,5X, 110HCUM DENS =,F6.1)
    RETURN
    END

    REAL FUNCTION F1(X,XVAL,YVAL,NDIM)
    DIMENSION XVAL(NDIM)YVAL(NDIM)
    CARRIES OUT LINEAR INTERPOLATION
    IF(X.LE.XVAL(1)) GOTO 1
    IF(X.GE.XVAL(NDIM) GOTO 2
    DO 3 I=1,NDIM
    IF(XVAL(I).LE.X) GOTO 3
    AM=(YVAL(I)-YVAL(I-1))/(XVAL(I)-XVAL(I-1))
    C=YVAL(I)-AM*XVAL(I)
    F1=AM*X+C
    RETURN
  3 CONTINUE
  1 F1=YVAL(1)
    RETURN
  2 F1=YVAL(NDIM)
    RETURN
    END

    REAL FUNCTION F3(TDAY,MO)
    CONVERTS A DAY NUMBER TO DAYS AND MONTHS WRITTEN THUS:
    2408
    INTEGER MO(12)
    F3=TDAY
    DO 1 I=1,12
    F3=F3-MO(I)
    IF(F3.LE.0.0) GOTO 2
  1 CONTINUE
```

```
   I=12
 2 F3=(F3+MO(I))*100.0+I
   RETURN
   END
```

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