

MODELLING APHID POPULATIONS

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SUMMARY: The application of two types of model to aphid populations is discussed, with particular reference to the lime aphid (*Eucallipterus tiliae* L.). The role of detailed simulation models is briefly reviewed and it is shown that a model of the lime aphid developed in Britain can represent the differing population behaviour of the same species in New Zealand. A much simpler, general herbivore/plant model is then applied to the lime aphid in Britain and gives as good agreement with observed data as did the detailed simulation model.

INTRODUCTION

This paper considers two approaches to the modelling of aphid populations. Using the lime aphid (*Eucallipterus tiliae* L.) as an example, it discusses the well-established role of detailed simulation models in the study of aphid population dynamics then considers the possible application of a simple, general herbivore/plant model to aphids.

DETAILED APHID MODELS

Aphid simulation models arose from the need to find a method of studying and understanding the dynamics of populations in which generations overlap, reproduction is continuous, age-distributions are generally unstable and it is impractical to follow the progress of individual cohorts. Such features preclude classic methods of age-specific life-table (key factor) analysis and may also account for the noticeable absence of aphids and aphid models from ostensibly general tests on animal population ecology.

These simulation models are generally extremely detailed and although broadly similar in construction differ in their individual emphasis. Those of Gilbert and Hughes (1971), Gutierrez *et al.* (1974) and Gilbert and Gutierrez (1973) considered evolutionary strategies of aphids and their parasites, and the first two addressed the problem of biological control. Gilbert and Gutierrez (1973) also emphasised the importance of climatic effects while models by Hughes and Gilbert (1968), Dixon and Barlow (1979) and Barlow and Dixon (1980) showed the factors involved in population regulation. Finally, Frazer and Gilbert (1976) used simulation as the basis for a rigorous analysis of the process of predation in the field. Whatever the emphasis in these studies, the first step common to most is an

attempt to account for what is observed by assembly of the detailed component processes studied separately in the field or laboratory (Gilbert *et al.*, 1976). The extent to which it is achieved varies considerably, particularly since several models have been checked against only one set of data, but the process represents the greatest contribution of detailed simulation models to our understanding of aphid population dynamics.

Thirteen species have now been modelled, one of which is the lime aphid. In Britain, populations of this aphid characteristically build up to a single peak each season, reached early in the year if densities are initially high and later if they are low (see Fig. 2). Following the peak, numbers decline and over-wintering eggs are laid by sexual forms at the end of each season. The result is an inverse relationship between densities at the beginning of successive years (compare initial densities in 1968 and 1969 in Fig. 2). The model embodies the detailed processes of egg-hatching, parthenogenetic reproduction, morph-determination, egg-laying, development, growth in size of the aphids, emigration of winged adults, predation, parasitism and other mortality. It incorporates the age-structure of the population and takes full account of temperature effects, but is not, like most other aphid models~based on the simplifying assumption of physiological time. As such, it reproduces the inverse relationship between densities in successive seasons and gives good agreement with field data over a period of 8 years in Britain (Barlow and Dixon, 1980). However the aphid is also found in New Zealand and here the picture appears to be somewhat different, at least during the first year in which populations have been sampled (1979/80). Densities on five trees in Palmerston North remained low, with slight peaks in spring and autumn and a depression during summer (Fig. 1). Sexual forms were produced about 6 weeks later than in Britain, relative to the time of appearance of the first generation, and exposure of the sampled trees to high winds was also

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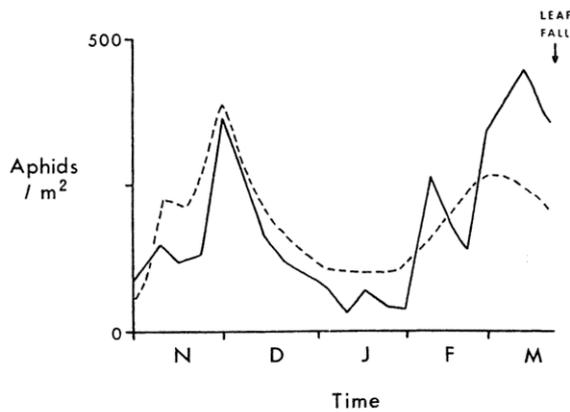


FIGURE 1. Population trends for the lime aphid over 5 trees in Palmerston North, New Zealand, 1979/80. ----- observed, - - - - - model.

considerably greater, particularly during the middle of the season. Predators were very few. Wind speed is known to affect aphid mortality (Barlow and Dixon, 1980) and incorporation of an arbitrary but realistic relationship, together with the other differences described above, caused the model to reproduce correctly the pattern of population change observed in the 1979/80 New Zealand season (Fig. 1). It appears therefore, that wind may be of considerable significance in these populations and that a priority in field work should be to establish the precise relationship between wind speed and aphid mortality in the study area.

A SIMPLE APHID MODEL

While detailed models are of undoubted value, simple predator/prey ones have been applied with considerable success to herbivore/plant interactions (Noy-Meir, 1975; Caughley, 1976a and b). Such models treat the population as a whole, ignoring age-structure, and aim to embody and reproduce the absolute essentials of its behaviour. They generally consist of a pair of equations, one for the herbivore and the other for its resource, while a third equation may be required where predators are important and their numbers continually affected by those of the herbivore (see for example May *et al.*, 1979). Aphids are clearly herbivores and the easiest aspect of their population dynamics to measure in the field is the change in their total density. Can such models be applied to aphids, therefore, to give a correct and biologically meaningful representation of the characteristic patterns of population change observed in the field?

A typical simple model of a herbivore and its resource is given by the following equations:

$$\text{Resource (R): } \frac{dR}{dt} = rR(1-R/K) - bH(1-e^{-fR}) \dots 1$$

$$\text{Herbivore (H): } \frac{dH}{dt} = H [c(1-e^{-gR}) - d] - H(1-e^{-S/H}) \dots 2$$

where r, b, f, c, g and d are constants. S is explained below. The first equation states that the resource grows or recovers in logistic fashion to an upper limit K (the first term), and is depleted at a rate which depends on the number of herbivores but which declines when the resource becomes very scarce (the second term). In the second equation, the first term represents resource-dependent growth of the herbivore population; its instantaneous rate of increase is positive (maximum c-d) when the resource is abundant and negative (minimum -d) when the latter is sparse. The second term in the herbivore equation represents the effects of predators. In this model their numbers are assumed to be independent of those of the herbivore, and their maximum consumption rate, summed over all predators, is given by S. The predation term therefore gives a total prey consumption rate of S when prey are abundant (H large), falling to zero as H declines, a Holling Type 2 functional response.

In applying such a model to aphids one obvious difficulty lies in the nature of aphid feeding; the host plant is not defoliated so the effect is difficult to measure. However, reciprocal effects of aphids on their hosts and vice versa are well-established, and in a number of instances an aphid-induced decline in plant quality is thought to have contributed directly to a population crash (Davis, 1957; Sluss, 1967; Frazer and van den Bosch, 1973; Gaynor *et al.*, 1979; Barlow and Dixon, 1980). The mechanism of such an effect is unknown but may involve accumulation of honeydew or toxins from aphid saliva in the phloem, a nutrient drain on the host, or physical occlusion of vessels as a reaction to aphid feeding. R in the model must therefore be considered as an index of resource quality rather than an absolute measure of its quantity, reflecting in part the extent to which the plant has been previously infested, and conveniently assigned values from 0 to 1. In the case of the lime aphid, the aphid/host interaction is particularly complex. One of the most important mechanisms causing a population to decline is increased emigration of adults, all of which are winged. This flight tendency is related both to condition of leaves at the time (Kidd, 1977) and to condition of the adult aphids

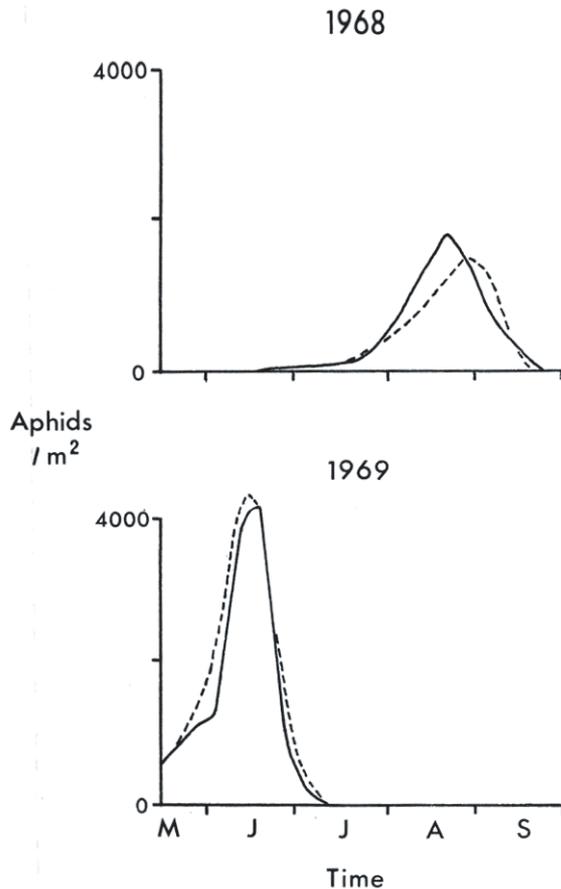


FIGURE 2. Population trends for the lime aphid in Glasgow, Scotland. ----- observed, - - - - - simple model with parameters of equations 1 and 2: $c=0.16$, $d=0.11$, $r=0.01$, $g=2$, $f=10$, $b=2 \times 10^6$, $K=1$, and initial values $R_0=1$, $H_0=3.6$ aphids/ m^2 leaf area (1968) or $400/m^2$ (1969).

themselves, but the latter is determined by nymphal experience of crowding perceived through the leaf (Kidd, 1977). It does not appear unreasonable, therefore, to consider the population's instantaneous growth rate to be affected directly or indirectly by plant conditioning. Before the simple model can be applied to the lime aphid, however, equation 2 must be modified by making c and S time-dependent. c , the positive component of the aphid's rate of increase, declines as the season progresses because an increasingly greater proportion of sexual morphs are produced. These mate and produce overwintering eggs, so curtailing the current season's population growth; finally leaf-fall supervenes. S represents

potential prey consumption by the most important predator, the two-spot coccinellid *Adalia bipunctata* L., and increases to a peak during the year as the single generation of beetles becomes larger and more voracious. The extent and timing of this peak depends on the initial number of aphids, so the pattern of S throughout the year is considered as an input in the model.

Figure 2 shows the two extremes of population growth observed during the year in Glasgow, Scotland, corresponding to low (1968) and high (1969) initial aphid densities, together with those generated by the simple interactive model. Agreement is good, the only qualitative discrepancy being at the beginning of 1969 before reproduction begins in the field and the density therefore remains fairly constant. Unlike a detailed simulation model, the simple one cannot reproduce such gross changes in age-structure without the incorporation of an additional factor which modifies the aphid's rate of increase accordingly. This was thought to be unwarranted given the limited time over which the effect is significant, and with this exception the simple model gives as good agreement with field data as a detailed simulation (cf. Barlow and Dixon, 1980).

DISCUSSION

The main disadvantages of detailed simulation models are that they tend to be cumbersome, difficult to understand and specific to individual situations. On the other hand they provide understanding in depth, relating phenomena at the population level to behaviour and physiology. Simple interactive models are the reverse in most respects. The level of understanding they provide is high, virtually qualitative, but they are nevertheless truly functional and can clearly be used for predictive purposes. They are also more general: versions similar to the one described above have been applied to reindeer and sheep (Caughley, 1976a) the moth *Cactoblastis cactorum* (Caughley, 1976b) and the spruce budworm (Ludwig, Jones and Holling, 1978; May, 1977) while there is every likelihood that elephants in East Africa, the larch bud moth in Switzerland and many other herbivores could be added to this list.

The aim in this paper has been to show briefly that both approaches can provide valuable insights. The one highlights the difference between lime aphid population behaviour in Britain and New Zealand, and suggests reasons for this difference. The other calls into question our knowledge of the role of aphid-induced plant changes; the eruptive pattern of population change commonly exhibited by aphids

is strongly suggestive of a herbivore/plant interaction accentuated by the effects of predators. Further research should also enable more biological meaning to be attributed to the individual parameters of the simple model, so rendering it less qualitative and more quantitative.

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