12 Population Dynamics

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Introduction

It is the abundance of many aphids that makes them such serious pests. Therefore, it is important for aphid pest management to have a good understanding of their population dynamics both in terms of theory and practice. Although this aspect of aphid biology is well studied, there has been a lack of long-term studies of the population dynamics of aphids living on herbaceous plants, including crops. This is because any single arable crop field supports only a small fraction of the shifting population in a region, and even a dramatic event there will have little or no impact on the regional population dynamics (Mackauer and Way, 1976). As a result, this chapter will draw on research on non-pest species where their study may provide insights relevant to crop pests.

Not surprisingly, the pest status of aphids and political concern over the prophylactic application of pesticides has attracted the attention of modellers since the 1960s (Hughes, 1963; Hughes and Gilbert, 1968; Gilbert and Hughes, 1971; Gosselke *et al.*, 2001). Attempts were made to forecast the abundance of aphids and propose expert systems to help farmers optimize prophylactic measures and minimize their costs (Mann *et al.*, 1986; Gonzalez-Andujara, 1993; Ro and

Long, 1999). These studies usually concluded that forecasting is a better strategy than either no control or prophylaxis, where yields are average and above (Watt, 1983; Watt *et al.*, 1984). The advisory systems, however, did not receive general acceptance and disappointingly few forecasting systems are in use. Analysis of some of the existing models of aphid population dynamics reveals the reasons. For example, a model that describes the summer population dynamics of the *Sitobion avenae* (grain aphid) (Carter *et al.*, 1982; Carter, 1985) was modified and extended to include the population dynamics of the aphidophagous predator *Coccinella septempunctata* (7-spot ladybird) (Skirvin *et al.*, 1997a,b). It is claimed to give better predictions than the Carter *et al.* (1982) model, but there are few data against which it can be validated. The main weakness of the Skirvin *et al.* (1997a) model is that it gives the same prediction for identical initial conditions, which is contrary to what is observed in the field.

Early models of the population dynamics of *Myzus persicae* (peach–potato aphid) (Scopes, 1969; Tamaki and Weeks, 1972, 1973; Tamaki, 1973, 1984; DeLoach, 1974; Taylor, 1977; Whalon and Smilowitz, 1979; Tamaki *et al.*, 1980, 1982; Mack and Smilowitz, 1981, 1982; Smilowitz, 1984; Ro

and Long, 1998) were improved recently by Ro and Long (1999). However, even this model is not validated against data that were not used to derive the parameters, which devalues the claim that it gives a good prediction. In addition, it also makes the unwarranted assumption that the decline in aphid abundance is caused by predators.

A simulation model developed to investigate the interrelationship of factors influencing the population dynamics of *Rhopalosiphum padi* (bird cherry–oat aphid) in barley crops during autumn and winter (Morgan, 2000) accurately predicts outbreaks and peak aphid populations within 20% of that observed in all but one case. However, this model is not suitable for long-term predictions, as it requires the daily input of maximum and minimum temperatures, which invalidates its predictive value as those temperatures themselves cannot be predicted with sufficient accuracy. Another model for this species was developed by Wiktelius and Pettersson (1985) but not used for forecasting, and the need for further research stressed.

A whole family of models of *Aphis craccivora* (cowpea aphid) (Gutierrez *et al.*, 1974) and *Acyrthosiphum pisum* (pea aphid) population dynamics (Gutierrez and Baumgärtner, 1984a,b; Guttierez *et al.*, 1984), and that of their natural enemies (Gutierrez *et al.*, 1980, 1981) were developed by Gutierrez and his group, but even these were not used for long-term predictions. Similarly, a computer simulation model developed to investigate spatial and population dynamics of apterae of the *Diuraphis noxia* (Russian wheat aphid) on preferred (wheat) and non-preferred (oat) hosts by Knudsen and Schotzko (1991) is suitable only for short-term (14 and 21 days) predictions. A transition matrix model developed to simulate the population dynamics of *Aphis pomi* (green apple aphid) (Woolhouse and Harmsen, 1991) has also not been validated against an independent data set.

Recently, spatio-temporal or metapopulation models have been published (Weisser, 2000; Winder *et al.*, 2001). These are a promising development, but modellers employing this approach need to consider whether aphid migration, rather than predator-inflicted mortality, is the regulating factor. The question remains, whether aphid metapopulation dynamics are driven by predators or, as predicted by theory (Kindlmann and Dixon, 1996, 1999), the predators are responding to aphid abundance, which is self-regulated by migration.

In general, the failure of models to predict aphid population dynamics for practical purposes is due to the extremely wild oscillations in aphid numbers caused by intrinsic (size, fecundity, mortality, migration rate) and external (weather, especially temperature) factors. As a consequence, predictions are unlikely to be robust enough for reliable forecasting, mainly because they depend on the course of weather during the season, which cannot be predicted. In addition, most of the models tend to be very complex, which stems from the belief of their authors that complexity means better accuracy, which is not always the case (Stewart and Dixon, 1988). This is because the measuring errors associated with each of the large number of parameters yield highly variable predictions. Thus, there is a serious gap in our knowledge, which needs to be filled in order to confirm or refute the understanding arrived at mainly by studying aphids living on woody plants. For a further discussion of forecasting, see Harrington *et al.*, Chapter 19 this volume.

Biological Background

Aphid biology relevant to population dynamics

Most aphid species can reproduce both asexually and sexually, with several parthenogenetic generations between each period of sexual reproduction. This is known as cyclical parthenogenesis and, in temperate regions, sexual reproduction occurs in autumn and results in the production of overwintering eggs, which hatch the following spring and initiate another cycle. Many pest aphids, however, overwinter, not as an egg but as nymphs or adults, and others as

both eggs and active stages (see Williams and Dixon, Chapter 3 this volume). For their size, the parthenogenetic individuals have very short developmental times and potentially prodigious rates of increase (de Réaumur, 1737; Huxley, 1858; Kindlmann and Dixon, 1989; Dixon, 1992). Thus, aphids show very complex and rapidly changing within-year dynamics, with each clone going through several generations during the vegetative season and being made up of many individuals, which can be widely scattered in space. The survival of the eggs and/or overwintering aphids determines the numbers of aphids present the following spring.

The study of the population dynamics of aphids living on herbaceous plants, including agricultural crops, is difficult because their host plants vary in abundance and distribution from year to year. Tree-living aphids, in addition to being very host-specific, live in a habitat that is both spatially and temporally relatively stable. Therefore, it is not surprising that most long-term population studies on aphids have been on such species (Dixon, 1963, 1966, 1969, 1970, 1971, 1975, 1979, 1990; Dixon and Barlow, 1979; Barlow and Dixon, 1980; Dixon and Mercer, 1983; Chambers *et al.*, 1985; Wellings *et al.*, 1985; Dixon *et al.*, 1993b, 1996). However, some of the theoretical results obtained from these studies are quite general and can be applied to other aphid species.

Within a year, aphid dynamics are very complicated and, in looking for the mechanism of regulation, this needs to be taken into consideration. An initial dramatic increase in population size in spring is typically followed by a steep decline in abundance during summer, and sometimes a further increase in autumn. During spring and summer, all the generations are parthenogenetic and short-lived (1–4 weeks). In autumn, sexual forms are also produced, which mate and give rise to the overwintering eggs from which fundatrices, the first parthenogenetic generation, hatch the following spring. The parthenogenetic generations overlap in time and environmental conditions change rapidly. Therefore, an individual throughout its life, as well as individuals born at different but close instants in time,

can experience quite different conditions, which results in aphids evolving different and varying reproductive strategies.

The within-year dynamics of aphids are determined largely by seasonal changes in host quality. Aphids do best when amino acids are actively translocated in the phloem. In spring, the leaves grow and import amino acids via the phloem; in summer, the leaves are mature and export mainly sugars; in autumn, the leaves senesce and export amino acids and other nutrients. Thus, on trees, the leaves are most suitable for aphids in spring and autumn. The differences in within-year population dynamics of aphids are due to differences in the effect these seasonal fluctuations in host plant quality have on the *per capita* rate of increase and intraspecific competition in each species. This annual cycle, of two short periods when the host plant is very favourable and a long intervening period when it is less favourable, is well documented for tree-dwelling aphids. This has greatly facilitated the modelling of their population dynamics. In general, the aphid-carrying capacity of annual crop plants tends to increase with the season until the plants mature, after which it tends to decrease very rapidly. Thus, the aphid-carrying capacity of trees tends to be high in spring and autumn and low in summer, whereas the carrying capacity of short-season crops in particular tends to be low early in the year, peaking mid-year, and then declining. This is an important point that will be returned to later in this chapter.

Much is known about the biology of the parthenogenetic generations of aphids, in particular the optimum behaviour for maximizing the instantaneous population growth rate, r_m, under various environmental conditions (Kindlmann and Dixon, 1989, 1992; Kindlmann *et al.*, 1992) and the optimal strategies for migration (Dixon *et al.*, 1993a). An individual-based model (Kindlmann and Dixon, 1996), which incorporated all that is known about the biology of tree-dwelling aphids, simulated most of the observed features of the population dynamics. It provided a theoretical background for the commonly observed phenomenon that the larger the numbers are at the beginning

of a season, the larger and earlier the peak. Migration was shown to be the most important factor determining the summer decline in abundance, while changes in aphid size and food quality account for why the autumnal increase is less steep than in spring. Finally, the model suggests the possibility of a 'seesaw effect' (a negative correlation between spring and autumn peak numbers) in some cases, a phenomenon observed in census data (Dixon, 1970, 1971).

There is regularity in the population fluctuations from year to year. Very regular 2-year cycles, as indicated by suction trap catches, have proved very attractive to modellers, who have applied time series analysis to the data (e.g. Turchin, 1990; Turchin and Taylor, 1992). The conspicuous cyclicity observed in yearly totals of the number of some species of aphid on trees, however, is due mainly to the cyclicity in the peak numbers in spring, which are closely correlated with the yearly totals. It is driven by the inverse relationship between the size of the spring peak and the autumnal rate of increase, the 'seesaw effect' (Kindlmann and Dixon, 1992). This effect is present in some (Dixon, 1971), but not present or very weak in other (Dixon and Kindlmann, 1998), empirical data. In *Drepanosiphum platanoidis* (sycamore aphid), where the total numbers on the host tree are relatively constant from year to year, there is a within-year seesaw in the abundance of aphids in spring and autumn. As most of the aphids that migrate over long distances, rather than between trees, do so in autumn, the result is the 2-year cycles observed in the suction trap catches (Dixon and Kindlmann, 1998). Time series and correlation analyses reveal that the dynamics are often predictable in spring and late in autumn, but not during summer, as the size of the spring peak is not transferred into summer numbers of aphids (Kindlmann and Dixon, 1992).

It is argued that aphid population density is regulated by density-dependent processes acting within years, which is reflected in the year-to-year changes in overall abundance (Sequeira and Dixon, 1997). Some results suggest a curvilinear density-dependence, with strong density-dependent regulation at low densities and weak at high densities (Jarosik and Dixon, 1999).

Biology of natural enemies relevant to aphid population dynamics

Aphid colonies are characterized by rapid increases and declines in abundance (Dixon, 1998) that are not synchronized in time, as they feed on different host plants with different phenologies (Galecka, 1966, 1977). On a large spatial scale, at any instant, populations of aphids exist as patches of prey, associated with patches of good host-plant quality (Kareiva, 1990). That is, aphid predators exploit patches of prey that vary greatly in quality both spatially and temporally.

The adult insect predator is winged and can move easily between patches, whereas its immature stages cannot. Thus, the best strategy for an adult is to distribute its offspring between patches in a way that maximizes the expected number and fecundity of offspring that survive to maturity. The developmental time of aphidophagous predators, like coccinellids, often spans several aphid generations. Thus, the ratio of generation time of these predators to that of their prey (generation time ratio, GTR) is large, and optimum foraging strategy therefore depends not only on the present state of an aphid colony, but also on its quality in the future. The optimum oviposition strategy is therefore likely to be determined by expectations of future bottlenecks in prey abundance.

In addition, predators like coccinellids and chrysopids are cannibalistic (Agarwala and Dixon, 1992, 1993). This behaviour is adaptive, as eating conspecific competitors will increase the fitness of a predatory larva. Therefore, eggs laid by predators late in the existence of a patch of prey are at a disadvantage, as they are highly likely to be eaten by larvae of predators that hatch from the first eggs to be laid. Avoiding laying eggs in patches already exploited by larvae is likely to reduce cannibalism and intraguild predation. Empirical data indicate that several different species of insect predator have evolved mechanisms that enable them to

oviposit preferentially in patches of prey that are in an early stage of development and avoid those that are already being attacked by larvae (Hemptinne *et al.*, 1992, 1993, 2001). Laying eggs in the presence of conspecific larvae is strongly selected against in these predators, because to lay more eggs results in these eggs being eaten by older conspecific larvae. In addition, laying eggs late in the development of a patch of prey is maladaptive, as there is insufficient time for all the larvae to complete their development. The response to the presence of conspecific larvae reduces the number of eggs laid per patch.

Thus, oviposition commonly occurs only during a short 'egg window', early in the existence of each patch of prey (Hemptinne *et al.*, 1992). When predators are abundant and suitable, patches of prey are rare; however, many eggs may nevertheless be laid in a patch during the 'egg window'. In such circumstances, strong density-dependent cannibalism (Mills, 1982) greatly reduces the abundance of the predators relative to that of their prey. Therefore, these predators have little impact on aphid population dynamics (Dixon, 1992; Kindlmann and Dixon, 1993, 1999; Dixon *et al.*, 1995). They may, however, have short-term impact on local populations valuable to farmers. This is well illustrated by the fact that most of the IPM Case Histories (Chapters 21–30 this volume) recognize the value of natural enemies and the need to limit damage to them when selecting and applying insecticides. Powell and Pell (Chapter 18 this volume) discuss practical biological control of aphids entirely in terms of interventions to manipulate the unfavourable enemy:pest ratio that occurs naturally. Without intervention, there is poor synchronization in time and numbers between natural enemies and their aphid prey on arable crops. In an international study of *M. persicae* populations on potato conducted by 16 workers over 2 years in 10 countries (Mackauer and Way, 1976), the majority of data sets recorded aphid population increases regardless of predator presence, and the latter only affected reductions at times when the potential increase rate of the aphids was low.

Hymenopterous parasitoids can mature on one aphid and would appear to be potentially more likely to regulate aphid abundance. However, their effectiveness is often reduced by: (i) their longer developmental time relative to their host; (ii) the action of hyperparasitoids which, in many cases, are less specific than primary parasitoids; and (iii) their vulnerability to attack from aphid predators (Dixon and Russel, 1972; Hamilton, 1973, 1974; Holler *et al.*, 1993; Mackauer and Völkl, 1993). In addition, because of the risk of hyperparasitism, primary parasitoids are likely to cease ovipositing in a patch where many aphids are already parasitized, as high levels of primary parasitism make the patch attractive to hyperparasitoids. By continuing to oviposit in patches of aphids already attacked by conspecifics, these natural enemies may reduce their potential fitness (Ayal and Green, 1993; Kindlmann and Dixon, 1993).

In the initial phase of aphid population increase on the shorter-season arable crops such as spring-sown cereals, there are often slight dips or plateaux, followed by sudden acceleration. This is attributed to the activity of polyphagous predators (mainly carabid beetles, spiders, and earwigs), and referred to by Southwood and Comins (1976) as the 'natural enemy ravine'. They suggested that the outcome of a spring invasion of aphids is often determined by the balance between the number of invaders and the size of the autochthonous population of polyphagous predators. Carter and Dixon (1981) offered an alternative explanation: the lack of population growth in the initial phase of the population dynamics was attributed to the intermittent nature of aphid immigration, which is amplified by the pre-reproductive period of the offspring of the immigrant aphids. However, it is more likely that the ravine in population dynamics is a consequence of not being able to detect population increase at low population density using small sample sizes (Jarosik *et al.*, 2003). Small sample sizes were used in the studies cited by Southwood and Comins (1976) as evidence for a natural enemy ravine. In the study of Smith and Hagen (1959), it was 200 lucerne stems. In that of van Emden (1965), it was

90 mustard plants. Wratten (1975) used 30 stems of wheat. The study of Carter and Dixon (1981), in which an alternative explanation for the ravine was proposed, was also based on small sample sizes, with the maximum sample size of 600 tillers of winter wheat. Honek and Jarosik (2000) and Honek *et al.* (2003) also found no evidence that polyphagous predators affect cereal aphid population dynamics in the field. In the habitat they studied, carabid beetles were the dominant guild of polyphagous predators. However, these carabids are mainly seed predators (Honek *et al.*, 2003) and their activity was only loosely correlated with aphid density (Honek and Jarosik, 2000). In addition, aphids have a low nutritional value and are not a preferred food of carabids (Bilde and Toft, 1999). However, in many crops other than cereals, there is a clear mid-season trough in aphid density between an early and a late peak similar to that which occurs on trees (see p.). Examples of this trough, attributed to unfavourable host plant condition with its depth influenced by natural enemy activity, can be found in several of the IPM Case Histories, e.g. brassicas (Fig. 21.1) and cotton (Fig. 23.3).

Theory of Aphid Population Dynamics

Features of aphid population dynamics that should be incorporated in models

If it is accepted that natural enemies do not regulate aphid populations, the modelling process is greatly simplified. The important features of any model are:

- Each year aphids show an initial dramatic increase in population size.
- This increase is typically followed by a steep decline in abundance.
- Sometimes there is a further increase in abundance.
- Migration is the most important factor determining the decline in abundance.
- Within-season aphid dynamics often show a 'seesaw effect' – a negative

correlation between initial and final peak numbers.
- The greater the initial aphid numbers, the larger and earlier the peak.
- Very regular, 2-year cycles are characteristic of aphid between-year population dynamics.
- Aphid population density is regulated by density-dependent processes acting within years, which can be potentially strong at low densities.
- Long-term aphid dynamics appear to be little affected by the activity of insect natural enemies.

We present several simple models based on estimates of relatively simple parameters, which may be useful for prediction of aphid dynamics complying with these rules.

Regression model

This model assumes one can divide the population dynamics into three periods: initial increase, subsequent decline, and late season increase. After converting population densities to logarithms, it is possible to assume a linear increase or decrease of density in time.

Let $x(t)$ be the natural logarithm of the population density at time t; let $x(0) = x_0$; let s_1, s_2, and s_3 be the rates of initial increase, subsequent decline, and late season increase, respectively; let x_1 be the natural logarithm of the population density when migration begins, which for simplicity coincides with the first peak in population density, and let x_2 be the population density after the decline in abundance (the trough). Then $x(t) = x_0 + s_1t$ before the peak is reached, $x(t) = x_1 - s_2t$ during the decline in abundance, $x(t) = x_2 + s_3t$ late in the season. Because of the inverse relationships between the initial rates of increase, rates of decline, and late season rates of increase, and initial numbers, $s_1 = -k_1x_0 + q_1$, $s_2 = k_2x_1 - q_2$ and $s_3 = -k_3x_2 + q_3$, where k_1, k_2, and k_3 are the slopes, and q_1, q_2, and q_3 the intercepts of the three rate relationships. Then it follows:

$$x_1 = x_0 + (-k_1x_0 + q_1)T_1$$
$$= q_1T_1 + (1 - k_1T_1)x_0 \tag{1}$$

$$x_2 = x_1 - (k_2 x_1 - q_2)T_2$$
$$= q_2 T_2 + (1 - k_2 T_2)\, x_1 \qquad (2)$$

$$x_3 = x_2 + (-k_3 x_2 + q_3)T_3$$
$$= q_3 T_3 + (1 - k_3 T_3)x_2 \qquad (3)$$

$$x_0, n+1 = k_4 x_{3,n} \qquad (4)$$

where k_4 is the slope of the relationship between the numbers next spring and late this season, $x_{i,n}$ means x_i in year n (omitted if year is n and no confusion can arise) and T_1, T_2, and T_3 are the duration of the periods of initial increase, subsequent decline, and late season increase, respectively.

Assuming that for a species, k_i, q_i and T_i are the same each year, then from Equations (1)–(4) it follows:

$$x_{i,n+1} = K + k_4(1 - k_3 T_3)(1 - k_2 T_2)$$
$$\times (1 - k_1 T_1)x_{i,n}, \qquad (5)$$

where K is a constant and $i = 0, 1, 2, 3$.

If we make $Q = k_4(1 - k_3 T_3)(1 - k_2 T_2)(1 - k_1 T_1)$, then Equation (5) simplifies to:

$$x_{i,n+1} = K + Q \cdot x_{i,n}, \qquad (6)$$

which is a model for the between-year population dynamics. Equation (6) is a linear difference equation and therefore its predictions can be derived easily from the values of its parameters K and Q. The equilibrium of this system is $x = K/(1 - Q)$ and is positive (and therefore biologically realistic), if and only if either $K > 0$ and $Q < 1$, or if $K < 0$ and $Q > 1$. If the equilibrium of Equation (6) is not positive, then it predicts either an infinite increase in population size, or its eventual extinction. If the equilibrium of Equation (6) is positive, then it is stable, if and only if $-1 < Q < 1$. If $0 < Q < 1$, then Equation (6) tends not to oscillate, if $-1 < Q < 0$, then the system tends to oscillate.

Definition of Q allows many biologically interesting interpretations of these mathematical predictions, but it is beyond the scope of this text to list them all. For example, one interesting case is when the regulatory term in one of the three periods is large and the remaining two are small, so that one of the brackets defining Q is negative, but larger than -1, while the other two brackets are positive. Then Equation (6) predicts oscillations.

If the density-dependent terms are small in all three periods, so that all three brackets defining Q are positive, then Equation (6) is unlikely to predict oscillations, and there are lots of other scenarios.

Equations (1)–(3) accurately describe the within-year population trends observed in two species of aphids, *D. platanoidis* and *Myzocallis boerneri* (Turkey oak aphid) (Dixon and Kindlmann, 1998), and are therefore realistic. They are able to simulate most of the characteristic features of both within- and between-year aphid dynamics described in the preceding section. Their serious drawback is the large number of parameters that have to be estimated. In addition, the assumption that k_i, q_i, and T_i are the same each year is not always satisfied, especially the duration of the initial period, which is known to vary relative to the initial numbers of aphids: the greater the initial number of aphids, the larger and earlier the peak (Dixon and Kindlmann, 1998).

Regression model with stochasticity

The minimum number of aphids present during the trough does not depend on the peak numbers (Dixon and Kindlmann, 1998). If the peak is large, then there is intense competition for resources, and the aphids present at the beginning of autumn are small and have a low fecundity (Dixon, 1990), which affects the population rate of increase in autumn (Dixon, 1975). When the summer peak is small, the autumnal rate of increase can be either small or large (Dixon and Kindlmann, 1998). This variability may be a consequence of higher predation in some years, as predators attracted to large numbers of aphids in summer may have a marked effect on the few aphids that remain after the summer migration, or of meteorological factors like wind (Dixon, 1979). The autumnal rate of increase, however, is positively correlated with the size of the peak the following year (Dixon and Kindlmann, 1998). Summarizing, aphid dynamics are often not very deterministic. This is sometimes seen in the low values of the correlation coefficients of the relationships defining the

individual phases in aphid dynamics (Dixon and Kindlmann, 1998). Thus, there are advantages in replacing Equations (2) and (3) with:

$$x_2 = x_1 - (k_2 x_1 - q_2)T_2 + r.RND_1$$
$$= q_2 T_2 + (1 - k_2 T_2)x_1 + r.RND_1 \qquad (2a)$$

$$x_3 = x_2 + RND_2.(-k_3 x_2 + q_3)T_3$$
$$= RND_2 q_3 T_3 + (1 - RND_2 k_3 T_3)x_2 \qquad (3a)$$

where RND_1 is a random number from $< -0.5; 0.5 >$ and r is a constant, which together simulate the extremely low numbers, the stochasticity of migration, and the sampling error. RND_2 is a random number from $<0; 1>$, which takes into account that the population may be negatively affected in autumn.

This model has the advantage of taking into account the underlying stochasticity, but its predictions are stochastic. Interestingly, in the absence of the stochastic element, the cyclicity in the yearly totals of *M. boerneri* is more definite, but the amplitude of the fluctuations is smaller. That is, this model's prediction of the trend in yearly totals more closely reflects reality than does the model with no stochasticity (Kindlmann and Dixon, 1998).

Logistic model with variable 'carrying capacity'

A distinctive feature of aphid dynamics is that the decline in numbers is caused mainly by their own dynamics and not by other species. Thus, the commonly used logistic growth model cannot be used. The amount of soluble nitrogen in the leaves (an indicator of nutritive quality) is high in spring when the leaves are actively growing, falls to a low level in summer, and then increases in autumn prior to leaf fall (Dixon, 1963, 1971). Accepting that the concentration of soluble nitrogen in the leaves is a good indicator of changes in host quality, it is reasonable to assume that aphid-carrying capacity may show a similar trend. This would lead to a logistic model with carrying capacity varying in time, $x' = rx(1 - x/K(t))$. Figure 12.1 shows the predicted dynamics, when the

carrying capacity is assumed to vary between Kmax and Kmin following a cosine function: $K(t) = (K_{max} - K_{min}).((\cos(t\pi/d) + 1)/2) + K_{min}$. The dynamics are similar to those observed – an initial increase followed by a steep decline and a further increase. The greater the initial numbers of aphids, the larger and earlier the peak. However, it can be shown that the population trajectories can never cross – in other words, if 2 years are compared in which the initial aphid numbers in one year are larger than those in the other, the same holds for autumn abundance. Thus, this model does not predict the seesaw effect.

Cumulative density model

In this model, it is assumed that the regulatory term that slows down the instantaneous rate of increase is cumulative density, rather than a term that is proportional to instantaneous density, as in logistic growth. This is based on the assumption that it is the sum of the numbers of individuals multiplied by their life span, which determines the slowing down of the instantaneous rate of increase. The logistic growth never yields a decline in population density with time – a phenomenon typical of aphid population dynamics. In the absence of an effect of natural enemies, an autoregulatory term that causes a decline in population density with time is needed. Cumulative density is a potential candidate, as it could influence food quality and hence slow down population rate of increase. Accepting this, aphid population dynamics can be described by the following set of differential equations:

$$\frac{dh}{dt} = ax, \qquad h(0) = 0, \qquad (7a)$$

$$\frac{dx}{dt} = (r - h)x, \qquad x(0) = x_0 \qquad (7b)$$

where $h(t)$ is cumulative density of aphids at time t, $x(t)$ is density of aphids at time t, a is a scaling constant relating aphid cumulative density to its own dynamics, and r is maximum potential growth rate of the aphids. Thus, while in the logistic model
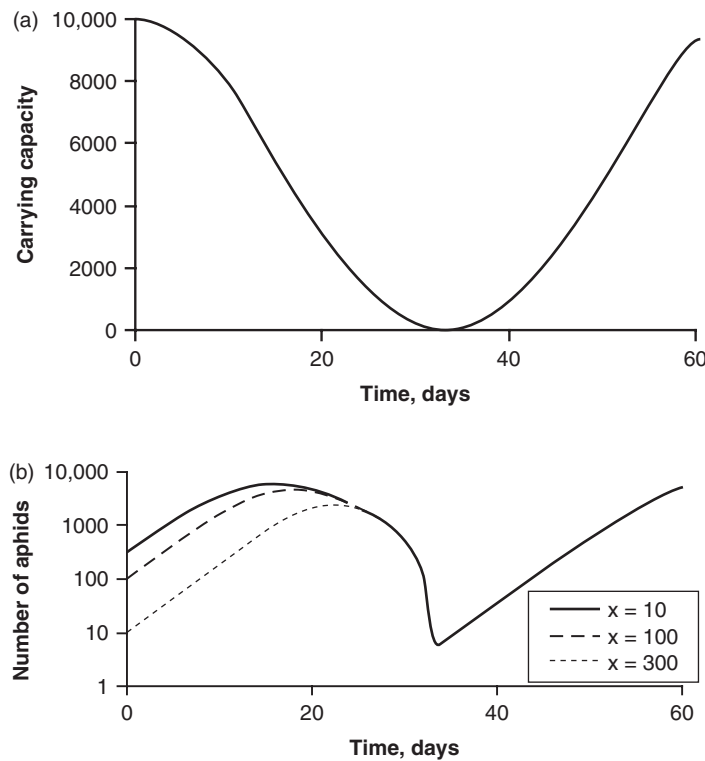
Fig. 12.1. (a) Carrying capacity and (b) aphid density as a function of time for various initial densities of the aphid, predicted by the logistic model using a variable carrying capacity: $r = 0.3$; $K_{max} = 10{,}000$, $K_{min} = 1$; $d = 33$. Initial aphid densities (x) in insets.

it is assumed that the growth rate linearly declines with population density, here it is assumed that the growth rate linearly declines with aphid cumulative density. This models the decline in population density with time, so typical of aphid populations.

This model predicts that with increasing initial aphid density, the peak density becomes larger, and is achieved earlier. This is illustrated in Fig. 12.2. This model also successfully simulates most of the features of aphid dynamics. One example of the fit of this model to empirical data is shown in Fig. 12.3.

Logistic model with variable carrying capacity and growth rate affected by cumulative density

Empirical data indicate that if the number of aphids present early in a season is large, then there is intense competition for resources and the aphids present at the beginning of autumn are small and have a low fecundity,

which affects the population rate of increase in autumn (Dixon, 1975, 1990). Simulation of this can be achieved by combination of the previous two models, which gives:

$$\frac{dh}{dt} = ax, \qquad\qquad h(0) = 0, \qquad (13a)$$

$$\frac{dx}{dt} = (r - h)x\left(1 - \frac{x}{K}\right), \qquad x(0) = x_0, \qquad (13b)$$

$$K(t) = (K_{max} - K_{min}).$$
$$\times ((\cos(t\pi d) + 1)/2) + K_{min}. \qquad (13c)$$

This model, unlike the logistic model with a variable carrying capacity, yields a seesaw effect (Fig. 12.4). However, the basic practical problem of how to measure the time varying 'carrying capacity', K, remains.

Comparison of the different population models

The 'regression model' is descriptive, contains more parameters, and is thus more flexible, but is more data demanding than
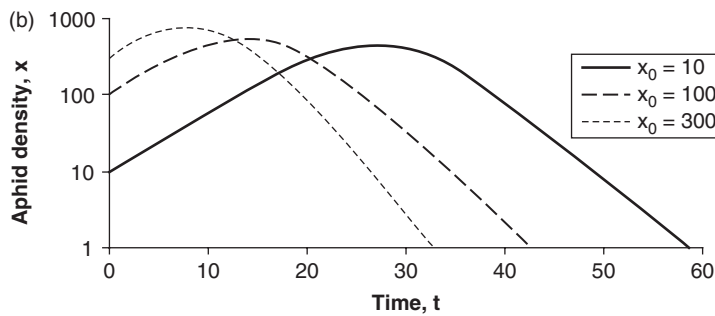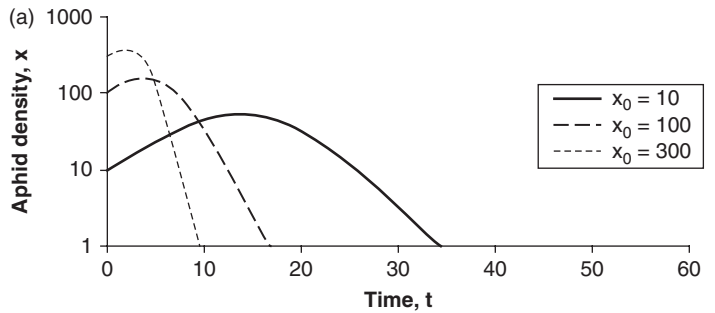
Fig. 12.2. Aphid density as a function of time for various initial densities of the aphid predictions of Equation (7): $r = 0.3$; (a) $a = 0.0005$, (b) $a = 0.00005$; initial aphid densities in insets.
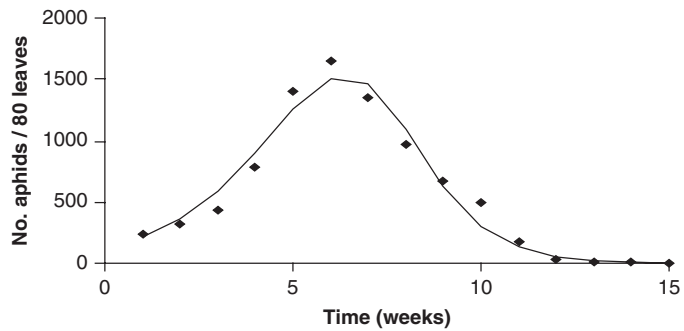

Fig. 12.3. Aphid density as a function of time predicted by Equation (7) (solid line), relative to the census data for the aphid on a Turkey oak tree in 1995; estimated parameters: $r = 0.71$; $a = 0.00015$, initial aphid density $x_0 = 215$.

the logistic growth model with variable carrying capacity. It divides a season into three periods: initial increase, subsequent decline, and final period of increase. Its parameters can be obtained easily from regressions of population densities on time, provided reliable data are available. Its serious drawback is that many of the parameters have to be estimated and the assumption that k_i, q_i, and T_i are the same each year is not always satisfied. Thus, this model is a good theoretical tool, but unlikely to be useful for predicting aphid dynamics.

The logistic growth model with variable carrying capacity is a logical consequence of

the observation that food quality undergoes changes during the season. The problem with this model is that it requires an estimate of the trend in the carrying capacity during a season, which may be impossible to measure directly. An indirect measure, e.g. the concentration of soluble amino acids, is used instead. Its major drawback, however, is that it does not predict the seesaw effect.

The 'cumulative density model' is based on the intrinsic ecology of aphids, does not describe a specific scenario, and requires fewer data. However, it describes only the dynamics during the initial and
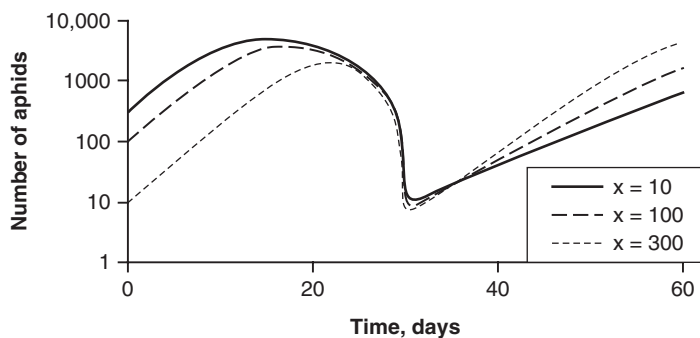
Fig. 12.4. Aphid density as a function of time for various initial densities of the aphid – prediction of the logistic model with variable carrying capacity: $R = 0.3$; $K_{max} = 10,000$, $K_{min} = 1$; $d = 33$. Initial aphid densities (x) in inset.

decline periods. The increase in abundance later in the season remains to be modelled.

The model with variable carrying capacity and growth rate affected by cumulative density combines the advantages of the two previous models and is the most flexible of the models. However, it also requires an estimate of the trend in the carrying capacity during a season. As stated above, it is likely to be V-shaped for tree-dwelling aphids and Λ-shaped for aphids infesting annual crops. Although a single peak is found with cereal aphids, it is rather atypical and due to the short time before plant decline that the aphid population increase starts. Thus, in case of multiple peaks occurring during one season, each peak has to be modelled separately.

Natural Enemies and Aphid Abundance

Although there is no evidence that natural enemies are capable of regulating the abundance of aphids, they may affect aphid abundance, and their activity may therefore be of economic benefit to the farmer. In some years with low cereal aphid numbers, they may even obviate the need to spray altogether (see Poehling *et al.*, Chapter 25 this volume). In killing aphids, natural enemies are therefore potentially capable of reducing the population rate of increase of aphids. This will depend, however, on the strength of the density-dependent processes acting on the aphid's rate of increase. If the natural enemy load associated with a pest aphid is high, then it might reduce its abundance. Thus, increasing the diversity and abundance of the natural enemies in crops might

reduce the abundance of pest aphids. The challenge is to show that it does and that it is a cost effective way of protecting crops.

Practical Problems

For forecasting pest aphid abundance and for making decisions in integrated control programmes, it may be necessary to have accurate estimates of aphid abundance and population growth rates.

Field estimates of abundance and population growth rate

The crucial parameters of the models, maximum potential growth rate of aphids and its parabolic decline, are difficult to assess for aphids living on herbaceous plants, including crops. The seasonal trends in aphid abundance on crop plants can be determined, however, providing there are no constraints on sample sizes. For example, this was done using census data from 268 winter wheat plots collected at 3- or 7-day intervals over a period of 10 years for aphids on wheat leaves and 6 years for those on the ears (Jarosik *et al.*, 2003). Aphids can become very abundant on wheat, which they colonize in spring. The initially very sparse populations of aphids grow and reach maximum densities, usually in the last days of June, and then decline sharply in abundance. An estimate of the maximum potential population growth rate of the aphids, i.e. the intrinsic rate of population

increase, can be obtained by fitting linear regressions, in which population growth is linearized by log transformation of population size *N*, and by expressing time in day-degrees (*DD*) above the lower developmental threshold (Honek and Kocourek, 1990; Honek, 1996). The model corresponding to exponential population growth is then:

$$ln[N(DD)] = ln[N(0)] + rDD$$

where *ln[N(DD)]* is the response variable, *ln [N(0)]* is the intercept, *r* is the slope of the regression line and the population growth rate, and *DD* is an explanatory variable. The explanatory variable is the sampling date expressed in *DD*, which is from the beginning of immigration until the peak of aphid abundance. The population growth rate *r* is an estimate of the achieved intrinsic rate of increase (Jarosik *et al.*, 1996).

To test for the parabolic decline from exponential growth, the square of the explanatory variable can be calculated and subtracted from the regression:

$$ln[N(DD)] = ln[N(0)] + rDD - rDD^2$$

If this causes a significant reduction in deviance, there is evidence of parabolic decrease in population growth with increase in aphid density (e.g. Crawley, 1993).

The use of log aphid counts and normal distribution of errors in the statistical analyses is preferable to the use of generalized linear models with a Poisson or negative binomial distribution of errors (McCullagh and Nelder, 1989). The reason is that, in spite of the fact that aphid distributions are highly clumped, they usually differ significantly not only from a Poisson distribution, which describes a random distribution, but also from the negative binomial distribution, which is usually used to assess population densities where the distributions are clumped (Ekbom, 1985, 1987; Elliot and Kieckhefer, 1986; Krebs, 1989; Elliot *et al.*, 1990; Jarosik *et al.*, 2003).

Importance of sample size

In a study of cereal aphids (Jarosik *et al.*, 2003), no population growth was detected at very low densities on individual plots.

The probability of identifying exponential growth increased with aphid density and made it possible to determine the crucial density for the transition from undetectable population growth at low density to exponential growth as density increased. At high densities, the populations grew exponentially, and the growth rates did not show a parabolic decline as aphid density increased.

However, significant exponential growth was always detected in pooled data. This was strikingly different from the dynamics on individual plots, because significant exponential growth was revealed even at very low densities. The second important difference was that the growth rates decreased significantly at high densities, in accordance with the cumulative density model, illustrated in Figs. 12.2 and 12.3.

The detection of significant growth using pooled data, when no growth was detectable using data from individual plots, is attributable to the much larger sample size of the pooled data. The sample size on individual plots was 300 tillers or ears at low densities. The pooled sample sizes ranged from 2400 to 30,600 tillers (average 12,900) and from 1200 to 22,800 ears (average 10,500).

Sample size is important when assessing species abundance (e.g. Southwood and Henderson, 2000). Using the density for the transition to exponential growth, a sample size of 300 tillers or ears appeared clearly insufficient for the correct assessment of aphid abundance (Ekbom, 1985, 1987; Ward *et al.*, 1985a; Elliot and Kieckhefer, 1986; Elliot *et al.*, 1990). Thus, the random population fluctuation without apparent population growth, which occurred at low densities on individual plots, appears to be attributable to small sample size. It does not mean that these populations were not growing.

There is no simple solution to the problem of sampling low aphid densities. The required sample sizes are very large, and therefore time-consuming. The use of presence–absence counts, instead of counting the numbers of aphids, is not a solution, because the saving in time is associated with a decrease in accuracy, and hence a further increase in the required sample size (cf. Ward *et al.*, 1985a,b; Elliot *et al.*, 1990). The nigh

impossibility of obtaining accurate estimates of aphid abundance when aphids are scarce further supports the notion that the natural enemy ravine may be an illusion. The studies cited in support of the ravine concept sampled aphid densities similar to those used in the study on cereal aphids. This is important, because at high densities it would be possible to detect the ravine using a smaller sample size. Therefore, there is no evidence from these studies that the ravine might be present when the densities are higher, as in the cereal aphid study, and could be detected by a smaller sample size.

Trap estimates of abundance

Another way of estimating the abundance of a pest aphid is by using traps (see Harrington *et al.*, Chapter 19 this volume). As in field sampling, it is important to ask the following question: 'What constitutes a series of trap catches that is suitable for statistical analysis?' In this respect, the selection procedures of several analyses are of interest. Redfearn and Pimm (1988) chose time series that 'contained at least 10 years in which at least one individual was collected', and Woiwod and Hanski (1992) and Hanski and Woiwod (1993) removed from their analyses all series for which the mean annual abundance was less than five individuals in order to remove time series with many zeros. However, it is not possible to state unequivocally that catches below ten differ from one another (Thacker, 1995). For this reason, the data selected by Redfearn and Pimm (1988) and Woiwod and Hanski (1992) could be considered too liberal. When assumptions of year-to-year differences in abundance are to be made, time series with many values below ten are suspect (Thacker, 1995). Variances of series containing many zeros are difficult to compare with certainty (Wolda and Marek, 1994). A selection procedure based solely on mean catches is also difficult to recommend for all series, as it does not consider the spread of the data values. Of two series with identical means, that with the higher variance is more suitable

for use, as conclusions about year-to-year changes in abundance can be more reliably drawn. Therefore, the selection process could be improved by including variance, unless a very conservative mean value cut-off is used. That is, if a catch is low, it is possible to say with certainty that the aphid population is low. However, the existence and magnitude of any population trends are rather more difficult to elicit. So, for example, if the catch sequence goes 4, 4, 4, the real population underlying that may have quadrupled or quartered over those three time periods. But if the sequence is 500, 500, 500, then the population being sampled is more abundant and very stable (Thacker, 1995).

The foregoing discussion assumes that the aerial population accurately reflects the abundance of an aphid on its host plant (cf. Howard and Dixon, 1990). This may not always be the case. For example, the yearly catches of *D. platanoidis* by a suction trap positioned 1 m above the ground and close to sycamore (*Acer pseudoplatanus*) trees accurately reflected the abundance of aphids on these trees and, like the total numbers on the trees, showed relatively little change from year to year (Dixon, 1990; Dixon and Kindlmann, 1998). In contrast, the yearly catches recorded by the Rothamsted Insect Survey (RIS) trap 106 km away fluctuated from year to year. The reason for this is that the size of the annual catch taken by the RIS trap is determined mainly by the aphids caught in June, October, and November (Fig. 9.13 in Dixon and Kindlmann, 1998). The sum of the catches in these 3 months taken by the suction trap close to the trees is well correlated with the yearly total catches of the RIS trap. That is, the RIS trap is, in this case, catching aphids mainly in the second half of a year. In addition, the ratio of the catches of the local and RIS traps each month did not remain constant throughout the year. Early in a year, the local trap caught many more aphids relative to the RIS trap than later in a year. That is, the flight behaviour of the aphid is changing during the course of a year and, as a consequence, the RIS trap, in this case, does not accurately reflect the trends in aphid abundance on the host tree (Dixon and Kindlmann, 1998).

In summary, providing it is known that the catches accurately reflect the abundance of a pest aphid on a crop plant, suction trap catches may reliably indicate year-to-year changes in abundance, and trends in abundance within years of abundant species. However, the catches may be a more reliable indicator of the timing of aphid migrations, which is important when interested mainly in virus transmission by aphids.

Consequences for Pest Management

If, at low aphid densities, population growth on cereals is undetectable, then the switch to exponential growth as density increases, assuming significant damage to this crop occurs mainly during the exponential phase of population increase, could be used to predict when, and if, the damage boundary (*sensu* Pedigo *et al.*, 1986) is likely to be exceeded. Distinguishing the early phase of population growth thus might have important consequences for aphid control (Jarosik *et al.*, 1996, 1997). However, pooled results showed that there is actually no transition from undetectable population growth to exponential increase in the case of cereal aphids (Jarosik *et al.*, 2003). The apparent transitions are just a consequence of low population density, when population increase is undetectable using small sample sizes. Small trap catches present similar problems.

In summary, for aphids on cereal crops, the required sample size at low densities for measuring exponential growth is more than 500 tillers and, in most cases, much larger sample sizes are required (cf. Ward *et al.*, 1985a; Elliot and Kieckhefer, 1986; Ekbom, 1987; Elliot *et al.*, 1990). Moreover, estimates of sample size are very unreliable at low densities (Ward *et al.*, 1985b), and the required sample size increases rapidly to infinity if the densities are less than, for example, an aphid per tiller. Such densities are typical of the onset of aphid population growth. This also applies to trap catches. Therefore, because the sample sizes needed for a reliable decision are extremely large, and therefore costly, it is likely that their use in forecasting will be limited.

Conclusions

In terms of theory, we have a good understanding of aphid population dynamics, and the models accurately predict the population trends observed in the field. This is particularly the case for aphids living on woody plants. On the practical side, progress has been disappointing. This is mainly because of the difficulty of obtaining accurate estimates of population size when aphids are scarce. In spite of this, there have been some successes in aphid pest management. Therefore, we should be optimistic and believe that a better understanding of the seasonal trends in aphid abundance in the field may result in better ways of determining when aphid control should be applied. In certain cases, it may even be possible to use them to forecast future trends.

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