Population dynamics: cycles and patterns

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12 Population Dynamics: Cycles and Patterns

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Introduction

The aim of the study of population dynamics is to identify the causes of numerical change in a population and explain how the interaction between these causes results in the observed changes. Figure 13.1, this volume, illustrates many of the components involved. These components have been allocated separate chapters in this volume, and the next chapter takes one important crop pest species, *Sitobion avenae* (English grain aphid)*,* and uses a modelling approach to illustrate how the components integrate to describe its population dynamics over different spatial scales.

This chapter looks at the abundance on crops of several aphid species and what explanations for the patterns observed can be proposed from field-derived evidence.

Analyses based on age-specific life tables and key factor analysis, which are well-established techniques for many other insects (Southwood, 1966), are not available in their normal format to aphidologists. Such analyses require a census of the different life stages of the insect over several generations; this is impossible when generations largely overlap, as they rapidly do with aphids following initial establishment. Also, the polyphenism of aphids, with high numbers of a local population being dispersing alatae, can result in sub-populations on widely differing host plants. Some of these may be crops, and others wild plants; up to now this has severely limited our understanding of the population dynamics of the regional population of an aphid species.

Given the complexities when sub-populations occur on a succession of hosts, long term studies of aphid population dynamics have focused on monoecious aphids on long-lived plants such as trees. It is then possible to census a resident aphid population over an extended period of time. The best-known example is probably the work of Dixon and his co-workers over many years on the sycamore aphid, *Drepanosiphum platanoidis* (Kindlmann *et al*., 2007).

Overwintering Populations

Most aphids that are crop pests are of primary interest on an ephemeral crop plant, but also utilize other plants at other times. Until now, the emphasis on studying their population dynamics has been on the population cycle on the crop, which only on a regional and not on a field scale is likely to be relevant to the long term population dynamics of a species.

The annual nature/management of most crops means that the aphids often need to disperse to other hosts for overwintering, though in mild winters in the UK some aphids can overwinter on autumn-sown or perennial crops; this then leads to an earlier build-up of the population in spring (Oakley and Walters, 2008). Overwintering populations of *Rhopalosiphum padi* (bird cherry–oat aphid) can of be found on autumn-sown cereal crops, and Morgan (2008) theorized from a simulation model with barley that decreasing the mortality rates of apterous nymphs by as little as 5% over the autumn and winter amplified summer peak densities by as much as 60-fold.

Most crop pest aphid species are able to reproduce sexually, and in temperate regions this typically occurs in autumn (Dixon, 1973). After mating, oviparous females produce eggs that overwinter. Aphids may overwinter as eggs or in the mobile stages. Some species adopt one or the other strategy exclusively but some have different options in different clones (Chapter 4, this volume). Aphid population dynamics over winter are dependent primarily on temperature and predation. The impact of these factors determines levels of mortality and can be direct, interactive or mediated through their effect on plant condition.

Only a small proportion of the alatae leaving crops will find a suitable host for overwintering (Ward *et al*., 1998). Where species overwinter on wild herbaceous plants (e.g. *M. persicae* – Davis and Radcliffe, 2008) or grasses scattered over large areas, sampling populations is nigh on impossible. Much of our knowledge on winter mortality in the field (where there are a variety of mortality factors) therefore comes from species that overwinter on trees, and particularly in the egg stage. However, much laboratory work has been done on the cold-hardiness of many aphid species feeding on crops (reviewed by Bale, 1999), which has shown the ability of eggs to survive temperatures as low as -40°C although nymphs and adults start to die at temperatures as high as -5°C. Winter temperatures in Southern England thus do not generally affect eggs but can lead to mortality of newly hatched nymphs (Way and Banks, 1964). Harrington and Taylor (1990) followed field populations of *M. persicae* through the winter on brassicas and found that a major cause of mortality was low temperature inhibiting movement to suitable new feeding sites within a plant.

Correlations between *D. noxia* abundance and remote-sensed imagery have allowed the development of models using vegetation indices to be used as proxies for overwintering aphid abundance. Soil and topography are important factors, possibly due to desiccation increasing aphid mortality rates (Merrill *et al.,* 2009). Mortality of overwintering *D. noxia* nymphs and adults correlates strongly with the accumulated hours below 0°C (Armstrong and Peairs, 1996). Havelka *et al.* (2014) found that >87 day degrees below -5°C led to complete mortality of anholocyclic *D. noxia* populations.

Temperature and predation can interact by affecting the development and activity of predator populations. Favourable temperature conditions for overwintering active aphids are also suitable for parasitoids which then effectively control aphid populations, whereas in the absence of parasitoids, aphid populations increase rapidly (Legrand *et al.,* 2004). With some species such as *M. persicae,* however, higher populations are found in winters with higher temperatures, regardless of the presence of several predator groups, which do not appear to affect winter survival (Harrington and Cheng, 1984).

Leather (1993) gives data from 13 sources on the egg mortality over winter of 6 aphid species (Table 12.1). Mortality ranged from 23 to 99%, and included 8 instances of 70% or over. Such high mortalities would be largely due to predation. *Aphis fabae* (black bean aphid) eggs on spindle trees (*Euonymus europaeus*) suffer mortality between 18 and 73% with evidence of predation by birds and anthocorid bugs, although some eggs fail to hatch despite developing fully, even when predators are absent (Way and Banks, 1964). Eggs of *A. glycines* show similar high levels of mortality (~70%) (Welsman *et al*., 2007). The impact of predators may be affected by temperature (see above).

Spring Populations

Few data seem available on the effect of abiotic factors on the development of populations in spring at the overwintering sites, but the positive effects of temperature on aphid development time and fecundity are well established (Chapter 5, this volume). Higher spring temperatures increase numbers and rainfall decreases populations of *M. persicae* (Cocu *et al.,* 2005).

Predation probably has a limited impact on aphid populations in the spring. Although many predators were found on bird cherry in the spring, a high proportion of the *R. padi* population was winged by the time predator numbers peaked, suggesting that emigration to grasses explains the population decline on the winter host rather than predation (Leather and

Lethi, 1982). A similar situation occurs for *A. fabae*, where fundatrices hatch 3-6 weeks before natural enemies become common, suggesting a time lag between aphid and predator populations and that predation does not significantly affect aphid populations at this time (Way and Banks, 1968).

Onset of Dispersal to Crops

The dispersal of aphids to crops is usually a consequence of a switch from the production of wingless to winged offspring. In host-alternating aphids the number of wingless generations that occur following egg hatch on the woody winter host before winged emigrants appear is usually genetically determined. In aphids passing the winter in the mobile stages the proportion of alatae usually increases as the population becomes crowded, and as the young spring growth of the winter host plant becomes mature and less suitable for the aphids (Chapter 4, this volume).

Intra-specific competition as population density increases leads to an increase in the proportion of winged aphids and a slowdown in the reproductive rate of wingless adults (Way and Banks, 1968). If high numbers of aphids overwinter, there will be fewer parthenogenetic generations than at lower densities before winged forms are produced (Wiktelius, 1984). However, some host-alternating aphids can persist on their primary hosts under certain conditions. The rose aphid (*Macrosiphim rosae*), for example, can continue to produce sexual morphs on roses; these aphids then join in the sexual phase with those returning in the autumn from secondary hosts (Blackman and Eastop, 2006)..

Arrival on Crops

The timing of immigration will be affected by differences in temperature conditions between years, and climate change is obviously highly relevant here. In general, higher spring temperatures advance the onset of migration and rainfall delays it (Cocu *et al*., 2005).
A point often ignored is that insect and plant phenologies often have different drivers. The timing of aphid dispersal to crops is largely dependent on temperature whereas many aspects of the development of plants are to a great extent governed by photoperiod, which remains consistent from year to year. Since under a climate change scenario photoperiod remains constant, it is likely to have a considerable impact on the interaction between aphids and their host plants.

Some areas which suffer from aphid pests do not host overwintering populations. In Minnesota, USA, *M. persicae* migrates from the south to colonize herbaceous plants before moving onto potato crops (Davis and Radcliffe, 2008).

In a survey of a large agricultural region, Macfadyen *et al.* (2015) found that the timing of emigration by aphid crop pests overwintering in the mobile stages close to the crop occurred shortly after crop emergence. By contrast, host-alternating aphids such as *A. glycines* tend to have a delayed arrival in relation to the phenology of the crop (Hodgson *et al.*, 2005). Indeed, Ragsdale *et al.* (2004) report a lengthy gap between the production of alatae on *Rhamnus* spp. in the spring and the arrival of the aphid on soybean. This suggests that a third host plant was involved. Aphids that initially colonize crops can be from transient migrant populations as well as local overwintering populations from adjacent hedgerows and natural vegetation. Using genetic profiling of aphids caught in suction-traps, Vialatte *et al.* (2007) showed that *S. avenae* tend to come mainly from local overwintering sites in years with a major aphid outbreak on wheat crops.

The prediction of the likely size of aphid populations arriving on crops has been discussed in Chapter 16, this volume.

The Population Cycle on Crops

Methodology

Most aphids that are crop pests are of primary interest on an ephemeral crop plant, and utilize other plants at other times. Until now, the emphasis on studying their population dynamics has been on the population cycle on the crop. This is unlikely to be relevant to the long term population dynamics of a species (see earlier); a population explosion or crash there will have little or no impact on the dynamics of the regional population (Mackauer and Way, 1976). Thus Onstad *et al.* (2005) found little similarity among 14 soybean fields in Illinois, USA, in 3 summers either in the number of *A. glycines* or synchrony in their population dynamics.

Speculation as to the reasons for the changes of aphid numbers on a crop have often been based on nothing more than numbers of apterous aphids and alatoid nymphs counted in a sequence of visual inspections of the crop, coupled with counts of predators, mummies and diseased aphids noticed at the same time. Smith (1966) sought to identify the relative importance of the different factors involved in population changes between successive samples of *Acyrthosiphon spartii* on *Cytisus scoparius* (broom) by calculating aphid increase rates from

laboratory data and working out predation from the number of predators seen multiplied by the voracity of the different predator taxa in the laboratory. Unfortunately aphid increase and predator voracity calculated at constant temperature does not reflect what happens in the field where the temperature fluctuates. For aphids, fecundity is very different between fluctuating and constant temperatures, though the direction of difference varies between studies (Chapter 5, this volume). For natural enemies, Hodek (1957) showed that *Coccinella septempunctata* larvae doubled their food consumption at naturally fluctuating temperatures in comparison with their voracity at constant temperature equivalent to the mean of the fluctuating temperature. Moreover, plants grown under controlled and usually artificially-lit conditions are of quite different and often poorer quality as hosts for aphids. Furthermore, predator voracities in the laboratory ignore the time spent searching in the field, but perhaps more importantly predator numbers encountered while sampling aphids are likely to be serious underestimates (see later). As a result, Smith (1966) overestimated aphid increase rates and underestimated predation by insect taxa to the extent that he had a huge gap of unexplained mortality, for which he invoked predation by birds.

Others have attempted to measure mortality factors and emigration directly in the field. van Emden (1963), working with *B. brassicae* on Brussels sprouts, marked 120 leaves with colonies and visited them every 4 days to look for non-emerged mummies, cast skins of departed alatae, signs of activity of predators such as moist smears and sucked aphids, new mummies formed etc. When no more aphids were left on a leaf, a substitute was marked on a nearby plant. No attempt was made to measure aphid increase rate in the field, but counts of the aphid population on the crop at the same sampling intervals were made.

van den Berg *et al.* (1997) and Mills and Latham (2009) made direct observations of aphid colonies for standardized time windows to assess predation; however, much predation happens at night. van den Berg *et al.* used clip cages to try to measure aphid increase rate in the absence of predators.

In the end, data on changes in aphid reproductive rate will have to be included in a population dynamics exercise and, at present, we do not have a satisfactory numerical approach for such an analysis conducted on a crop. The principal barrier is that changes in aphid reproductive rate are crucial; they are continually affected by temperature and other weather variables and also by host substrate condition, which also varies continually with weather and as leaves mature and then age (van Emden, 1965; van Emden and Bashford, 1969). Perhaps not surprisingly, therefore, Tenhumberg *et al.* (2009) found a large discrepancy between the mean *Acyrthosiphon pisum* (pea aphid) population derived from a single adult when modelled on the basis of temperature (531) and the empirical population (2394). However, Hughes (1962 – full

methodology details are given by Hughes, 1976) explored the possibilities of developing a time-specific rather than an age-specific form of population analysis of a crop aphid. His life table was based on the concept of an 'instar period', taken as a constant if measured on the physiological time scale of day degrees above the threshold temperature for development. His analysis was based on 'twin samples' taken one instar period apart (Fig.12.1). On the first sampling occasion, leaves were collected and the aphids in the different instars counted. A second batch of leaves was taken with predators, mummies and diseased aphids removed and kept in the laboratory, so that the number of new mummies and diseased aphids appearing in one instar period was known. The potential rate of increase (new first instar aphids) during the instar period was calculated from the relative number of aphids in the first, second and third instars, on the assumption that these formed a geometric series (tested by chi-square). Thus the actual population in the second sample could be compared with an 'expected' population assuming no mortality. Once the measured subtractive factors had been taken into account, any gap remaining ('residual mortality') was regarded as the maximum mortality attributable to predation. The technique has been criticised by Carter *et al.* (1978) on the basis that stable geometric series of the first three instars will rarely occur in the field. It is also true that, since chi-square is scale dependent, the instar series will need to be based on large numbers to give the test adequate discrimination.

Hughes's method has not been widely used, but probably more because of the labour involved in instar identification than for statistical reservations. The concept that an increasing proportion of younger aphids in a population indicates a high potential increase rate is reasonable, and Hughes's calculation is one approach. The evidence is that it gives estimates of residual mortality that are within the range of predation impact that can be expected, certainly in contrast with residual mortalities obtained when laboratory data are applied to the field. During the International Biological Programme of 1964-1974, the biological control of *M. persicae* on potatoes was studied in 10 countries in 1970-71 (Mackauer and Way, 1976). The Hughes technique was used by 8 workers in 5 countries, producing 34 twin-sample data. Only 4 produced measurable negative residual mortalities, and in every case these data were taken at very low population levels. Even then, chi-square showed a significant deviation of numbers in instars I-III from a geometric series. Aalbersberg *et al.* (1988) found the technique worked well for *D. noxia* except during the population crash at the end of the season, when negative residual mortalities could be found.

Factors causing numerical change

Initial reproductive rates vary considerably between species. Aphid pests of perennial crops such as *Aphis spiraecola* (green citrus aphid) on citrus have a rapid population increase in the spring, originating from the initial immigrant alates then supplemented by alates from other host plants nearby (Zehavi and Rosen, 1987; Lebbal and Laamari, 2015). On annual crops, aphid populations are characterized by a typical logistic curve (Chapter 13, this volume), with initially low levels of reproduction. Infestations of *D. noxia* that disappear early in wheat (before the appearance of the first node) do not cause any economic yield loss (Kriel *et al.,* 1986). Predators may rapidly follow aphid pests from adjacent native vegetation into the crop (Macfadyen *et al.,* 2015), but at the start of the infestation predation rates are typically insufficiently high to counter new aphid immigrants and populations inevitably begin to rise (Costamagna *et al*., 2013a).

Abiotic factors

Changes in aphid populations are affected by weather with temperature and rainfall the most important factors. Developmental time, reproductive capacity, longevity and mean generation time are all positively correlated with increasing temperature up to a threshold level which differs from species to species (Slosser *et al.,* 1989; Chapter 13. this volume). Up to 90% of variation in population change of *D. noxia* is explained by accumulated 'heat units' and rainfall (Legg and Brewer, 1995). High temperatures become detrimental, e.g. temperatures above 25°C are detrimental to *A. pisum* population growth (Campbell and Mackauer, 1977). In the summer of 1976, temperatures in southern England caused a collapse of cereal aphid populations, and adult syrphids and coccinellids searching for food became highly apparent to the public; there were many reports of coccinellids biting people (H. F. van Emden, unpublished).

Increasing temperature (up to an optimum) of course increases the rate of reproduction of predators as well as that of aphids, and different rates of such change with temperature in predators and aphids have the potential for improving the impact of predators at different, especially lower, temperatures (van Emden, 1966 – using data of Dunn, 1952). Low temperatures can be beneficial to aphid populations in delaying the colonization of the crop by natural enemies (Nakata, 1994).

Bouts of heavy rainfall can knock aphids off plants, resulting in sudden and sometimes dramatic reductions in aphid populations, especially when in combination with high winds (Walker *et al.,* 1984; Atsebeha *et al*., 2009). Some aphids, e.g. *S. avenae* in the crevices between the ear kernels (Watt, 1979), have behaviour which renders them less susceptible to being knocked off the plant. High levels of rainfall can create suitable conditions for fungal infection of

aphids, although aphids which are found in more humid microhabitats (e.g. *Metopolophium dirhodum* (rose–grain aphid) and *D. noxia* as contrasted with *S. avenae*) are less affected (Feng *et al.*, 1991).

Humidity can also be important for some aphid species. *Aphis spiraecola* requires high levels of humidity (~40%RH) for population growth with humidity lower than this leading to population decline (Dubey and Singh, 2011).

Natural enemies

Other chapters in this volume (Chapters 11 and 20 respectively) review the natural enemies of aphids and their practical use in biological control of aphids. Here we limit ourselves to naturally occurring natural enemies as drivers of population change in the field.

Natural enemies have variable impacts on aphid populations on the crop. Different predator groups respond differently to aphid presence and population levels. Whether natural enemies can control aphid pests seems to vary with species of aphid, and often with year for the same aphid species. Much predation of aphids in winter wheat occurs at night and involves ground-dwelling staphylinids (Holmes, 1984) and spiders, which are not included in estimates of predator numbers made during the houra of daylight. When plant conditions are favourable (see later) predators or parasitoids rarely have a major impact at the early logarithmic phase of aphid population growth (Tomanović *et al.,* 2008; Lozzia *et al.,* 2013; Ullah *et al.*, 2014). However, when crops are grown in structurally complex landscapes they are colonized by natural enemies earlier, which may result in more effective control of aphids during this phase of population growth (Raymond *et al.,* 2015). Specialist predators such as coccinellids often closely track population changes in aphid crop pests so that highest predator densities are found at the aphid peak in the crop (Hutchinson and Hogg, 1985; Idris and Roff, 2002; Soni *et al.,* 2013). Thus densities of syrphids also track changes in *A. pisum* populations throughout the season, as do rates of parasitization (Nakashima and Akashi, 2005). Such correlations are indicative of a positive density-dependent numerical response, and there is often no impact on the aphid population. This indicates that, in contrast to the numerical response, functional responses are often negatively density-dependent; i.e. in the exponential phase of aphid population growth, the time taken by predators to find and consume prey is too long for them to be able to keep up with the increase rate of their prey (Costamagna *et al.*, 2013a). On soybean, however, the aphids located on the upper nodes have the highest reproductive potential and, because the predators concentrate there, *A. glycines* is controlled effectively (Costamagna *et al.*, 2013b). The peak of

predator abundance is usually later than the aphid peak, again indicating that effective control by natural enemies is not occurring. For example, both *M. persicae* and *Aphis gossypii* (melon or cotton aphid) peaked on vegetable crops three weeks before the predator; the aphids were not effectively controlled in these crops (Vuong *et al.,* 2001).

The impact of parasitoids is often increasingly reduced after the first generation by hyperparasitoids (Summy and Gilstrap, 1983; Walker *et al.,* 1984); hyperparasitization not infrequently approaches 100% by the end of the season. Only when parasitization levels surpass 30% do *A. gossypii* populations start to decline (Slosser *et al.*, 1989), and aphid populations in wheat collapse when parasitization rates reach 50% (Abdel-Rahman *et al*., 2000).   Parasitization rates quoted are usually much lower than this; the < 9% recorded by Hutchinson and Hogg (1985) is perhaps more typical. However, estimates of parasitization based on mummies are probably considerable underestimates, since many parasitized aphids leave the plant to mummify on the ground (Gowling and van Emden, 1994). Summy and Gilstrap (1983) regard the removal of numbers of immature primary parasites in alate *Schizaphis graminum* (greenbug) as significant. Estimates of both parasitization and predation usually ignore such 'non-consumptive' mortality; the activity of natural enemies causes a significant proportion of aphids to be lost after falling off the plant (Fig. 23.4 – Gowling and van Emden, 1994). On the other hand there may also be some overestimation of parasitization, particularly when aphid numbers are declining, since unemerged mummies have greater 'longevity' on the crop than unparasitized aphids.

Aphid pathogens rarely seem to cause significant reductions in aphid numbers during the season, though Deguine *et al.* (2007) regarded them as primarily responsible for a mid-season decline in the population of *A. gossypii* in cotton (see later). However, pathogens can be important mortality factors in the end-of-season decline from peak numbers; Plantegenest *et al.* (2008) attributed 75% of the decline in *S. avenae* numbers in winter wheat to this cause.

Host plant condition

Plant growth stage has a strong influence on aphid population changes, as this will often determine the soluble nitrogen concentration of the phloem sap, which for aphids is often the limiting factor on reproductive rate (Dixon, 1973). Young, growing crop plants where nitrogen is being mobilized in the phloem are often where aphid population growth is most rapid. Within-year changes in aphid numbers on trees regularly show spring and autumn peaks with a long intervening period of lower populations; Kindlmann *et al.* (2007) attributed this pattern to

changes in host plant quality, with amino acids being translocated to the young leaves in the spring and being exported from senescing leaves in the autumn.

Variation in tissue condition within plants can have large effects with younger leaves more attractive to aphids, supporting higher rates of population increase (van Emden and Bashford, 1969; Costamagna *et al*., 2013b). Some aphid species, for example *B. brassicae* (van Emden, 1965) and *A. glycines* in soybeans (Tilmon *et al.,* 2011) largely remain on the leaves they colonize, and so the amino acid status of their substrate changes as the season progresses. *Sitobion avenae* and *M. dirhodum* are both common cereal pests but respond differently to plant condition, mainly due to their preference for different parts of the plant. The reproductive rate of *S. avenae* on young cereal ears is far higher than on leaves, whereas that for *M. dirhodum* is highest on the leaves and the aphid is rarely found on the ear (Watt, 1979).

As pointed out earlier, photoperiod is an important driver of plant phenology and therefore plant condition. Since the arrival of aphids on a crop is more related to abiotic factors such as temperature, the amino acid status of the crop when the aphids colonize will not be predictable. *Aphis spiraecola* and *Macrosiphoniella millefolii* populations increase rapidly when photoperiod reaches 14 hours because this triggers stem elongation of commercial yarrow (*Achillea collina*) (Lozzia *et al*., 2013) and *A. gossyppii* populations on cotton begin to increase shortly after the onset of the bloom (O'Brien *et al.,* 1993) which is a photoperiod-timed event with major increases in amino acid transport.

Variation in the condition of plant tissues can have large effects, with younger leaves most attractive to aphids and supporting highest rates of population increase. Both *M. persicae* and *A. fabae* have higher rates of increase on younger flowering soybean plants than when these are at or past the full pod stage, with most aphids and the highest rate of increase on the young upper nodes (Costamagna *et al.,* 2013b). Early in the season, *A. glycines* is found on newly expanding trifoliate soybean leaves. As the season progresses it is found lower in the canopy, further from the terminal bud. This reflects changes in the distribution of nitrogen in the plant phloem (Tilmon *et al.*, 2011).

Declines in aphid populations can also be attributed in part to changes in nutritional status of plant tissues. *Macrosiphum euphorbiae* (potato aphid) populations feeding on potato plants consistently decline once potato tubers have started filling (Parker *et al.,* 2000); fecundity then drops by 25-45% as the amino acid composition in the phloem of the potato plants changes (Karley *et al*., 2003). In most crops, maturation is important in reducing reproductive rates of aphids, but mycoses and natural enemies have rated as important in driving the decline (Feng *et al.,* 1991; Soni *et al.,* 2013). However, the decline is probably primarily due to plant condition with natural enemies merely accelerating its rate.

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The importance of crop plant condition for aphid population development is reflected in the approaches to reducing levels of crop damage by using aphid-resistant crop varieties (Chapter 22, this volume) and cultural measures (Chapter 21, this volume).

Emigration

The departure from the crop of alatae represents a local loss of individuals. Since it is triggered primarily by crowding and maturation/deterioration of the host plant, its main effect on population size is at the end of the season, and is discussed later.

The development of populations on crops

Numerical changes in aphid populations on crops follow a relatively consistent pattern in different aphid species and crops, although patterns may change unpredictably from year to year because of the importance of photoperiod on the amino acid status of the crop when the aphids colonize (see earlier).The main phase of population growth often follows a sigmoidal pattern (e.g. Fig. 12.2 and Chapter 13, this volume) with a rapid initial increase followed by a slowdown leading up to a peak in population before a rapid decline (often called the 'crash'). Of course there is variation in the amplitude and phase of the rate of increase and the size of the peak population. A sigmoidal rise to a peak, though found at some time during the season in most species, does not always start with the arrival of aphids on the crop.

van Emden's (1965) study of *B. brassicae* on marked cabbage leaves showed a small initial peak of reproduction following immigration until predation became a significant factor, but as leaves started to senesce from late August onwards, the aphid population rocketed in spite of greatly increased mortality from aphid predators.

This pattern could be illustrated three-dimensionally (van Emden, 1966) by plotting the number of aphids on different sample dates and the number of predators in the sample (as a kind of 'predator index') on the two horizontal axes and the percent predation in the re-visited colonies on the vertical axis (Fig. 12.3). This shows a double-peak pattern of aphid density, with the numbers kept low for most of July by increasing predation. However, even increased predatory pressure in August failed to prevent an explosion of aphid numbers into the autumn. The double-peaked pattern reported for aphids on woodland trees (Kindlmann *et al*., 2007) and citrus (Lebbel and Laamari, 2013) (Fig. 12.4), and attributed by Kindlmann *et al*. to changes in amino acid

status, was therefore also seen with the brassica crop, and the autumn peak dramatically shows that the increase in amino acids later in the season accelerates aphid reproduction beyond the control capacity of the mortality factors. Similarly Hutchinson and Hogg (1985) recorded that mortality of *A. pisum* attributable to predation on alfalfa ranged from zero to about 30%, but that even at the highest predator densities *A. pisum* populations increased exponentially.

Predation, however, clearly does determine the duration and level of the trough in aphid density between the two peaks. Parajulee *et al*. (1997) successfully increased predator numbers in cotton by relay-intercropping it in strips with a variety of spring and summer crops, and found that this not only reduced *A. gossypii* numbers but also caused the population to show two peaks in contrast to the single peak in non-intercropped cotton (Fig. 12.5). The pattern of a trough between two peaks, caused by unfavourable plant condition but with its depth determined by natural enemy activity, is frequently found in annual crops (e.g. in *Theriophis trifolii maculata* (spotted alfalfa aphid) on lucerne (Tambe and Kadam, 2015); Fig. 27.2 in the IPM Case Histories and Fig. 12.6). An increase in the movement of amino acids in the phloem also occurs during the development of inflorescences. This often precedes autumn leaf and/or plant senescence in annual crops, but in crops such as brassicas which flower in the following year if not harvested, dense aphid colonies appear on the flowering stems. This would result in a third population peak after the depression of the population during the winter.

At the other extreme, aphids such as *S. avenae* show an exponential rise to a single peak followed by a crash in the population as the plants mature and senesce. However, this exponential rise is delayed for some time after aphids have arrived on the crop (Fig.12.2B). The general importance of amino acid status leads suggests that the trigger for the rise is the switch from vegetative to reproductive growth.

 Quite commonly with cereal aphids, there is a brief 'hiccup' in the exponential phase (Fig. 12.6). This can even take the form of a very temporary reduction in the size of the population on the plant, with sample points otherwise strictly on an exponential curve changing to one below and the next above; the exponential rise to the peak is then continued. Such 'hiccups' are often ignored in drawing the curve; that this phenomenon occurs later for *S. avenae* than for *M. dirhodum*, which feeds lower down on the wheat (Fig. 12.7), suggests a host plant change is probably again involved. Similar 'hiccups' are seen with *A. spiraecola* and *S. avenae* in Fig. 12.2 and with *Rhopalosiphum maidis* in Fig. 12.6A.

Although aphid reproductive rate and temperature are closely correlated in the laboratory, the over-riding importance of host plant quality is clearly shown in Fig. 12.3 by reference to the four time periods and the contemporaneous predatory activity. In period 1, with a negligible increase in the aphid population, mean daily temperature was 16.5ºC (range 14.0–17.0). When

aphid numbers increased sharply between 19th and 23rd August, mean temperature was a little lower in period 2 at 16ºC (range 13.5–17.0), and even lower in period 3 (mean 13.5ºC, range 12.50–14.50). At the time of a later surge in aphid numbers (period 4), mean temperature was down to 10.5ºC (range 7.0–12.0). *Diuraphis noxia* populations in Orange Free State, South Africa, show a striking double peak (Fig. 12.8) which appears quite unrelated to weather conditions (Kriel *et al*., 1986).

Many of the phenomena described above reflect the main conclusions from the international study of *M. persicae* on potatoes (Mackauer and Way, 1976 – see earlier):

1) Parasitoids, even in the absence of hyperparasitoids, had little impact on the aphid population.

2) Fungal attack was only sporadic, and there were no signs early in the season, even where humidity conditions were favourable.

3) Predation (residual mortality) was heavy surprisingly often, but even so only induced a decline in the *M. persicae* population after the crash or at other times when aphids were increasing at well below their maximum rate, even on a relatively poor host (potato). As an example, a twin sample in Italy (where the potential increase rate was only 1.24) can be contrasted with one in Scotland (where PIR was 1.99). At the former site 17.6% predation was accompanied by an 8.6% aphid population decline whereas at the latter an 8.8% increase in the population occurred although predation was much higher (43.7%).

4) There was a low and steady rate of emigration, and natural enemies were removing potential migrants even well after the population peak.

Emigration at the End of the Season

Crop maturation (see above), crowding, plant deterioration due to aphid damage as well as unfavourable weather, cause a crash in the aphid populations at the end of the crop season.This crash can be very rapid; Basky (1993) found that a peak *D. noxia* population of nearly 4000 per wheat plant on 3rd July had completely vanished by 20th. As mentioned above, part of this crash is a consequence of host plant condition reducing aphid reproductive rate (Karley *et al*., 2003), accelerated by natural enemies including pathogens (Plantegenest *et al*., 2008). Feng *et al.* (1991) considered that parasitoids and pathogens were more important than crop maturation in causing the post-peak decline of cereal aphids. This is in contrast to most other studies; e.g. Karley *et al.* (2003) were consistently able to associate the crash in aphid numbers on potato with changes in

the phloem amino acid composition of the potato leaves. However, another aspect of the crash is the effect of plant deterioration in switching reproduction from apterae to alatae (Wiktelius, 1984; Parker *et al.,* 2000; Chapter 4, this volume), which emigrate from the crop to alternative habitats (usually trees or wild herbaceous plants). This phenomenon does not appear to be triggered in response to predation but by the impacts of crowding (Costamagna *et al.*, 2013b).

Models have estimated that emigrants suffer high levels of mortality as autumn approaches, with less than 5% of alate emigrants surviving more than 10 days after landing on a new host (Fabre *et al.,* 2010). In the end, only 0.6% of *R. padi* successfully find their winter host (Ward *et al*., 1998). Variability in alata production and emigrant survival as well as predation of emigrants on their off-season hosts are probably the reasons why autumn egg numbers change dramatically from one year to the next on the same overwintering sites (Welsman *et al*., 2007).

Longer Term Regulation of Aphid Populations

At the start of this chapter, we pointed out that aphids were unsuitable subjects for building age-specific life tables as a basis for understanding their population dynamics. Nevertheless, Mackauer and Way (1976) carried out the first age-specific analysis made with field data of aphids (*M. persicae*). They got round the problems aphids present by using a whole year as their age-specific time division; in this way their census datum (the 'population index' published by Broadbent and Heathcote (1961) from trapping records in potato fields for the years 1942-1959) could be used as the 'one discrete generation' in their analysis. When the log. difference from the previous year is plotted against the population index and the points are joined in chronological order, a clockwise spiral results (Fig. 12.9). This is characteristic of an efficient mechanism of population stability, but one in which the density-dependence is delayed and which overcompensates for large deviations from the equilibrium (Varley and Gradwell, 1968). The most likely mechanism suggested was aphids leaving the summer hosts when moving to and between weed hosts and predation by natural enemies in the spring. Davis *et al.* (2014) have used a 17-year time series of three cereal aphid species (*R. padi*, *M. dirhodum* and *D. noxia*) compiled from a trapping network spanning the northwestern USA, and found that the abundances of all three species were consistent with the operation of delayed density-dependence. Alyokhim *et al.* (2005) used a graphical method, similar to that used by Mackauer and Way (1976), with peak numbers of *Aphis nasturtii* (buckthorn aphid), *Macrosiphum euphorbiae* and *Myzus persicae* on potato from 1949-2003. They found strong evidence of direct

density-dependent regulation of the populations of all three species. There was also evidence of delayed density-dependence for *M. euphorbiae*. The periodicity of population fluctuations for *A. nasturtii* and *M. persicae* was 6.1 years and 3.9 years, respectively. Effects of density-independent weather factors were relatively minor compared to density-dependent regulation. Thacker *et al.* (1997) found apparent delayed density-dependence in *A. fabae* egg counts between 1980 and 1992 at Rostock, Germany. They concluded that this was an artefact of unusual cyclical weather in this 12-year period; however, it seems unlikely that such unusual weather cycles could be the explanation for the density-dependence shown for aphids by the other authors cited above.Way and Banks (1968) had previously pointed to the frequent alternation of high and low years of *A. fabae* on bean crops. They suggested that immigration was affected by predation on spindle trees in a biennial pattern since, after high aphid numbers in the summer, many predators would overwinter and reduce the population the following year. The resulting low *A. fabae* summer population would produce a low overwintering predator population, thus a high number of aphids would arrive on crops the following spring. A similar mechanism leading to a biennial pattern was recorded for *A. pisum* in Serbia (Tomanović *et al.,* 1996). High autumn parasitization leads to more parasitoids emerging in the spring, leading to a reduction in the aphid population and therefore low parasitoid numbers in the autumn.

In suction-trap catches, *D. platanoidis* also has a 2-year cycle of abundance. The total number of *D. platanoidis* on a tree is relatively constant from year to year, in spite of this cycle. This paradox results from what Kindlmann and Dixon (1992) refer to as the "seesaw effect", describing an inverse relationship between the spring peak and the increase in numbers in autumn culminating in long-distance migration. Again the changes are density-dependent, strongly increasing numbers at low densities but more weakly at high densities (Jarošík and Dixon, 1999). The stronger density-dependent changes at low densities relate to the reduced intrapecific competition for space that then prevails, since the unexploited carrying capacity of the tree is high.

Conclusion

Although attempts over the years to understand the causes of population change of aphids on crops from field-collected data have provided good evidence for what underlies the one-, two- or three-peak cycles, all the methodologies can be criticized and validation of the interpretations by

experiment has proved difficult or impossible. The time-specific life table approach has emerged as the best way to analyse population change, and it should perhaps now be revisited.

Hutchinson and Hogg (1985) sought to improve Hughes's (1962) method in their studies with *A. pisum,* replacing the calculation of 'potential increase rate' based on instar frequencies with the intrinsic rate of increase (r_m) estimated on a day-degree scale under field conditions in clip cages (i.e. in the absence of natural enemies). They found this gave a reliable estimate of the potential population growth rate.

One of the most important innovations of Hughes's method was to analyse population changes in 'instar period' units. The power of computers to model changes almost continuously (by small fractions of an instar period) is a substantial step forward, at least to the point where the likely 'what if?' outcomes of possible pest management interventions can be reliably predicted. This approach is explored in the chapter which follows.

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Table 12. 1 Overwintering mortality of eggs of six aphid species in the field (modified from Leather, 1993, which includes the full references).

Aphid species	% mortality
Acyrthosiphon pisum	67.0-70.0
	83.0
	72.0

|	
Aphis fabae	40.0
Metopolophium dirhodum	66.0
	59.0-62.0
Myzus persicae	30.0-60.0
Rhopalosiphum padi	70.0
	70.0
	80.0
	48.1-87.5
Sitobion avenae	50.0-99.0
	23.0-62.0
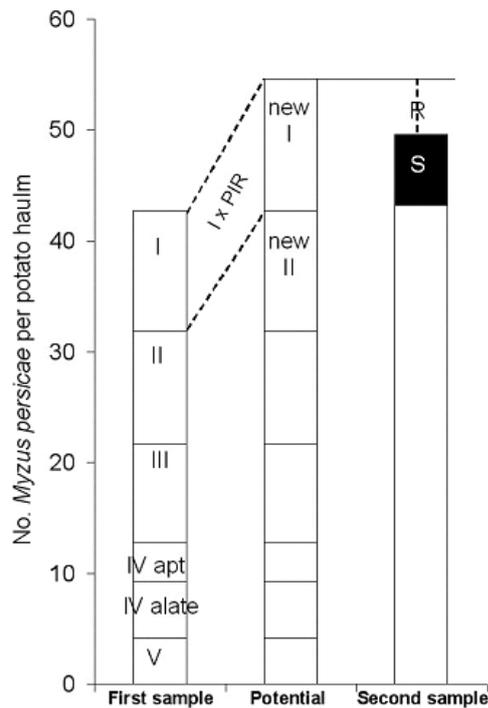
Fig. 12.1. Example of a time-specific age analysis from twin sample data for *Myzus persicae* in potatoes from the International Biological Programme (see text). I-V, aphid instars; apt, apterous; PIR, potential increase rate calculated from proportions of aphids in the first three instars; S, measurable subtractive processes; R, residual mortality (modified from Mackauer and Way, 1976).
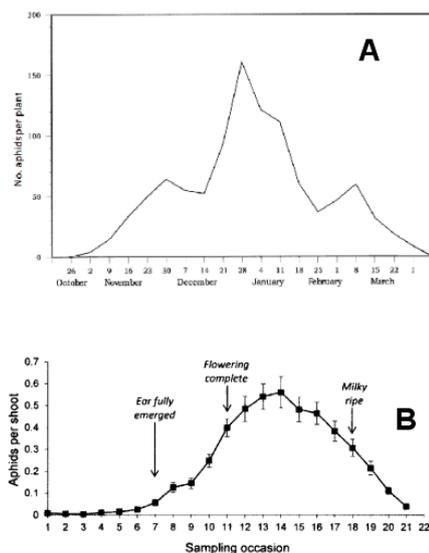
Fig. 12.2. A, Seasonal population build up of *Aphis spiraecola* on *Cosmos bipinnatus* during 2006 (simplified from Dubey and Singh, 2011); B, Population growth of *Sitobion avenae* (aphids/shoot) on wheat in 2002 (from Winder *et al.,* 2014, with permission).
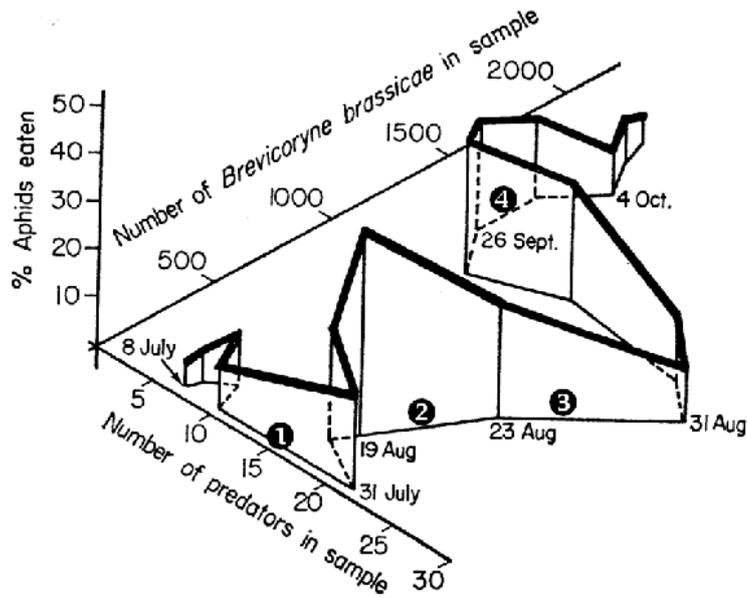
Fig. 12.3. A graphical representation of the effectiveness of aphid predators, showing good control of *Brevicoryne brassicae* on cabbages early in the season (from van Emden, 1966). For symbols ❶-❹, see text.
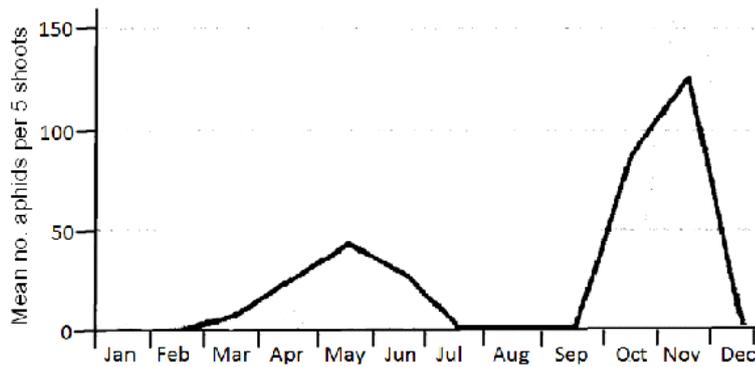
Fig. 12.4. Monthly fluctuations of the mean no. aphids per 5 shoots on clementine in a citrus orchard in 2012 (simplified from Lebbal and Laamari, 2015).
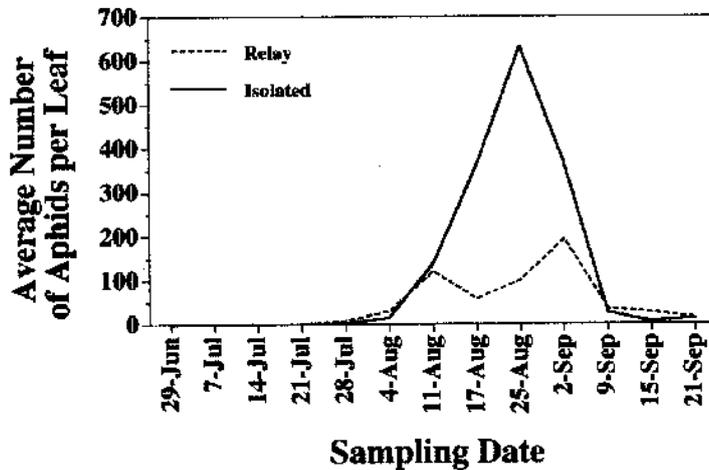
Fig. 12.5. Abundance of cotton aphids in strip-intercropped (------) and isolated (——) cotton averaged over three years (from Parajulee *et al.,* 1997, with permission).
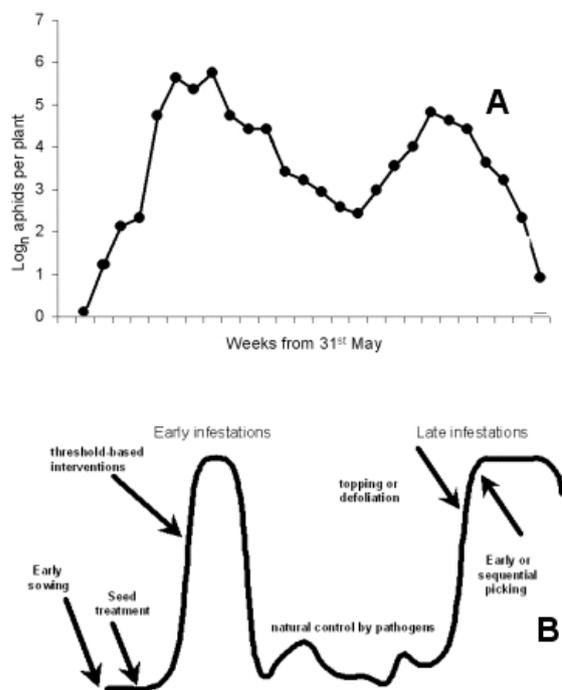
Fig. 12.6. A**,** Abundance of *Rhopalosiphum maidis* on grain sorghum in 1989 (modified from Michels and Burd, 2007); B, Stylized representation of the dynamics of *Aphis gossypii* on cotton (from Deguine *et al.,* 2007).
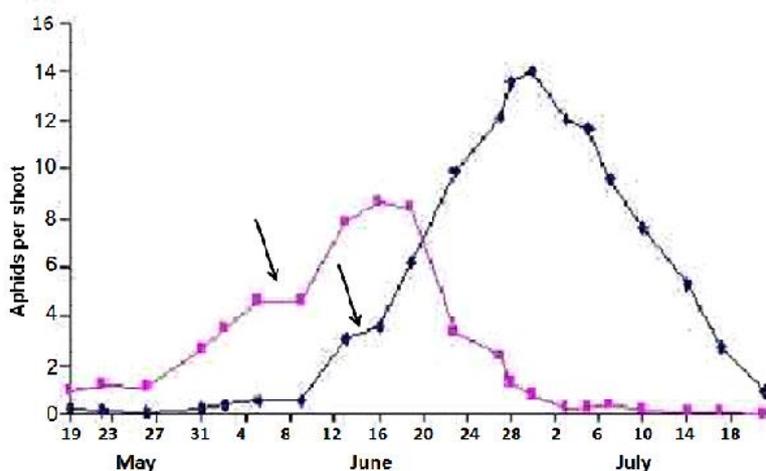

Fig. 12.7. Abundance of *Sitobion avenae* (black line and diamonds) and *Metopolophium dirhodum* (purple line and squares) on wheat. Arrows indicate the 'hiccups' mentioned in the text (data courtesy of J. M. Holland).
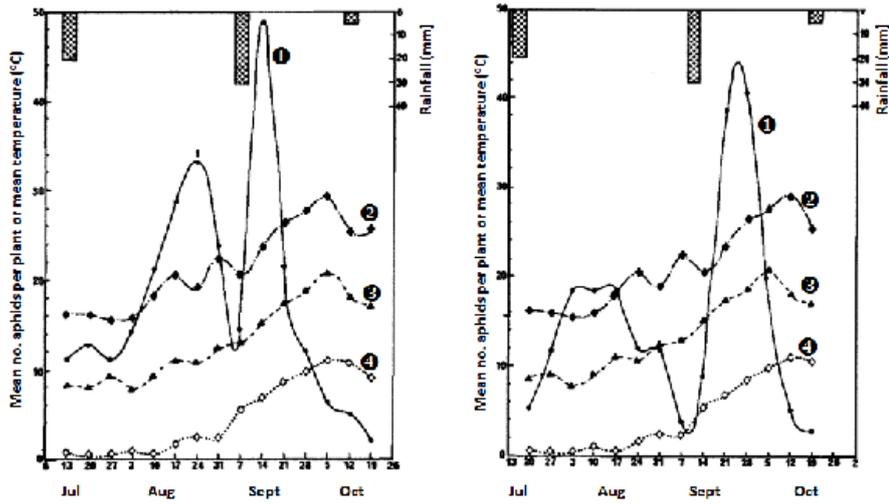
Fig. 12.8. Abundance of *Diuraphis noxia* in relation to climatic conditions and wheat growth stage at two sites in 1982. ❶, mean number of aphids per plant; ❷, mean maximum temperature; ❸, mean temperature, ❹,mean minimum temperature (redrawn from Kriel *et al.*, 1986). Note that the first peak was already in steady decline before the heavy rain in early September.
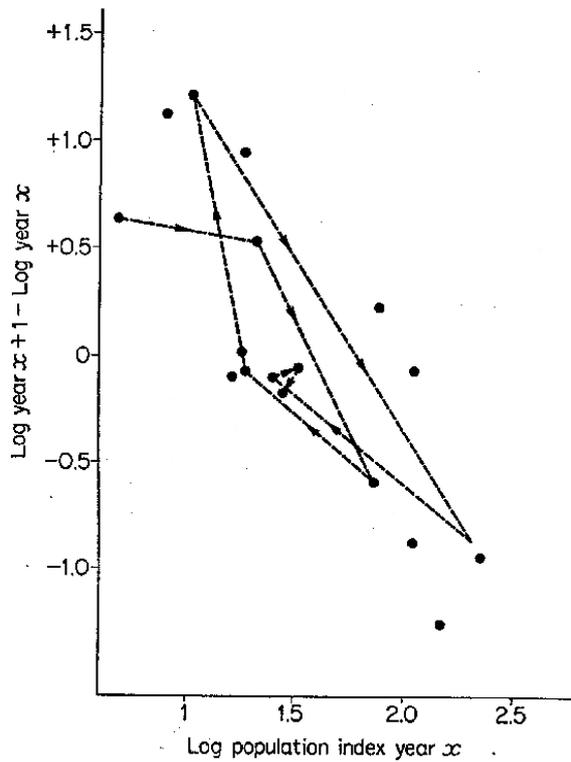

Fig. 12.9. Changes in *Myzus persicae* abundance from year to year plotted against abundance in the earlier year. The population data have been taken from Broadbent and Heathcote's (1961) trapping data for1942-1959 (from Mackauer and Way, 1976). Points for 1942-1950 have been joined in sequence as an example of a clockwise spiral pattern (see text).

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