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Full Table of Content

Monitoring Change in the Distribution and Abundance of Insects

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Monitoring Change in the Distribution and Abundance of Insects

L. R. TAYLOR

Introduction

Twenty years ago, in this Report, it was argued that pest control requires a national, if not international, scale of organization (Williams, 1952). Opinion at that time was influenced by the growing recognition of the great numbers of insects in the air and the vast areas that are regularly quartered in search of host plants, some of which are crops of agricultural or horticultural importance.

New agricultural hazards have since emphasised the need to see pest control as more than a local farm problem (Taylor, 1973). Economic pressures are increasing field and farm size and specialisation and, as the traditional mosaic of mixed farming in small fields gives way to monocultures of a narrowing range of crop varieties, the effect on pest populations presents unassessed risks. The widespread use of highly sophisticated insecticides has selected resistant pest strains and produced other side effects. In this rapidly changing agricultural environment, aphid biotypes have appeared attacking new crops; the recent increase in aphid problems in Britain, noted by Baranyovits (1973) and others, is also widespread abroad (Kolbe & Linke, 1974) and the potential for developing new pests is unpredictable.

It is clearly desirable to use the minimum amount of insecticide consistent with effective control and the precise timing of application can be crucial. However, because most crop pests are migrants, accurate timing of control schedules demands accurate knowledge of pest movements.

Current population dynamics theory is incapable of forecasting either the likely effects of the changing environment on pest status, or the likely movements of existing pests. Fundamental work has so far concentrated on numerical change in populations, but these agricultural problems are largely spatial and concern, not only how insect *numbers* change, but how *distribution* is controlled.

The available information on the rate of change of distribution of insect populations is meagre. It is known that some species, many aphids for example, are compulsive nomads. They have no population centre where a species could be monitored to register seasonal changes in numbers as an indication of future trends in crop infestation. Periodic movements of whole populations result in complete redistribution of the species so that the only relevant measure of population size is one made over a large geographical area, at least over the whole of Britain. At the other extreme, there are insect species so insular that each population centre has been known for generations. *This property of the 'fluidity' of a species is a population parameter that must be measured and understood before population dynamics can be of much relevance to agriculture.*

Again; if imprecise control treatments are to be deplored for their side-effects and aerial movements of pests are unpredictable in the present state of knowledge, *spraying programmes can only become efficient by constant monitoring of pest populations over large areas because they must be adjusted annually to the size, and especially the timing, of infestations that result from migration.*

It is in response to these two central issues that the two branches of the Rothamsted Insect Survey have been developed. The initial stages of both problems resolve themselves into the technical and economic difficulties of measuring the total population of any single insect species with enough speed and sensitivity to follow changes in its distribution over an area as large as Great Britain.

This paper describes an attempt to measure such populations, the techniques used, and what must be known of the populations before such measurements can be made effectively.

The project

To assess most accurately when control treatments should be applied, the ideal would be to sample the pests on the crops immediately before treatment. This would require constant crop surveillance which is feasible only for a few easily accessible crops.

Insect sampling in the crop or on the ground is tedious and expensive; with all the resources of a wartime economy, the wireworm survey (Fryer, 1944) required a major operation by dozens of entomologists to deal with only three species. For most crop samples, each group of pests requires a separate sampling programme, and often an individual technique. Furthermore, because of their highly specialised feeding sites, the number of samples required is usually large and the cost high. The Rothamsted Insect Survey, therefore, samples the flying stages of insects and attempts to relate these aerial samples to the ground, or parent, populations.

The justification for aerial sampling, adopted in the Rothamsted Insect Survey, is not that it is ideal, but that it is feasible. In part this claim is based on the efficiency of aerial sampling and the spatial disposition of the insects which will be dealt with later (p. 214). Another great advantage of aerial sampling is that, if the technical problems of sampling for one species are solved, then most other species of the same major group can be sampled simultaneously at little extra cost. An initial disadvantage is that the relationship between the parent population on the ground and the ephemeral aerial fraction is not yet sufficiently understood.

Four major factors govern the technical approach to aerial sampling, and their solution determines whether the project is viable.

The first factor, insect size and the related aerial density, determines the choice of aerial sampling technique. Aphids are serious pests, although not the only ones; however, they form a conveniently homogeneous group with which to begin and for which aerial sampling methods have been most thoroughly worked out. For such small insects, present in the air at high population densities, an absolute sampling method is already available to relate numbers directly to the sampling medium and so yield true population estimates. Larger and less common insects must be sampled by other means; this usually entails increasing the local concentration of insects in the air to a measurable level by an attractant before the sample is collected, so introducing a relative 'attraction factor' into density estimates. One reason for the dual sampling system adopted, therefore, is to investigate the problems arising in both kinds of methods; relative sampling for low density pests, and absolute sampling for high density pests.

Secondly, life-cycles determine the ease with which seasonal changes, or phenology, can be analysed. Some insects, like aphids, have complex life-cycles difficult to analyse, whilst many moths, including pest species, have simple cycles, which present easier material on which to develop the necessary analytical techniques.

Thirdly, one of the objects of the sampling is to make a comparative study of the dynamics of spatial distribution. Therefore, it is necessary to use populations of species of all kinds, from the persistently migratory or nomadic, to the non-migratory or static. Whilst aphids occupy the nomadic extreme, with population limits so tenuous that they may be difficult to locate and define, populations of moths range from nomadic to static and are more easily defined and more closely related to parent ground populations.

Finally, there is the cost of sampling. In pest control, identification must be rapid and

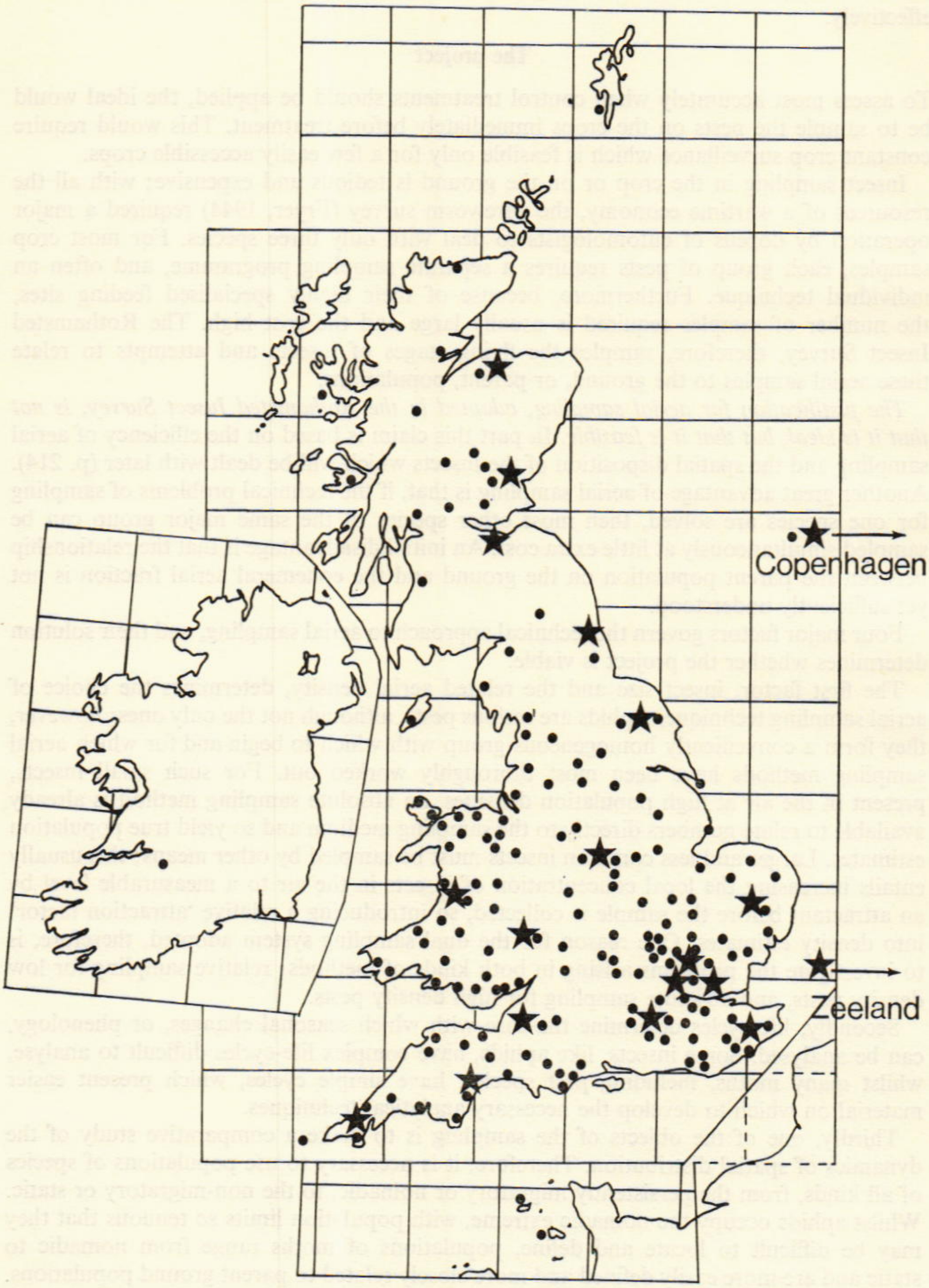

FIG. 1. Light trap (●) and suction trap (★) sites in the Rothamsted Insect Survey at August 1973.

accurate, but may be difficult if the pest group happens, like some aphids, to be taxonomically intractable. It must be done by experienced entomologists at a permanent centre and may be expensive, hence, sampling must be reduced to a minimum. More widespread sampling is necessary when studying fundamental population distribution processes, although speed is not so essential. Identification can be simplified by selecting the experimental species to avoid difficult taxonomic groups and the cost can be reduced by using the services of interested and talented amateurs as voluntary workers.

In order to satisfy both these requirements, the Rothamsted Insect Survey uses two parallel sampling systems (Fig. 1). A few highly efficient suction traps, so placed in uniform agricultural environments as to represent wide tracts of land, sample aphids that are professionally identified, mainly at Rothamsted. This rapid monitoring system provides an advisory service and also produces data enabling the short-term dynamics of migratory movement to be investigated. Simultaneously, a much more extensive network of light traps, sampling mainly moths that are identified by volunteers, provides data on spatial distributions allowing long-term differences between species, and the effect of changing environmental factors on both individual species and multispecies complexes, to be studied. For this latter purpose, the traps sample closer to the ground populations they attempt to represent, and are used in a range of sites that are as ecologically divergent as possible.

Development of the Survey

Although the need to monitor the changing distribution and abundance of insect populations was clear by the mid-1950s, no national organisation with the necessary facilities existed. Sampling techniques were available, but they had not been tested in large-scale surveys. In the event, the Light Trap Survey was started first because it was less costly than the Suction Trap Survey.

Light Trap Survey. In 1959 a project to investigate 'simultaneous changes in population levels in time and space', by sampling moths with light traps, was proposed to the Association of School Natural History Societies, but without success.

The standard Rothamsted Light Trap was restarted, therefore, on the edge of the century-old classical mangold experiment on Barnfield, to investigate the effects of post-war changes in agricultural practice on the insect fauna at the same site as that studied by Williams (1951) in the 1930s and 1940s. This trap completed its first year's sampling in 1960 and soon it was evident that the total insect population had fallen dramatically since the 1940s. Although the number of species seemed to have declined, the proportion of pest species seemed to have increased. (Later it became apparent that these issues were more complex.) This demonstrated the urgent need to survey the fauna and monitor its changes with changing agricultural practice and land usage.

TABLE 1

Light trap sites in August 1973

Category	No. of sites
Private individuals	43
Schools	33
Universities, colleges, museums, zoo	18
Field Centres, RSPB, Nat. Hist. Socs.	28
Forestry Commission, ADAS	13
Agricultural and Nature Conservancy Expt. Stns and Farms	21
Industrial organisations	2
Total	158

With this evidence, another appeal was made to amateur entomologists (French & Taylor, 1963) and in 1964 Mr S. C. Littlewood at Burleigh School, Hatfield, operated two traps (Littlewood, 1966). In 1965 seven traps completed a whole year's sampling. Since then, the increase has been maintained steadily, helped by publication of interim results (Lewis & Taylor, 1967; Taylor, 1968) and by the active interest of the Department of Education and Science through the Schools Science Fair. At the time of writing, August 1973, the project involves 158 trap operators (Table 1) and many other helpers. The original objective, traps at 200 sites, remains unchanged; some geographical areas remain inadequately represented (Fig. 1) but the range of agricultural and other ecological habitats now sampled is wide.

Because most operators are volunteers, light trapping does not continue indefinitely in the same places and sampling points cannot be chosen to a predetermined grid; therefore, a mapping programme capable of dealing with irregularly spaced data was needed. By 1968, the necessary minimum number of trapping sites for reasonable mapping were in operation and in 1971 the Symap V Program (Laboratory for Computer Graphics, Harvard) made such mapping possible. The species examined until now have been mainly pests, annual totals of which are published one year after collection because of the time taken to identify the catches and collate the records (Taylor & French, 1970, 1971, 1972, 1973, 1974a).

Suction Trap Survey. Early in the work it was realised that many of the defects of the light trapping system could be overcome by the simultaneous use of suction traps, but initially it was not financially possible to use them. However, about 1964, when restraint in the use of toxic chemicals became public policy (Agricultural Research Council, 1964), funds became available for the necessary trapping equipment, and for the appointment of staff to identify aphids. The initial stages of development were concerned with interpreting the sampling system and the general aerial populations.

The first suction trap began continuous operation at Rothamsted (Plate 1) in 1964. A second trap, 1·43 km from the first, gave samples that for practical survey purposes were found to be the same. These two traps were used to measure the sampling variance over a short distance (p. 214). A series of five traps, along a 643-km north–south transect down the east side of Scotland and England, was operating by 1966 and giving strong between-trap correlations of daily catches over distances up to hundreds of kilometers for whole insect Orders such as Thysanoptera, for whole Families such as Aphididae, and for single, small species such as the frit fly, *Oscinella frit* L., thus suggesting that large areas could be adequately sampled with a small number of suction traps.

A second transect of five traps, from Cornwall to Zeeland (662 km), was completed in 1970, perpendicular to the first. Trap sites at Aberystwyth and in the Midlands began to make mapping possible; the north–south transect was increased to 771 km by the addition of a trap at Elgin, and in 1971 the east–west transect was extended to Copenhagen (1321 km).

In 1966, a series of seven traps was established from Winnipeg in Canada, down the 97° line of longitude, to Denton in Texas, USA, to obtain comparable data (Taylor, Berry, Dry & Halgren, 1967). Later, additional traps at Rothamsted and at the Building Research Laboratory at Garston, near Watford, were established to obtain more information about the similarity or otherwise of samples from traps a short distance apart. By 1968, sufficient experience of sampling and identification had been obtained to introduce a Pest Warning Service.

The Aphid Pest Bulletin. The monitoring service for pests began in 1968 with weekly Bulletins, listing catches of 32 kinds of aphids taken in the suction traps. These Bulletins

Plates 1 and 2. The Tower site at Rothamsted Meteorological Station, now occupied by the standard suction trap of the Rothamsted Insect Survey at 12·2 m and a second trap at 1·22 m (Plate 1), was originally used for the measurement of vertical profiles of insect density by a series of 15 suction traps at 13 heights (Plate 2).

[*facing page 206*

were sent to about 50 people. Initial objectives were to assess cost, speed and efficiency of operation and the need by advisory entomologists for reliable current information about general population levels. From its inception, the Bulletin issued each Friday has listed the aphids caught five to twelve days earlier at sites in Britain. Aphids caught at sites overseas appear in the Bulletin issued one week later.

Of the 32 kinds of aphids listed in the first Bulletin in 1968, 23 remain unchanged in 1973. The 32 taxa now listed in the Bulletin comprise 27 species, three species' groups, the members of which are separated later, and two species' groups that are still too difficult to separate (see in Taylor & French, 1974a). Together with the moths already mentioned, four-week totals for these species have been published annually since 1969, but, unlike the moths, the aphid tables are published immediately the year's sampling is complete.

It was emphasised at the outset that the monitor programme was experimental; its feasibility and practicality had to be explored and fully tested under the pressure of operating conditions.

Initially the Bulletin service used only those traps already operating for experimental purposes. Now that the Bulletin is recognised as a useful early warning service by agricultural advisers, some traps have been sited for mainly advisory purposes, and the first survey trap to operate on a private, commercial farm (that of Mr. W. O. Watts, Berwick Ponds Farm at Rainham, Essex) became operational in 1973.

Both for pest monitoring and the study of population dynamics, local demands compete with synoptic; fine detail requires low level sampling which precludes national coverage at reasonable cost for insects like aphids. The suction traps listed here give maximum linear traverses and map-making cover, pre-requisites for synoptic usage, the area represented by traps sampling at 12·2 m above ground being considerable (see later). Their use for advisory work could, no doubt, justify the establishment of more suction traps, some sampling at lower levels, in order to define areas of local concentration of pest species. Perhaps more important for crop infestation, phenology needs to be studied on a local scale because migration in some areas is undoubtedly earlier than in others for reasons that are as yet obscure. Hence for advisory purposes, it is necessary to interpret the synoptic picture with the benefit of local knowledge.

Light traps may sometimes serve local needs if identification can be done locally and quickly. In Hungary a network of 132 light traps operates specifically for plant protection (Benedek, 1970), whilst an experimental forecasting service for the African Armyworm, *Spodoptera exempta* (Walk.), is based on light trapping in East Africa (Brown, 1970). The possibility of including insects other than aphids in the Bulletin is therefore being investigated, including those from certain light traps; some are already identified, but not immediately, and information can be used only in retrospect (Bowden, 1973; Crichton, 1971).

However, the present organisation of the Suction Trap Survey is nearing capacity and the only sites planned for the immediate future are in western Scotland and north-west England.

Sampling methods

Some of the techniques of aerial sampling and its interpretation had been developed before the Survey was started, but further improvements are continually being made. The aerial density of aphids and of some other insects is accurately measured with suction traps which have been standardised for insects of all sizes (Taylor, 1962); the model developed for survey purposes samples at 12·2 m above the ground. Moths and other insects are sampled at 1·2 m above the ground by means of standard light traps (see Williams, 1948) which give a selective sample that is related to the parent population

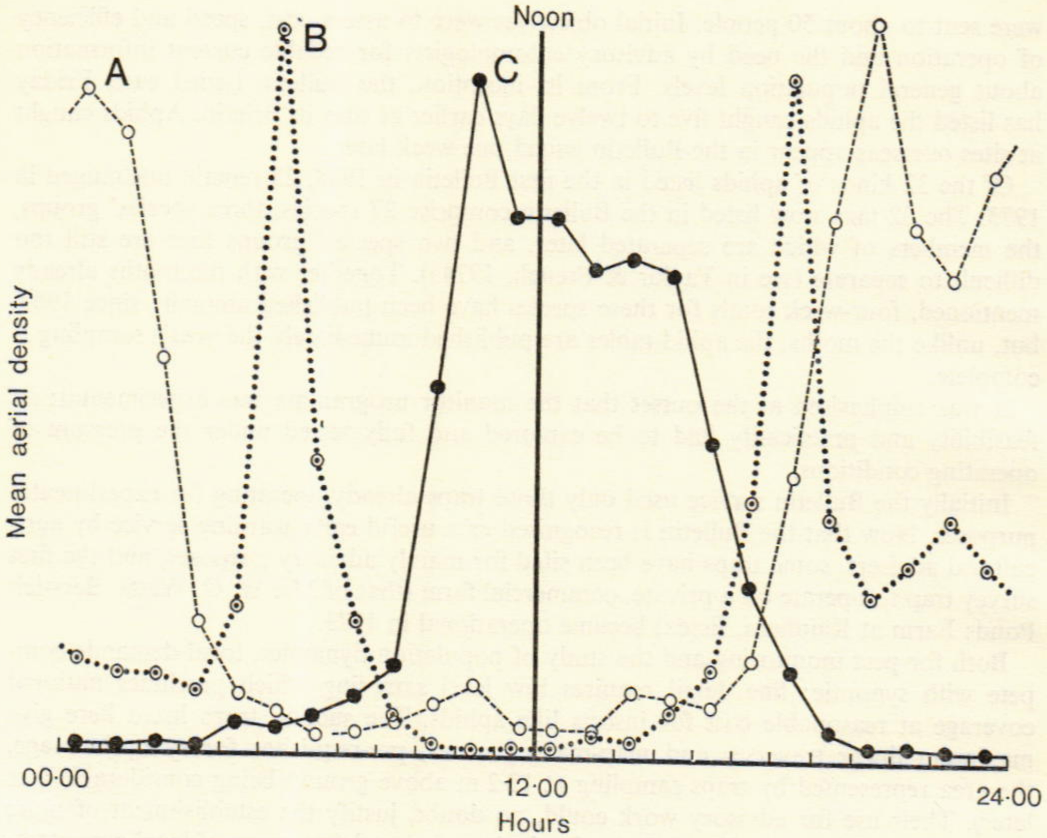

FIG. 2. Insects fly at specific times of the day and night, but few fly throughout the 24 hours. A, Gall midges (Cecidomyiinae); B, Fungus gnats (Mycetophilidae); C, Thrips (Thysanoptera).

by a factor, as yet unknown, but which continuing research is gradually elucidating (Taylor & Brown, 1972; Taylor & French, 1974b).

The major cost of aerial sampling is not the capital outlay on traps but the continuing cost of sorting and identifying catches. Of the many methods of sampling airborne aphids, the suction trap gives the most information for the least cost because of its greater efficiency (Taylor & Palmer, 1972). However, the composition of the aerial population varies greatly, and the correct choice of time and place for sampling can alter the proportions of particular groups of insects in the sample and so improve the cost-efficiency of the sampling method. Knowledge of the temporal fluctuations and spatial distributions of insects in the air is, therefore, vital for effective sampling.

Temporal fluctuations in the number of insects flying

Short-term fluctuations; diurnal flight periodicity. Insects fly at all times of the day and night (Fig. 2). Few species fly throughout the 24 hours and aphid flight (Fig. 3) is restricted to the daylight hours by light and temperature thresholds (Taylor, 1963) in all but a few exceptional circumstances (Berry & Taylor, 1968). Many other small, wind-borne, migrant pests such as thrips (Fig. 2), agromyzids, chloropids (e.g. frit fly) and many small beetles are also day-flyers. Others, such as moths and gall midges (Cecidomyiinae) are nocturnal, while fungus gnats (Mycetophilidae) and some plant bugs are crepuscular (Fig. 2). Sampling at specific times of day can thus include, or exclude, chosen groups.

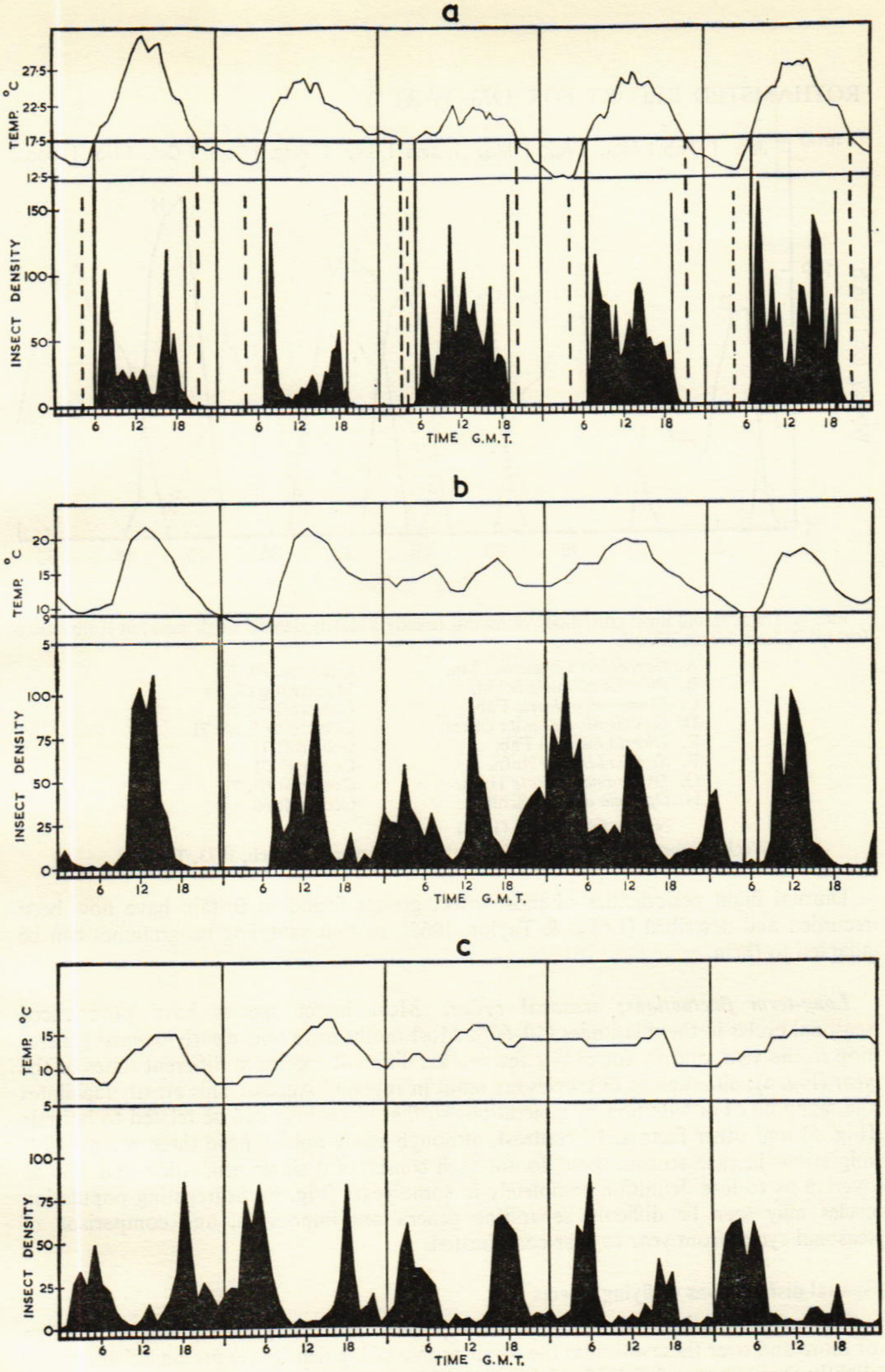

FIG. 3. Diurnal flight periodicity is often limited by flight thresholds. In the bean aphid *Aphis fabae* Scop. (a) a temperature threshold (17·6°C) releases morning flight but evening flight is stopped by a light threshold at 19.15 hours in July at Rothamsted. In the whitefly *Aleyrodes proletella* (Linn.) flight is continuous when temperature is above the threshold (9°C). In the moth *Lithocolletis messaniella* (Zell.) males fly in the early morning and females in the evening (after Lewis & Taylor, 1965).

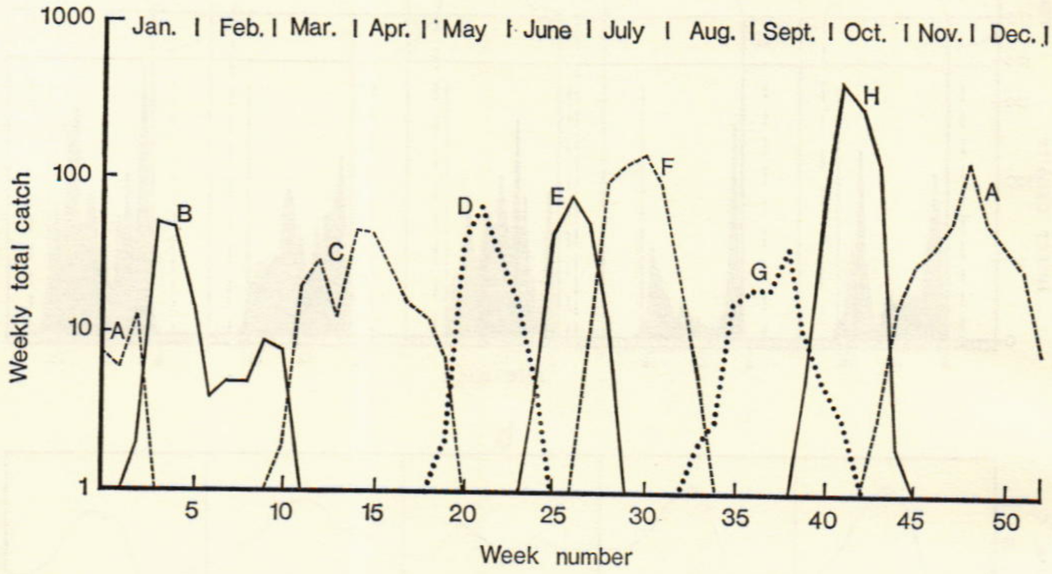

FIG. 4. The seasonal flight periodicity of moths, usually a clearly defined single peak, at Rothamsted (except B, from North Wales).

A.	*Operophtera brumata* Linn.	Geescroft 69, 70
B.	*Phigalia pilosaria* Schiff.	Maentwrog 68, 69
C.	*Erannis marginaria* Fab.	Geescroft 67, 70
D.	*Gonodontis bidentata* Clerck	Geescroft 65, 66, 71
E.	*Diarsia mendica* Fab.	Geescroft 71
F.	*Sterrha biselata* Hufn.	Geescroft 71
G.	*Dysstroma truncata* Hufn.	Geescroft 69, 71
H.	*Oporinia dilutata* Schiff.	Geescroft 69

Names from South (1961)

Week numbers are from a standard calendar (Taylor & French, 1973, Table 4).

Diurnal flight periodicities of most insect groups found in Britain have now been recorded and described (Lewis & Taylor, 1965), so that sampling programmes can be adapted to them.

Long-term fluctuations; seasonal cycles. Most insect species have pronounced seasonal cycles in these latitudes (50–60°). Most moths have one, clearly-defined generation in the year, and fly for only a few weeks, different species at different times of the year (Fig. 4); although most species are adult in July and August. This greatly facilitates the mapping of distribution by generations so that phenology can be related to latitude (Fig. 5) and other factors. In contrast, although many aphids have three recognisable migrations in each season, these do not each consist of a single generation and may so overlap as to lose definition completely in some years (Fig. 6). Segregating population cycles may then be difficult, separating generations impossible, and comparison of seasonal cycles from year to year complicated.

Spatial distributions of flying insects

Vertical distribution; the density × height profile. Insects fly at heights up to 1000 m or more and over these altitudes the mean profile of log density (ρ) on log height (z) is a slightly convex curve defined by Johnson (1957) as

$$\log \rho = \log C + \lambda \log (z - z_e),$$

where z_e represents a shift in the height axis.

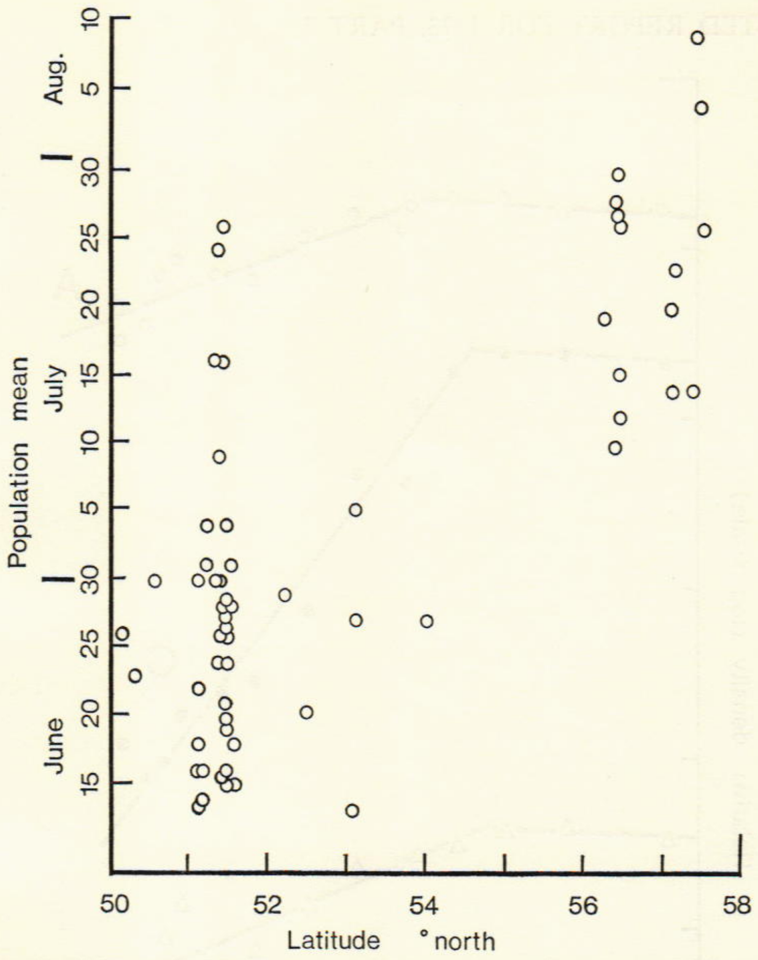

FIG. 5. Effects of environment, in this instance latitude, on phenology are more easily investigated with the simple seasonal cycles of a moth like *Diarsia mendica* Fab.

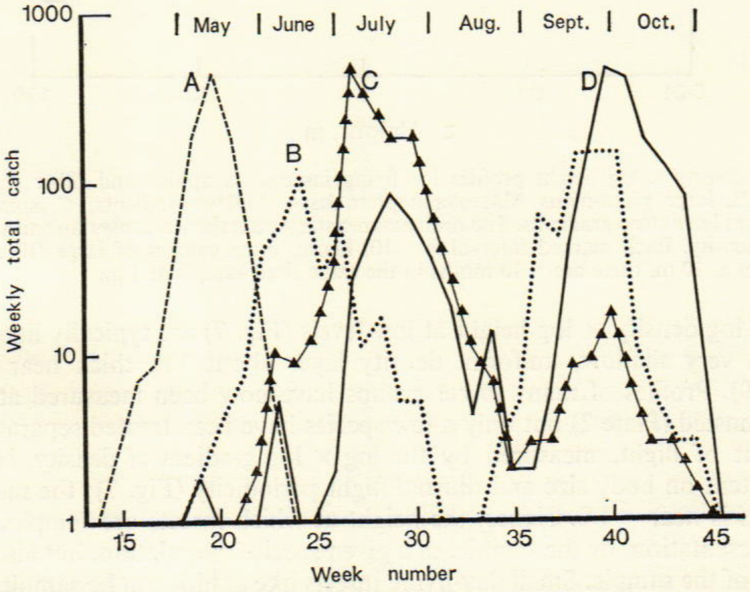

FIG. 6. Aphids often have three migratory cycles in the year, but these are not separate generations and may be ill-defined, making phenology difficult to elucidate: A, *Elatobium abietinum* (Walk.); B, *Brachycaudus helichrysi* (Kalt.); C, *Hyalopterus pruni* (Geoff.); D, *Rhopalosiphum insertum* (Walk.).

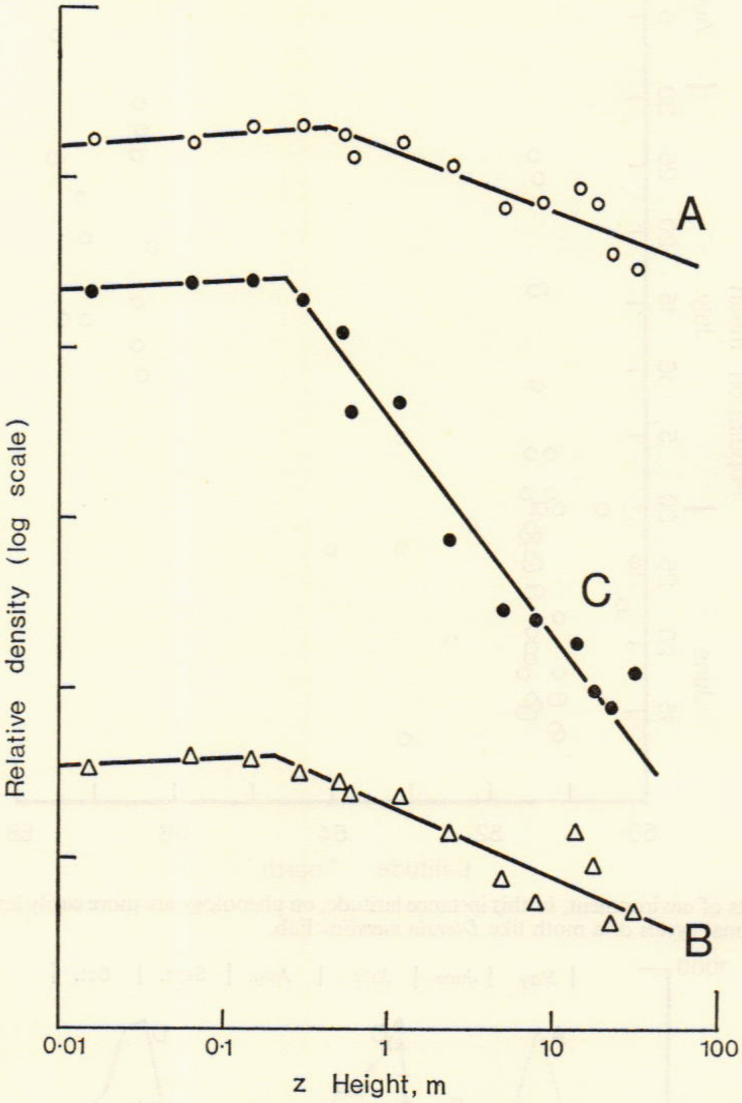

FIG. 7. Log density × log height profiles for flying insects. A, aphids and other small day-flying migrants and B, large night-flying Macrolepidoptera have shallow gradients; C, small night-flying Microlepidoptera have steep gradients. The ordinates are staggered; the scales overlap and are relative, not absolute, log density. Each marked interval is ×10, hence, when catches of large (B) and small (C) moths are equal at 10 m, there are ×10 moths in the same sized sample at 1 m.

Profiles of log density × log height at low levels (Fig. 7) are typically linear, $\rho = az^b$, except for a very shallow, uniform, density layer about 1 m thick near the ground (Taylor, 1960). Profiles of many insect groups have now been measured at a standard site at Rothamsted (Plate 2) but only a few species have been treated separately (Taylor, 1974). Height of flight, measured by the log × log gradient of density, $b(\rho)$, depends to a large extent on body size and diurnal flight periodicity (Fig. 7); the mean gradient for all insects is near $-1{\cdot}0$. Hence, the height at which insects are sampled affects not only the representation, by the sample, of a given species' population, but also the species composition of the sample. Small day-flying insects like aphids can be sampled effectively by collecting about 4000 m^3 of air per day at 12·2 m, and so exclude most of the small nocturnal insects by the sampling height, instead of by sampling in daytime only.

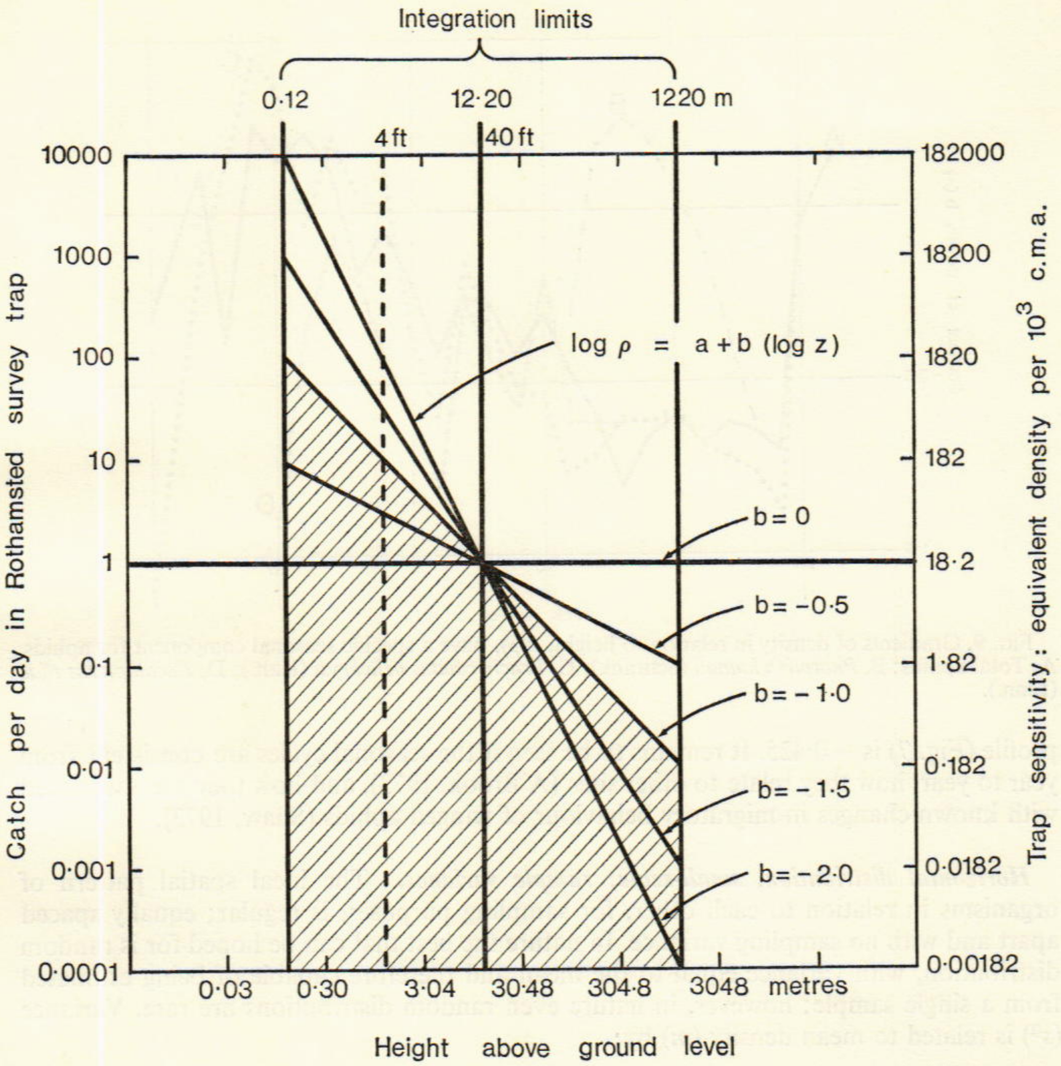

FIG. 8. With a linear log density (ρ) × log height (z) gradient of $-1{\cdot}0$, a single trap at 12·2 m is used to represent the profile integrated over the heights from 0·12 to 1220 m. For steeper gradients, the representation is less satisfactory (after Taylor & Palmer, 1972).

Gradient of density is not only important for selecting the appropriate group of insects; the estimate of total insect population depends on it (Fig. 8). It is unlikely that detailed profiles of density in relation to height, like those in Fig. 7, will be obtained for many species of aphid, because of the time and labour involved. However, the general form of the profile, as a mean in time, is fairly well established (Taylor, 1974), and the examples in Fig. 7 are typical. The gradient of density, $b(\rho)$, can thus be estimated somewhat crudely, from measurements at two heights.

One season's gradients for total aphids and three separate species, measured at 1·2 m (4 ft) and 12·2 m (40 ft) at the Tower site used for the original profile measurements, are plotted as weekly means of $b(\rho)$ in Fig. 9. Profiles for *Oscinella frit* L. had almost identical gradients in four successive months and led to the same expectation for other insects (Calnaido, French & Taylor, 1965). However, there are pronounced seasonal trends in $b(\rho)$ for aphids and these are different for different species. The weekly means range from just above zero to almost $-1{\cdot}0$; the mean gradient for all aphids in the full

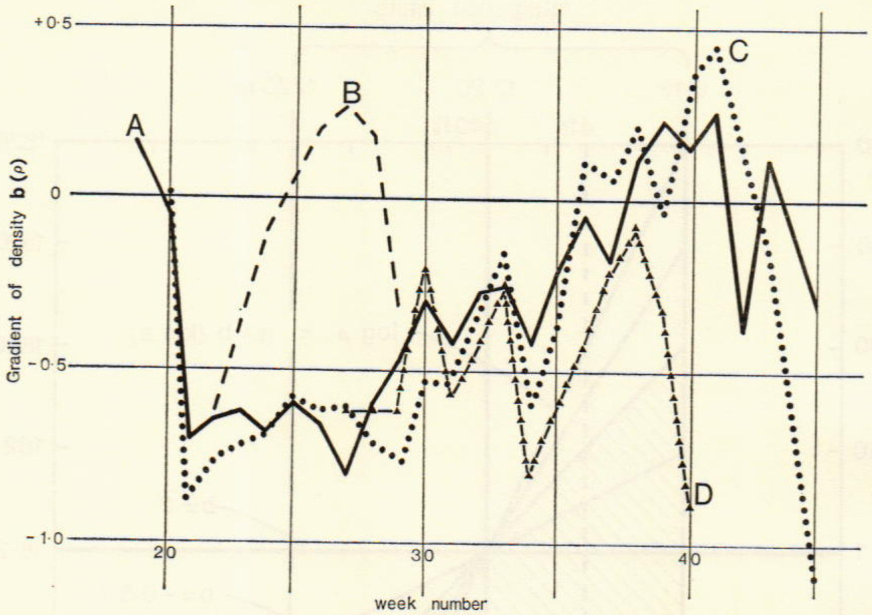

FIG. 9. Gradients of density in relation to height, $b(\rho)$, have a specific seasonal component for aphids. A, Total aphids; B, *Phorodon humuli* (Schrank); C, *Brachycaudus helichrysi* (Kalt.); D, *Eucallipterus tilae* (Linn.).

profile (Fig. 7) is −0·425. It remains to be seen if the seasonal cycles are consistent from year to year, how they relate to other sites (A'Brook, 1973), and how they are associated with known changes in migratory behaviour of winged aphids (Shaw, 1973).

Horizontal distribution, small-scale; sample variance. The ideal spatial pattern of organisms in relation to each other, for sampling purposes, is regular; equally spaced apart and with no sampling variance. In nature the best that can be hoped for is random distribution, with variance equal to the mean and therefore capable of being estimated from a single sample; however, in nature even random distributions are rare. Variance (s^2) is related to mean density (m) by:

$$s^2 = am^b$$

in all the organisms that have so far been studied (Taylor, 1961) and in sample distributions resulting from the aggregated dispositions of insects on crops, the log × log regression coefficient for aggregation, $b(s^2)$, almost always considerably exceeds 1·0. For example, for the bean aphid (*Aphis fabae* Scop.) on beans $b(s^2)$ is 1·72 (Taylor, 1970). By comparison, in samples of nearly all flying insects collected by suction traps at crop level, a and $b(s^2)$ are very close to 1·0 (Fig. 10); variances barely exceeding the mean. In other words, the aerial disposition of the individuals is random. The contrast between the two sets of data in Fig. 10 is self-evident; crop samples are not only expensive and inefficient to collect, they are poor value statistically compared with aerial samples.

Thus for aerial samples collected by suction trap, the variance can be calculated from a single sample and the information obtained is maximised. The sampling variance of light traps remains to be investigated.

Horizontal distribution, large-scale; effects of distance. As already mentioned, most flying insects are randomly distributed over small intervals in space. Hence the aerial density of aphids is homogeneous over short distances and the scatter of simultaneous

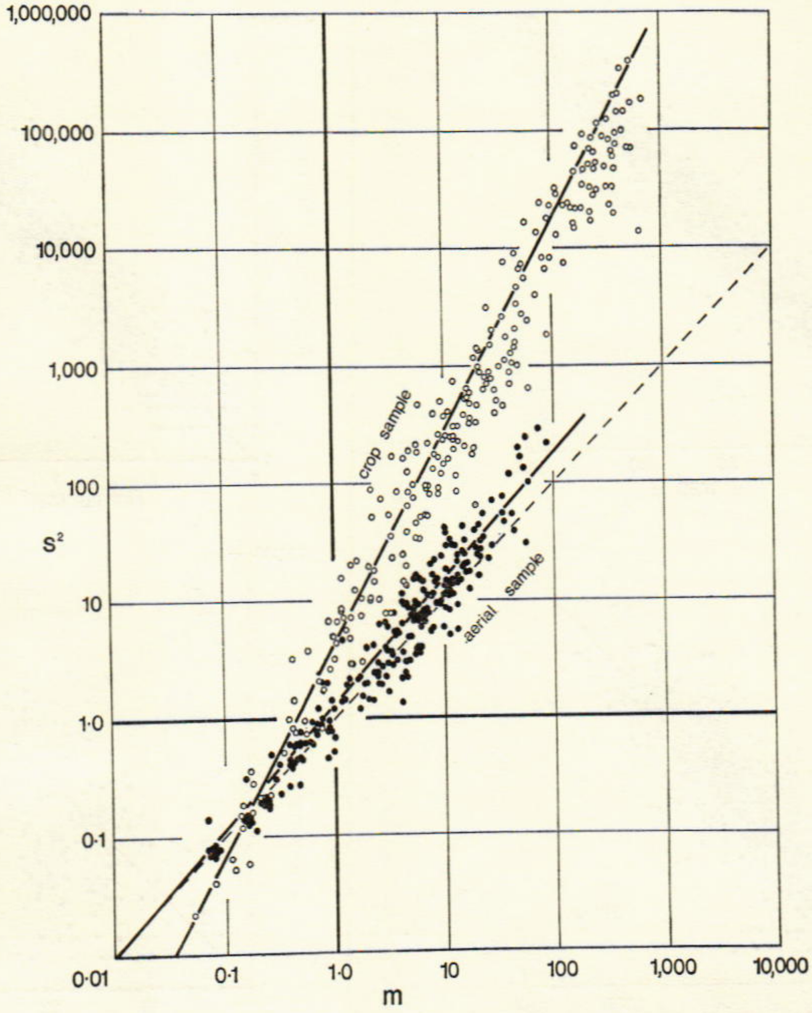

FIG. 10. Log variance × log mean relationship of samples from nearly random aerial insect density of many taxa (●) and of samples from highly aggregated aphids on crops (○).

samples from paired suction traps, side by side, can be appropriately equalised by a square root transformation (Fig. 11A). Greater separation leads to trends in population density, and aerial density differences become more heterogeneous (Taylor, 1971); simultaneous samples from paired traps then can be appropriately transformed by logs (Fig. 11B). The maximum distance between sample points that can be tolerated for a given level of sampling accuracy, is determined by the width of this scatter (Fig. 11C, D). The most manageable measure of this scatter found so far has been the correlation coefficient, r, for pairs of daily catches (in logs) over several weeks (Fig. 12). Regressions of logit $(r - 1)/2$ against $\sqrt{d}$, where d is the distance between the pair of sites, are linear (Fig. 13); the regression coefficient is probably species specific, and the pattern of traps necessary for a given level of population representation, therefore, differs for different species. For some, the regression is independent of the orientation of the two sites with respect to each other (Fig. 13A); for other species, correlation declines more rapidly with a north–west/south–east orientation than with a north–east/south–west one (Fig. 13B), and, when this happens, the north–west/south–east correlations can become negative at sufficiently great distances. Seasonal cycles of population density are in phase at sites

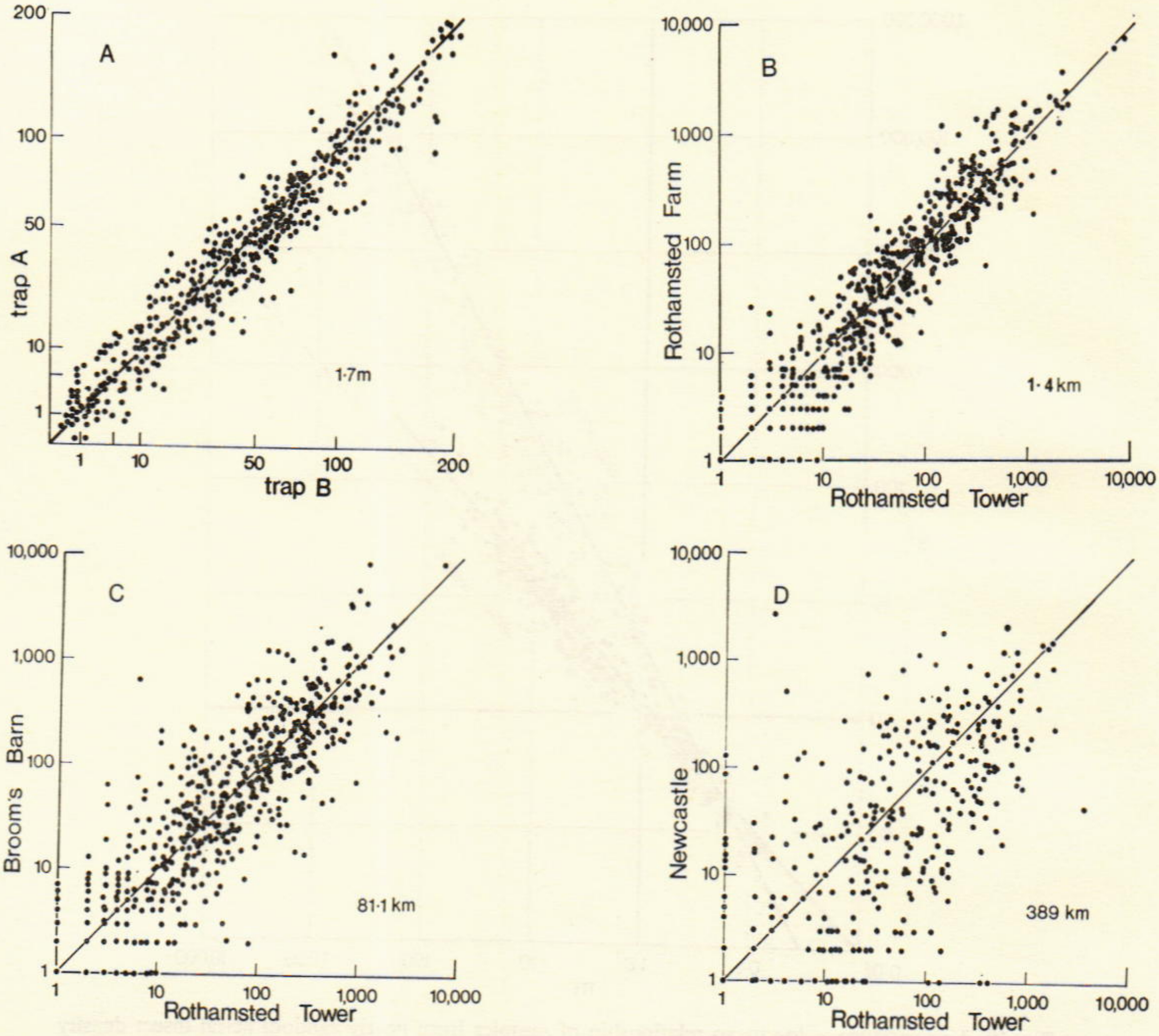

FIG. 11. A, Traps 1·7 m apart yield paired samples of most insects, appropriately transformed by square roots, i.e. from random distributions, giving the absolute minimum scatter. B, For traps 1·4 km apart, the transformation is logarithmic and the scatter similar in width to A between samples of 10 and 100. C, At 81·1 km the scatter has doubled in width but correlation is still very high. D, At 389 km catches are still positively correlated.

close together, but are sometimes out of phase as distance increases, especially with increasing latitude difference. There are also differences between species in the degree of synchronisation of seasonal cycles, shown in Fig. 14, which accounts for much of the specificity of the regression coefficient.

About 75% of the variance of r, depending upon the species, is accountable to latitude and longitude differences between sites, in a regression equation of the form

$$r = a + bx_1 + cx_1^2 + dx_2 + ex_2^2 + fx_1x_2,$$

where x_1 is the latitude difference between the sites and x_2 is the longitude difference; the coefficients differ between species and the coefficient f determines the axis of orientation of the set of samples. The behaviour of these coefficients has yet to be analysed and the remaining sources of variance found.

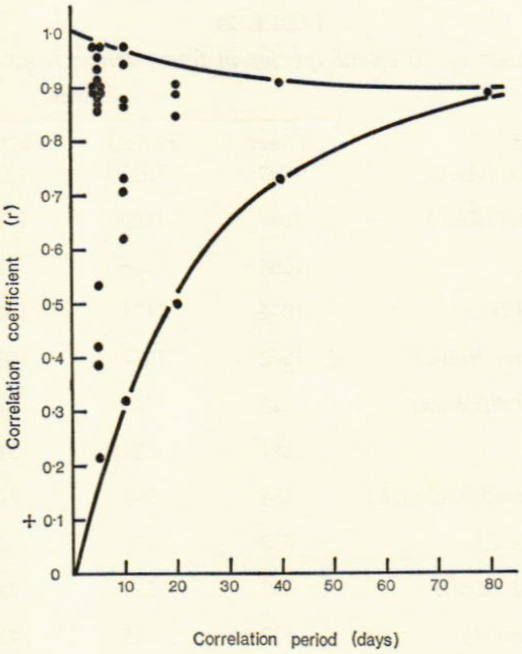

FIG. 12. Correlation of daily catches of aphids between two survey suction traps 1·4 km apart are widely scattered at short time intervals. Over such short distances the correlations narrow to a positive value at longer time intervals.

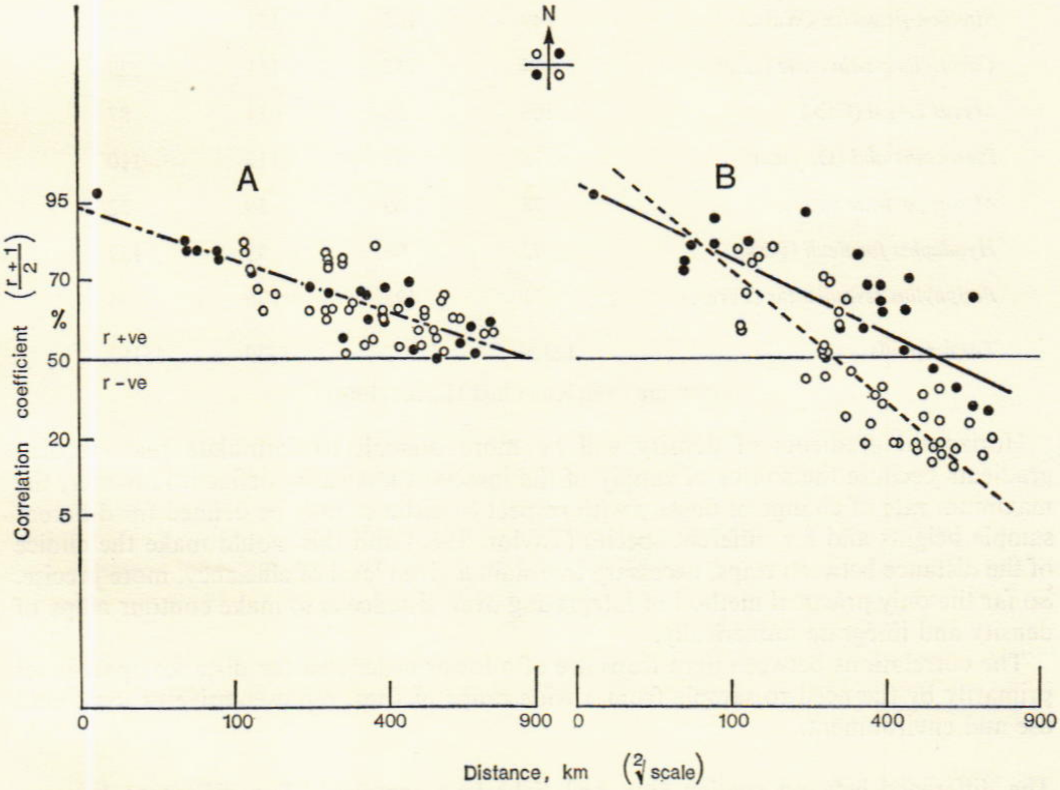

FIG. 13. The correlation of daily samples from pairs of traps declines with increasing distance and has a directional component in *Aphis fabae* Scop. (B) in 1969, but not in *Rhopalosiphum padi* (Linn.) (A), shown by correlations between pairs of traps orientated NW/SE (●) and NE/SW (○) of each other.

TABLE 2a

Total number of 20 aphid species in four suction traps in 1972

Species	Sites Tower	 Farm I	 Farm II	 Garston
Tuberculoides annulatus (Hart.)	1737	1023	1225	1740
Brachycaudus helichrysi (Kalt.)	1647	1800	1738	1216
Sitobion avenae (Fab.)	1264	1056	712	1407
Rhopalosiphum padi (Linn.)	1075	1174	1058	1637
Rhopalosiphum insertum (Walk.)	1062	1212	1036	750
Metopolophium dirhodum (Walk.)	715	755	671	693
Aphis fabae Scop.	561	524	517	662
Drepanosiphum platanoidis (Schrank)	484	398	317	806
Hyalopterus pruni (Geoff.)	430	471	481	508
Euceraphis punctipennis (Zett.)	337	238	237	1460
Cavariella aegopodii (Scop.)	327	445	419	370
Myzocallis coryli (Goeze)	191	195	186	215
Metopolophium festucae (Theo.)	167	201	159	51
Sitobion fragariae (Walk.)	149	135	171	222
Cavariella pastinaceae (Linn.)	134	157	111	228
Myzus cerasi (Fab.)	106	86	74	87
Pterocallis alni (De Geer)	78	99	115	110
Myzus persicae (Sulz.)	78	69	59	52
Hyadaphis foeniculi (Pass.)	73	90	91	139
Periphyllus testudinatus (Fernie)	71	122	136	74
Total aphids	12329	11912	11339	15192

Names are from Kloet and Hincks (1964)

Horizontal gradients of density will be more difficult to formulate than vertical gradients because the source of supply of the insects is less easily defined. However, the maximum rate of change of density with respect to distance may be defined for different sample heights and for different species (Taylor, 1965) and this would make the choice of the distance between traps, necessary to obtain a given level of efficiency, more precise. So far the only practical method of integrating over distance is to make contour maps of density and integrate numerically.

The correlations between light traps are of a lower order and the distance apart is set primarily by the need to sample from a wide range of sites, representative of local land use and environment.

The difference between suction trap and light trap samples. The difference between the samples from the two survey systems can be judged from Table 2 which gives the total annual counts of 20 species of aphids from four suction traps in 1972 (Table 2a)

TABLE 2b

Total number of 20 moth species in four light traps in 1972

	Sites			
Species	Barnfield	Allotments	Geescroft	Whipsnade I
Xestia xanthographa (Denis & Schiff.) (*Amathes xanthographa* Schiff.)	77	0	210	131
Agrotis exclamationis (Linn.) (*Agrotis exclamationis* Linn.)	64	28	13	217
Xestia c-nigrum (Linn.) (*Amathes c-nigrum* Linn.)	64	13	7	27
Mythimna pallens (Linn.) (*Leucania pallens* Linn.)	31	39	6	23
Diarsia rubi (View.) (*Diarsia rubi* View.)	46	8	20	78
Mythimna impura (Hübn.) (*Leucania impura* Hübn.)	39	1	23	96
Xanthorhoe ferrugata (Clerck) (*Xanthorhoe ferrugata* Clerck)	38	2	103	39
Hoplodrina alsines (Brahm) (*Caradrina alsines* Brahm)	31	4	72	25
Mesapamea secalis (Linn.) (*Apamea secalis* Linn.)	31	11	27	43
Rusina ferruginea (Esp.) (*Rusina ferruginea* Esp.)	30	5	60	11
Caradrina morpheus (Hufn.) (*Caradrina morpheus* Hufn.)	28	11	20	44
Idaea aversata (Linn.) (*Sterrha aversata* Linn.)	21	2	108	17
Spilosoma luteum (Hufn.) (*Spilosoma lutea* Hufn.)	20	5	55	52
Spilosoma lubricipeda (Linn.) (*Spilosoma lubricipeda* Linn.)	13	3	9	52
Hepialus lupulinus (Linn.) (*Hepialus lupulina* Linn.)	13	1	18	55
Hoplodrina blanda (Denis & Schiff.) (*Caradrina blanda* Schiff.)	13	0	104	10
Idaea biselata (Hufn.) (*Sterrha biselata* Hufn.)	13	1	346	6
Hydraecia micacea (Esp.) (*Gortyna micacea* Esp.)	12	12	3	19
Lacanobia oleracea (Linn.) (*Diataraxia oleracea* Linn.)	10	0	2	3
Thalpophila matura (Hufn.) (*Thalpophila matura* Hufn.)	10	3	4	8
Total moths	895	209	4451	2175

The first name is from Kloet and Hincks (1972); the synonym (in brackets) is from South (1961)

and a similar set of moth samples from light traps (Table 2b). Three of each set of traps are sited on Rothamsted Farm. The 20 species selected are the commonest in the first trap, located at the standard site for each survey, Rothamsted Tower suction trap and the nearby Barnfield light trap respectively, and are arranged in order of occurrence in that trap. The other traps are on the three nearest survey sites.

The uniformity of the aphid table is impressive. The two Farm traps (I and II) are only 12·2 m apart and their catches are expected to be similar, but they are both almost the same as that obtained in the Tower trap, whilst catches in the Garston trap, 11·7 km away, hardly differ from them. In fact, the total aphid sample differs by a factor of only 1·3 between traps.

In contrast, the commonest moth in the Barnfield light trap was not caught in the Allotment trap, in a similar situation only 200 m away, and the catches at all sites differ considerably; the Whipsnade I trap was 12·8 km away. Total moth count differs by a factor of 21·3 between traps.

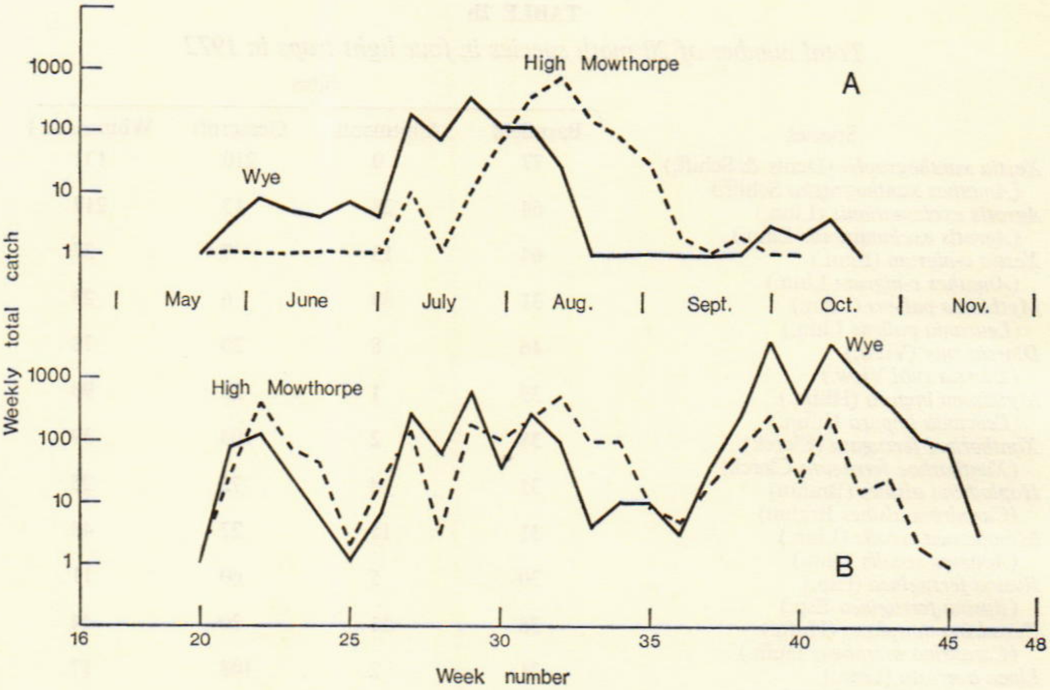

FIG. 14. Synchronization of seasonal cycles differs between species. A, *Aphis fabae* Scop.; B, *Rhopalosiphum padi* (Linn.); 1969. High Mowthorpe is in Yorkshire; Wye is in Kent. Week numbers are from a standard calendar (Taylor & French, 1973, Table 4).

This difference between the two sets of data is partly intentional, for the two surveys serve different purposes, but it is of considerable importance when considering how many traps are needed for making maps using one or other of the two systems. Whatever contribution the light trap bias may make to the differences of moths in Table 2b, *the similarity in aerial densities of aphids in 2a is real.*

Aerial and ground populations

As mentioned earlier, unless the aerial sample relates to crop samples, the survey monitoring exercise is of little practical value. The relationship between the aerial and ground populations seems to be more tenuous for aphids than for moths. In this section, therefore, only aphids are considered, especially from the viewpoint of aphid immigration into crops, rather than emigration from crops, about which a considerable amount is already known (see Johnson, 1969).

Unlike the deposition of inert spores or dust particles, the alighting of insects involves complex and specific behaviour on their part. Alighting is a controlled sequence of actions that are probably only possible when an insect is facing upwind and when its speed of flight exceeds that of the air; it may be followed immediately by take-off. Hence the number of insects passing over a crop does not necessarily give a satisfactory measure of their deposition into it, and deposition itself requires careful interpretation. The insect may select different plants on which to alight in order to feed, to reproduce or merely to rest. Hence the time spent on the plant may be short or long and the likelihood of capture by crop sampling correspondingly small or great. If virus is transmitted by a single, short, probe by an aphid there may be no corresponding accumulation of insects on the crop to register visits, especially if the crop is not a preferred host. In contrast, aerial sampling by suction trap records aerial density whatever the purpose of the flight. Hence, whilst aerial sampling may record insects that fail to infest a crop, crop sampling may fail to record insects that successfully infect it. Again, crop sampling registers those insects that arrive by walking, or survive the winter in the crop, to which the aerial sample is blind.

Thus the relationship between crop sampling and aerial sampling involves a behavioural component that can be very elusive. This relationship has been most thoroughly investigated for several species of grass aphids that are present in cereals and may present problems both as plant feeders and as virus vectors.

Cereals. From 1969 to 1972, Advisory Service (ADAS) entomologists collaborated with us by providing crop counts of seven species of cereal aphids on 24–44 spring-sown cereal fields throughout Scotland, England and Wales. The aphids sampled were *Rhopalosiphum maidis* (Fitch), in 1969; *R. padi* (Linn.), in 1969–72; *R. insertum* (Walk.), in 1970–72; *Metopolophium dirhodum* (Walk.) and *M. festucae* (Theobald), in 1969–72; *Sitobion fragariae* (Walk.) and *S. avenae* (Fab.), in 1969–72 (George, 1974). The crop sample was essentially that thought to be practicable as a routine sampling service (Dean & Luuring, 1970).

Attention was directed primarily to recording first arrivals in spring-sown crops of wheat and barley, and occasionally of oats. These dates of first arrival were then compared with the first records from the nearest suction trap, which on 26% of occasions was more than 40 km (25 miles) away. Out of a total of 732 field × trap comparisons of arrival dates, in 89% an aphid species was recorded by the trap before it was found in the field, if it was found there at all; in 9·6% the species was found first in the field; in no instance was a species found in the field but not in the nearest trap. Results were consistent from year to year except for an improvement in the prior detection of initial migrants by crop sampling, from 5·6 to 11%, as experience increased (Table 3).

In contrast, the behaviour difference between species is great and most instructive, if not yet fully understood. In Table 4 the species are arranged in sequence according to the percentage found first in the crop samples; this ranges from 0% in *R. padi*, to 25% in *M. dirhodum*. First arrival dates in individual crop samples for these two extreme species are plotted against first aerial arrival dates in Fig. 15.

TABLE 3

Number and percentage (in brackets) of first arrivals of all seven species of cereal aphids in field and air samples in four successive years

	1969	1970	1971	1972	Σ
Air only	66 (61)	83 (63)	122 (54)	132 (50)	653 (89)
Air before field	36 (33)	35 (27)	79 (34)	100 (38)	
Both together	0 (0)	0 (0)	2 (0·9)	2 (0·8)	4 (0·5)
Field before air	6 (5·6)	9 (6·8)	25 (11)	30 (11)	70 (9·6)
Field only	0 (0)	0 (0)	0 (0)	0 (0)	
None recorded	0 (0)	5 (3·8)	0 (0)	0 (0)	5 (0·7)
Σ	108 (100)	132 (100)	228 (100)	264 (100)	732 (100)

TABLE 4

Number and percentage (in brackets) of first arrivals of each cereal aphid species in field and air samples

	Air only	Air first	Both together	Field first	Field only	None recorded	
Rhopalosiphum padi (Linn.)	84 (69)	38 (31)	0 (0)	0 (0)	0 (0)	0 (0)	122 (100)
Metopolophium festucae (Theo.)	83 (68)	37 (30)	0 (0)	2 (1·6)	0 (0)	0 (0)	122 (100)
Rhopalosiphum maidis (Fitch)	15 (83)	2 (11)	0 (0)	1 (5·6)	0 (0)	0 (0)	18 (100)
Rhopalosiphum insertum (Walk.)	83 (80)	14 (13)	0 (0)	6 (5·8)	0 (0)	1 (1·0)	104 (100)
Sitobion fragariae (Walk.)	67 (55)	38 (31)	3 (2·5)	10 (8·2)	0 (0)	4 (3·3)	122 (100)
Sitobion avenae (Fab.)	26 (21)	76 (62)	0 (0)	20 (16)	0 (0)	0 (0)	122 (100)
Metopolophium dirhodum (Walk.)	46 (38)	44 (36)	1 (0·8)	31 (25)	0 (0)	0 (0)	122 (100)
Total cereal aphids	404 (55)	249 (34)	4 (0·5)	70 (9·6)	0 (0)	5 (0·7)	732 (100)

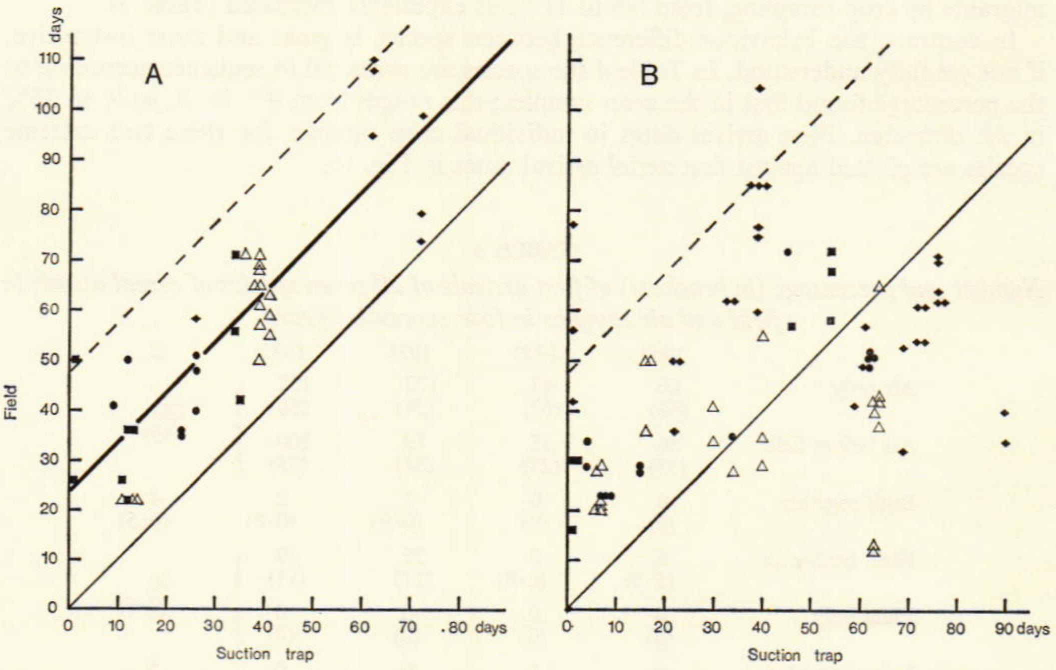

FIG. 15. Dates of first arrivals from survey trap and crop samples are consistent for (A) *Rhopalosiphum padi* (Linn.) but erratic for (B) *Metopolophium dirhodum* (Walk.); ■, 1969; ●, 1970; △, 1971; ◆, 1972. Coordinates are the number of days after the first record for the appropriate year. The 95% limits fitted in both figures are derived from *R. padi*.

The figure for *R. padi* (Fig. 15A) is simple and clear. In 1971, migration was fairly late and well synchronised, specimens appearing in all the trap samples within five days, whilst the crop samples were scattered over 21 days with a mean delay of 23 days after the mean suction trap date. The 1972 migration was also late but not quite so well synchronised, spatially or temporally. First arrivals in trap samples ranged over 10 days and crop samples over 36 days at a mean of 27 days after the mean trap date, except at one site (see Figure). In 1969 and 1970, migration was not well synchronised over the country, but the delay in the appearance of the aphids in crop samples, compared with the trap samples, as shown by the 95% limits in the figure, remained remarkably consistent. The length of the whole scatter along the *x*-axis is a measure of the annual variability in the timing of migration which makes crop protection so difficult.

Although migration is not often nationally synchronous, occasions like 1971 show that, even when it is, initial discoveries by crop sampling are not synchronised. The mean delay of 23·1 days may be a measure of the lower sensitivity of these particular crop samples, relative to the Survey suction trap sample; whilst the 95% limits of 23·8 days is the difference between individual fields. If so, the mean delay could perhaps be reduced by more intensive crop sampling, but the limits are a measure of the local knowledge needed to interpret aerial samples for individual crop infestations.

Fig. 15A may perhaps be so simple only because cereals are not currently preferred hosts for *R. padi* in Britain, so that the crop samples closely reflect the arrival of aerial immigrants which visit the crops but do not actively concentrate into it when they move from other sources. *M. festucae* and *R. insertum* behave in a similar way. In contrast, the distribution of *M. dirhodum* is far more erratic (Fig. 15B), and *S. avenae* and *S. fragariae* approximate to it. The limits derived from *R. padi* are transposed to the scatter for *M. dirhodum* in Fig. 15B and only about half the observations lie within them. Those insects outside the limits remain to be explained in terms of the difference in behaviour between *M. dirhodum* and *R. padi*; for example, they may result from low-level, short distance, movements concentrating insects into the crop from local, possibly overwintering, sources. This requires further investigation, especially since *R. padi* is a cereal pest elsewhere and a slight change in its behaviour or in farming practice might make it a pest in Britain.

Sugar beet. A similar comparison, on a different scale, has been made for the sugar beet aphids, *Myzus persicae* Sulz. and *Aphis fabae* Scop., sampled during routine crop inspection by fieldmen of the British Sugar Corporation in the areas served by two processing factories.

Two Survey traps were relevant to the crop samples; Broom's Barn trap, which is within about 40 km (25 miles) of the fields in the Bury St. Edmunds factory area, and Rothamsted trap which is within 100 km (63 miles) of the fields in the Felsted area. Three years' samples (1965/6/7) from these sites showed that the Survey traps were more sensitive in recording the first seasonal immigration of *M. persicae* and *A. fabae* than the crop inspection scheme (Heathcote, Palmer & Taylor, 1969). The crop sampling in these instances was extensive, ten plants in each of up to 176 fields in each area being examined for aphids each year (Hull, 1961), and the distance of some fields from the appropriate trap was considerable. This analysis is now being repeated over a period of eight years.

Potatoes. Although, in general, aerial samples appear to be more sensitive than crop samples for cereal and sugar-beet aphids, crop samples sometimes suggest the existence of airborne populations greater than the aerial samples suggest are available, assuming the crop sample to have been deposited from the airborne population. As part of the potato virus warning service operated by D. Hille Ris Lambers for Bladluisonderzoek TNO in Holland, large samples of 1000 potato plants, stratified over several fields, are threshed for aphids during the initial immigration of *Myzus persicae*. During June 1969, these samples yielded 100–3000 aphids per hectare around the Zeeland Survey trap. Assuming that *M. persicae* flies, on average, for 2 hours and has an aerial density × height gradient of −1·0—these being the expected values for the flight time of aphids and the mean gradient for all insects (Table 5, Taylor & Palmer, 1972)—this crop sample implies a trap catch at 12·2 m above the ground of 0·5–12 aphids per day, yet none were caught.

Assuming that both aerial and crop samples are efficient and reasonably accurate, which is likely, there are four possible reasons for this considerable discrepancy:

1. A density gradient of aphids of less than −1·0.
2. An accumulated flight time of less than 2 hours.
3. Movement of aphids into the crop after their primary deposition from the air (spatial concentration).
4. Accumulation of successive flights of aphids on to the crop (temporal concentration).

Because *M. persicae* is a mobile, polyphagous species, it seems quite likely that some of the aphids continue to move about after the first major flight is over. However, potato is not their specially preferred host, so that concentration, spatial or temporal, on the potato crop is unlikely to occur, nor was a continued rise in crop counts recorded (Hille Ris Lambers, personal communication) as would be likely if accumulation was the correct explanation. This is not intended to imply that deposition occurs randomly. The pattern of deposition depends on the layer of relatively still air, which is essential for an airborne insect to alight, around general topographical and other physical features, such as trees, the edges of growing crops, and wind-breaks (Lewis & Dibley, 1970). Once insects are within this layer, controlled re-distribution becomes possible; movement of insects into crops and active congregation by them can add to the deposition pattern to produce the familiar highly aggregated crop dispositions that are often found, for example by Dean & Luuring (1970) in cereal aphids. However, such aggregations are local, whilst the discrepancy being sought here is larger in scale and about one order of magnitude in size.

The third alternative, the length of time in flight, is difficult to assess for specific occasions in the field; expectation has to be based largely on laboratory experiments, which are species specific, and changes in aerial density profiles, which are not. A flight time of 0·5 hours, instead of 2·0, would increase the expected deposition rate, thus decreasing the expected trap catch from 0·5–12·0 to 0·1–3·0. At this level of expectation, a zero catch is less surprising. However, it seems likely that, if anything, 2 hours may be an under-estimate of total time spent in flight.

This leaves the fourth alternative. With a density gradient of −2·0 instead of −1·0, the deposition rate for a given trap catch at 12·2 m above the ground, is increased by a factor of ten. The insect density profiles upon which the gradient expectations shown in Fig. 7, were based, were obtained from an almost ideal site at Rothamsted (Plate 2), whereas at sites like that of the Goes trap on the Zeeland flats, unprotected from the North Sea gales, the wind shear in the first 10 m must be considerable. This may prevent the development of profiles like those at Rothamsted, and increase the gradient above that expected. Presumably the preliminary choice of a vertical gradient of −1·0 used for *Myzus persicae* was rather steep; the prospect of it being as steep as −2·0 must, therefore, be regarded with some suspicion. It is therefore, evident that more information is needed about specific profile gradients in relation to site and time.

It is also evident that any trap sample, however accurately measured, remains no more

FIG. 16. Annual density distribution maps for four aphids in suction traps, in 1971. Layering intervals are roughly geometric; 0, 1–2, 3–9, 10–31, 32–99, 100–315, 316–999, 1000–3161, 3162–9999. Symbolism is the same in all maps, except 16C, in which the intervals 1–2 and 3–9 have the same symbol, as have the intervals 10–31 and 32–99; the higher interval symbols are all displaced accordingly. A, *Rhopalosiphum insertum* (Walk.); B, *Cryptomyzus galeopsidis* (Kalt.); C, *Phorodon humuli* (Schrank); D, *Aphis corniella* (Hille Ris Lambers).

than an index of population density until the vertical profile of density can be integrated with some confidence. This is equally true for horizontal profiles of density, and becomes obvious in assessing total populations from maps.

Interim results

Long-term spatial distributions of single species. The strengths and weaknesses of the two sampling systems are evident by comparison of the four aphid maps in Fig. 16 with the four moth maps in Fig. 17. Phenological complications have been removed by summing samples over a whole year, so that the total season's production of migrant adults is shown. This is a measure of the annual capacity of the species to scour the country in search of host plants, or crops. In order to study regional variations in the timing of migration, phenological maps will shortly be produced.

Although we have fewer suction traps than light traps, especially in the north-west of Britain, there are other reasons why the aphid maps are simpler than those for the moths. The first two species, *Rhopalosiphum insertum* (Walk.) and *Cryptomyzus galeopsidis* (Kalt.) (Fig. 16A and B) are typical of many aphids and illustrate the extreme of migrant ubiquity. Widespread host plants, combined with great powers of dispersal, enable an aerial population distributed almost uniformly at 12·2 m above the ground to exploit the whole country.

Evidently the annual samples from even this small number of survey suction traps is adequate to represent these populations, and annual population changes might well be represented solely by mean sample density. No change in the distribution of species that behave in this way can be registered over an area so small as Great Britain. The scale of their population fluctuations is continental.

The next two species *Phorodon humuli* (Schrank) and *Aphis corniella* (Hille Ris Lambers) were chosen because of their strongly regional concentrations compared with most aphids (Fig. 16C and D). In all these maps, the layering intervals are roughly geometric (see legend Fig. 16); the density range for *P. humuli*, which has non-standard layering (see legend), from the 'high' in the Welsh Marches to the 'zero' in northern Scotland is over five orders of magnitude. The high density area is probably distorted slightly by the small number of traps, but a discrete population is strongly indicated; not completely isolated from populations on mainland Europe, but contained largely within the island in an area that is capable of arbitrary definition. The 'zero' areas are not, of course, devoid of insects but the density is very low, below the sensitivity of the sampling system.

Diffusion from the area of high density is great, as expected with aphids. Wild hops, the host plant, are rare north of the Scottish border, and hops are not cultivated north of Worcestershire. It seems likely that some of the aphids caught in the north of Scotland had travelled hundreds of kilometers. Similarly, the dogwood, *Cornus sanguinea* Linn, the host of *Aphis corniella* is restricted to England and Wales, except for introduced garden shrubs in Scotland, and the almost equally concentrated distribution of this species also offers a prospect for further analysis.

All these annual maps emphasise the highly developed distributive processes of aphids, their effective methods of searching the environment for hosts, and the even distribution of airborne populations compared with those on the ground. It remains to be seen if additional sampling sites greatly alter the synoptic maps for species like *P. humuli*.

The first moth, *Plusia gamma* (Linn.) the Silver-Y moth (Fig. 17A) is a well-known, long-distance, migrant pest of field crops that has much in common with aphids. In most years it floods the British Isles from southern Europe in spring and subsequently produces two generations, each supplemented by further incursions from abroad, until their

FIG. 17. Annual total maps for four moths in light traps. A, *Plusia gamma* Linn. in 1969; B, *Cerapteryx graminis* Linn. in 1970; C, *Agrochola lychnidis* Schiff. in 1970; D, *Abraxas grossulariata* Linn. in 1970. Names from South (1961).

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FIG. 18. Accumulated mean maps for *Cerapteryx graminis* Linn. A, 1968; B, (1968 + 1969)/2; C, (1968 + 1969 + 1970)/3; D, (1968 + 1969 + 1970 + 1971)/4. Number of sampling points: 1968, 47; 1969, 62; 1970, 72; 1971, 81.

FIG. 19. Difference maps for the years 1970–69. *Cerapteryx graminis* Linn.; areas of gain, A; loss, B. *Plusia gamma* Linn.; areas of gain, C; loss, D.

FIG. 20. Maps of daily distributions of the bird-cherry aphid, *Rhopalosiphum padi* (Linn.) for 1 (A), 2 (B), 3 (C), 4 (D) September 1971.

numbers are reduced almost to zero in winter, except in isolated places with a mild climate, because it lacks the ability to withstand the British winter. As with aphids, the annual map sums several migrant generations, with intervening non-flying stages, so that the final distribution at the end of a fairly successful season, such as 1969, is the result of the dispersive powers of the adult acting upon the areas of maximum reproduction. The distribution in other seasons may be quite different (Taylor, French & Macaulay, 1973). The maps are more detailed than those for the aphids, partly because there are more traps, but mainly because the low level aerial density reflects the ground population more closely than does the higher level aerial density of aphids, and is consequently less evenly distributed even with this highly mobile moth (see Table 2).

Cerapteryx graminis (Linn.), the Antler moth, severely damages upland pasture in some years and has been thought to be a migrant, perhaps because it reaches high densities locally and sometimes flies by day. Its population concentrations in the highlands tend to be discrete (Fig. 17B), reaching at least three orders of magnitude above its lowland densities. However, because its distribution changes little from year to year (Taylor, 1973, Fig. 4) it now seems doubtful whether it is, in fact, a migrant.

Agrochola lychnidis (Schiff.), the Beaded Chestnut moth (Fig. 17C) is, in contrast, largely restricted to the lowlands of the south-east. Like the Antler moth which feeds on a wide range of common grasses, the Beaded Chestnut is polyphagous, feeding on widespread Rosaceae of many kinds. Apparently it is not host plant distribution that circumscribes these moth populations. Also, like the Antler moth, the changes in the population of this species can obviously be followed with some accuracy.

Abraxas grossulariata (Linn.), the Magpie moth (Fig. 17D) is a familiar, but sporadic, pest of currants and gooseberries. Its distribution pattern is again different, with the main concentration in the centre of England. Whether its sporadic outbreaks are caused by changes in population density or changes in distribution will become more evident when sum and difference maps like Figs. 18 and 19 are available.

The localised nature of the Antler moth populations shows up well when successive years' maps are accumulated and means produced (Fig. 18). Fig. 18A shows the distribution in 1968, and the sequence B, C, D shows the effect of adding successive years' maps. There is no loss of definition as the process continues. By the third year, the map has assumed a near-stable condition. Further years could now be considered, not as isolated distributions, but as deviations from an expected condition.

The obverse is shown in Fig. 19A and B in which the areas gained and lost by the population between 1969 and 1970 are shown in the form of difference maps. The changes are essentially local, increase or decrease occurring around the borders or at the centre of the main population concentrations, and representing a local swelling or shifting of masses. In direct contrast, the difference maps between 1969 and 1970 for the Silver-Y moth (Fig. 19C and D) show a wholesale, and fairly even, loss over the whole country. Continued summations of maps of a species such as the Silver-Y would eventually result in a uniform distribution approaching Fig. 16A.

It is important, however, to consider the deficiencies of light traps in connection with these map manipulations. Because light trap samples incorporate a behavioural bias that may be correlated with site, difference maps tend to become less biased, whilst accumulated summation maps emphasise the bias. Hence the need to standardise light traps (see p. 207). Also, until traps are operating at enough sites, the loss or gain of a single trap can appreciably affect primary maps. In 1973, the coverage is adequate in England and Wales except for the Welsh Marches, Wiltshire Downs, northern Pennines and the English Lake District. Scotland is inadequately covered.

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FIG. 21. Four-week total maps for the peach–potato aphid *Myzus persicae* Sulz. for the season of 1971.

A, 23 April–; B, 21 May–; C, 18 June–; D, 16 July–; E, 13 August–; F, 10 September–; G, 8 October–; H, 5 November–2 December.

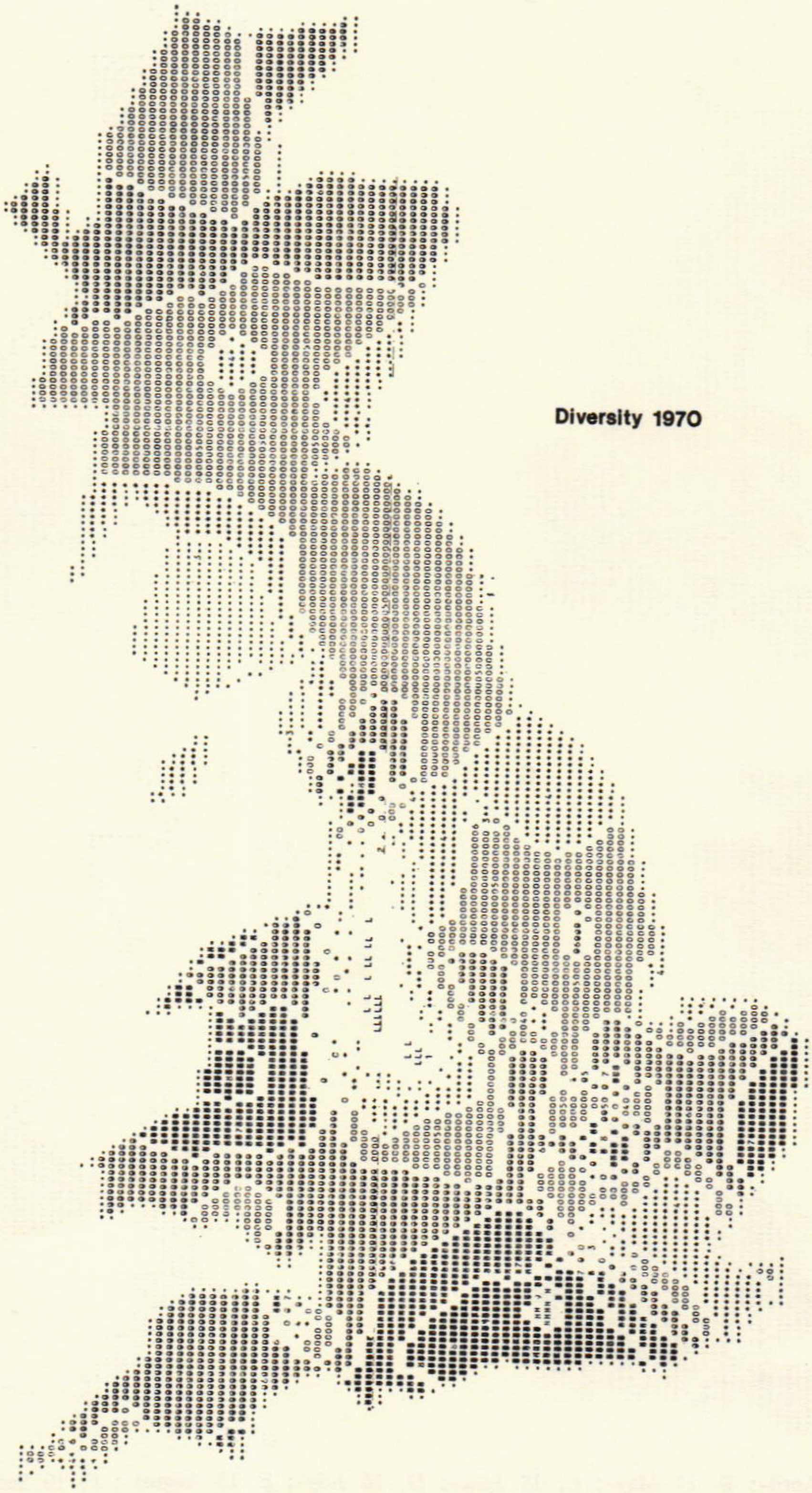

FIG. 22. Moth diversity (α) distribution map for 1970.

Short-term spatial distribution of single species. The short-term instability of aerial aphid populations is clearly shown during the autumn migration of *Rhopalosiphum padi* on four successive days in 1971 (Fig. 20); almost nothing remaining stable. The most consistent feature is the density banding across the highlands of Scotland and even this is largely an artifact, resulting from the absence of traps in the west. In England and Wales the only common feature is a tendency for patterns to form along a diagonal from the Wirral to Kent. No attempt has yet been made to examine changes at this level systematically, but experimental evidence suggests that successive daily maps represent, largely, different aphids. The capacity for effective flight in aphids is not usually retained for long; in some species only for a single day, so that successive maps may not be of the same population, unlike moths which have much longer flying lives. This could emphasise regional differences.

The annual distributions shown in Fig. 16 are summed over several, usually three, more or less distinct population cycles. These successive waves can be seen in the four-week maps of *Myzus persicae* in 1971 (Fig. 21). The difficulty of establishing calendar criteria for the timing of these migrations (see also Fig. 7, Taylor, 1974) is what makes forecasting of crop infestation dates so difficult.

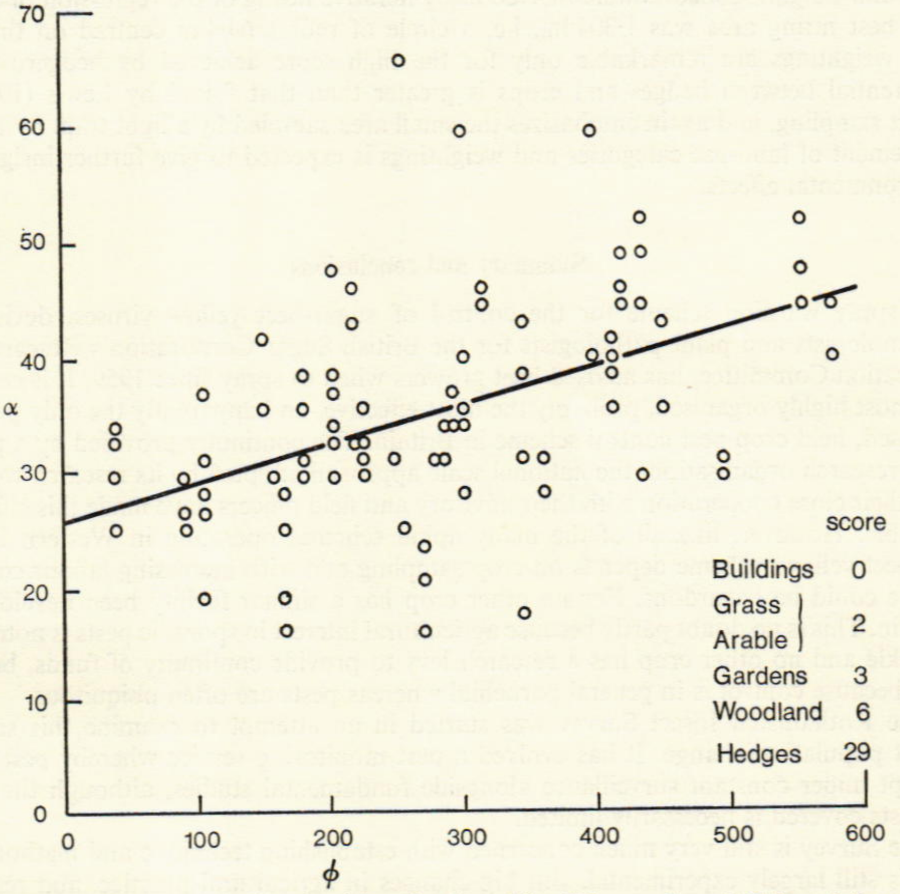

FIG. 23. Regression of moth diversity (α) on land-use (ϕ) within a radius of 64·4 m of the sample point; fitted line is $\alpha = 25{\cdot}94 + 0{\cdot}034\,\phi$. The index ϕ is a weighted area measure using the scores given in the figure.

Multi-species populations. Although the spatial distribution of individual species is of major concern in current pest control, to study the effect of a changing environment on insect populations requires a collective measure of the species structure of a sample so that the effect of parallel changes in different regions, where the species are different, can be investigated. The frequency distribution of individuals between species provides such a measure. The index of diversity, α, derived by Fisher, Corbet & Williams (1943) from the log-series distribution, or $\lambda = S^*/3\sigma$ from the log-normal (Kempton & Taylor, 1974), both of which fit moth samples from light traps, provide the necessary measure, sensitive to environmental changes.

Because α, like λ, is independent of sample size it is also independent of the attraction factor which affects the size of light trap samples from different sites (p. 207). Maps of α diversity (Fig. 22) are thus relatively free of bias. Hence changes from year to year, although they are currently affected by the small number of sample sites, are expected soon to become a sensitive indicator of areas of changing population structure. The log-series does not usually fit the frequency distributions of aphids but a direct comparison of the diversity of moth and aphid populations should be possible using λ.

Major factors affecting diversity are now being sought. Latitude accounts for about 20% of the variance of α between sites. Another 20% results from the land-use immediately adjacent to the trap (Fig. 23). The provisional land-use index, ϕ (Taylor, 1968) is a sum of the areas in certain categories, weighted as shown in the figure. The total area and weighting factors were arrived at by iterative fitting of the regression of α on ϕ. The best fitting area was 1·304 ha, i.e. a circle of radius 64·4 m centred on the trap. The weightings are remarkable only for the high score achieved by hedgerows; the differential between hedges and crops is greater than that found by Lewis (1969) by direct sampling, and again emphasizes the small area sampled by a light trap. Systematic refinement of land-use categories and weightings is expected to give further insight into environmental effects.

Summary and conclusions

The spray warning scheme for the control of sugar-beet yellow viruses, devised by entomologists and plant pathologists for the British Sugar Corporation's Research and Education Committee, has advised beet growers when to spray since 1959. It is certainly the most highly organised, probably the most effective, and apparently the only properly assessed, field crop pest control scheme in Britain. The continuity provided by a permanent research organisation, the national scale approach adopted by its research workers, and their close cooperation with their advisory and field officers have made this efficiency possible. However, like all of the many aphid schemes operating in Western Europe the beet yellows scheme depends on crop sampling and with increasing labour costs, its future could be hazardous. For no other crop has a similar facility been developed in Britain. This is no doubt partly because agricultural interest in sporadic pests is notoriously fickle and no other crop has a research levy to provide continuity of funds, but it is also because control is in general parochial whereas pests are often ubiquitous.

The Rothamsted Insect Survey was started in an attempt to examine this scale of insect population change. It has evolved a pest monitoring service whereby pest status is kept under constant surveillance alongside fundamental studies, although the range of pests covered is necessarily limited.

The Survey is still very much concerned with establishing technique and methodology and is still largely experimental. But big changes in agricultural practice, and resulting pest status, have still to come and the Survey is also concerned with the ability to detect these changes early and to respond to them.

Migration and the spatial aspect of population dynamics; the role of aggregation or heterogeneity in population distribution; the changing distribution of insects in relation to changing environment; the relation between land-use and population diversity; thresholds of population instability and the evolution, or creation, of pests; pest movement as a prelude to crop infestation; all these have a common spatial component requiring a synoptic sampling approach. Given this, the search for a solution through mapping seems inevitable, and the choice of sampling tools and experimental animals seems logical.

The choice now appears to have been satisfactory and the efforts made to understand the samples justified. It seems likely that radar could provide useful ancillary information on the very short-term movements of aerial concentrations of large insects (Schaefer, 1974). However, the prospect for radar identification of a difficult aphid like *Myzus persicae* must be remote, and radar does not provide an alternative to current methods.

The light trap samples are large enough to be useful, but at the same time small enough not to affect local populations and thereby ruin the experiment. Rare species are very seldom caught, and voluntary workers can handle the catches in their spare time. Many other personal and official projects have built up around the data; some are listed in *Rothamsted Report for 1972*, Part 1, p. 201. The suction trap samples have presented certain problems because sample size needs to be adjusted almost daily to prevent sorting and identification becoming too great a burden; these problems are being overcome. The weekly Bulletin is now used by both public advisory services and private industry. Advisory purposes may require additional samples if usage increases, but the maps are already prompting many questions and providing some answers. The need for a mapping programme was anticipated as the essential common ground for the two sampling systems and the appearance of SYMAP was fortunate; it serves initial stages well.

The successive maps are of aerial populations separated by the daily flight periodicities of the adult insects and seasonally by their earth-bound larval stages. The essential analytical problem is to find succinct expression for these successive spatial distributions in a temporal sequence. Continuous summation increasingly separates species according to their inherent spatial stability; horizontal gradients of density progressively build up in stable species and break down in spatially fluid ones. Step by step changes in difference maps show areas colonised and vacated. How many of the 557 species of moths, the 255 species of aphids, and the other kinds of insects so far sampled are suitable for this treatment is not yet known. Primary data, such as total population size and area, and secondary data such as rates of gain and loss, need to be extracted from the maps before more sophisticated analysis is possible, and trends will not show convincingly with the few years' data at present available.

This report, to explain the objectives that prompted this approach and to collate the evidence that justifies it, is perhaps overdue, but with such a long-term exercise, concrete results are slow to appear and unsubstantiated speculation ill-advised. The project owes its continued existence to the many people, both amateur and professional, who have worked so long and so patiently while awaiting results and, to them, I am deeply grateful. Those long awaited results now seem to be both tangible and relevant.

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