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INTERNATIONAL DISPERSAL OF INSECTS AND INSECT-BORNE VIRUSES

Internationale verspreiding van insekten en van virussen die door insekten worden overgebracht

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INTRODUCTION

This paper is about the international or long-distance dispersal of insect pests by natural means, with special reference to Europe. The most numerous examples, and some of the best, are from other parts of the world; but even in Europe it would be difficult to consider, in so short a time, all the pests that cross national boundaries. Instead, therefore, a few examples will be given to illustrate certain points, mainly about the mechanisms of dispersal. Problems of research and how, by more cooperative work, we may monitor dispersal more satisfactorily, will also be considered.

Concrete evidence about distances insects travel can be obtained either by capturing migrants over territory where they are not breeding, or by recapturing marked individuals released at a source. So far it has been impossible to capture marked individuals at very great distances (except for the Monarch butterfly; URQUHART, 1960). The first method, therefore, provides most information; and it can be supplemented by inference from a knowledge of insects' flight.

The long-distance spread of pests is most obvious in countries where agriculture is developed near tracts of waste or uncultivated land, either within or beyond the national boundaries, from which insects invade cultivated areas and become pests there. Some of the best examples of this are from North America. For example, the cotton leaf-worm, *Alabama argillacea*, annually invades the southern States from its permanent home in Central or South America. The beet leaf-hopper, *Circulifer tenellus*, breeds on desert weeds in Utah, but annually invades the sugar beet areas up to 300 km away. The leaf-hopper *Empoasca fabae* migrates northwards for up to 1600 km annually in the U.S.A. Species of noctuid moths fly from North Africa into the southern countries of Europe and become pests there. There are many such examples.

In most of Europe, however, agriculture and its pests are everywhere and uncultivated land is minimal or well mixed in with agricultural land. There, the long-distance spread of pests is less noticeable. Only when a new pest is introduced from another continent and spreads from a well-defined source is the process obvious. Intercontinental contamination is, however, usually done accidentally by man, as for example when the Colorado beetle was imported into Europe from America, or the Mediterranean fruit fly imported into the U.S.A. from Europe. Continuous inspection and quarantine attempt to minimise such transfers; but natural spread within continents, whether of such introduced pests or of those already there, goes on all the time and is almost impossible to prevent.

In northern Europe, therefore, though there are many entomologists, knowledge about the spread of pests that occur everywhere is cramped by the difficulty of associating the insects in any particular place with the source from which they come. Whereas in the more southerly regions, where migrants could perhaps more easily be traced especially across the sea, quantitative records are more scanty.

THE SCALE OF DISTANCES FLOWN

Insects can travel, in a single flight, distances that range from a few metres to over 3200 km. This is the scale for quick travel in Europe. Generally, the direction and speed of such long-distance flight depend on the resultant of the speed and direction of winds circulating within cyclones and anticyclones, and the speed and direction of movement of the pressure systems themselves; the air must also be warm enough to permit sustained, active flight whose duration is the major factor that, with the wind, determines the distance travelled. The insects' own air speed usually contributes little either to distance or to speed of long-distance displacement. The following examples illustrate this and demonstrate the scale of distances involved.

From June 28 to 30, 1958, the N.E. coast of Britain was invaded by unprecedented numbers of the Diamond Back moth, *Plutella maculipennis*, a feebly flying insect about as big as a clothes moth and a well-known pest of cruciferous crops. In places it was estimated at 30–60 million moths/acre and their progeny eventually caused much damage in many places across England. A weather ship at sea 480 km south of Iceland and over 800 km west of the northern tip of Scotland reported thousands at 1300 hr on July 4. Populations in England and in northern and southern Europe were too small to supply those that came, though Scandinavian countries had an influx.

An analysis of weather charts showed that winds, up to about 1200 m altitude, arriving at the weather ship on July 4 and at the N.E. coast on June 29 and 30 could be back-tracked to the western region of the U.S.S.R. or to the eastern Baltic area. There on June 27, the weather was hot and thundery and could have encouraged flight and convective transport to high altitudes, before subsequent displacement on the easterly winds (Fig. 1). From Norway to the

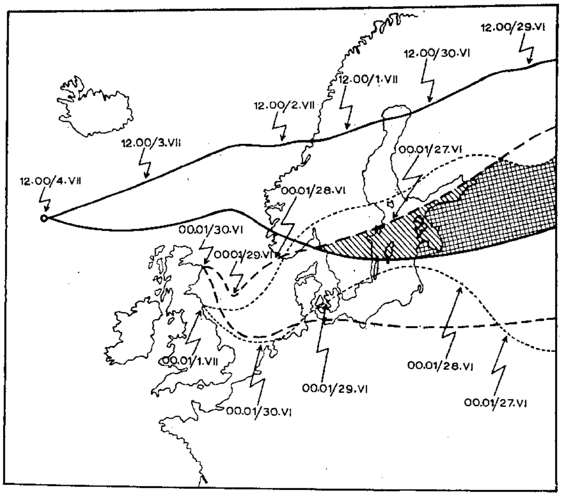


FIG. 1. *Plutella maculipennis.* Back-tracks of wind associated with the invasion of the United Kingdom in 1958.
Shaded area: The probable origin indicated where backtracks from different points of arrival cross each other.

Plutella maculipennis. *Verband tussen windrichting en binnenvliegen in het Verenigde Koninkrijk in 1958.*
De donkere gedeelten geven het waarschijnlijke gebied van oorsprong weer, waar winden die naar verschillende plaatsen waaiden, elkaar kruisten.

After FRENCH & WHITE, 1960.

weather ship was 1600 km and flight presumably did not cease at the ship; the distance from Russia was 3200 km (French & White, 1960).

Two points about this flight are particularly important. The insects almost certainly supported themselves by active flight for at least four days (for without this they would soon have fallen into the sea). The migration occurred in northern Europe where a maximum amount of information might be expected, but though infestations at the source must have been spectacular and widespread, we have been unable to obtain any information about them. Also in Britain, where observers are numerous, many more places must have been heavily invaded than were recorded. Similar journeys are probably frequent but, when made by smaller numbers, possibly pass unnoticed. However, when small numbers of other moths arrive, at times when there is no breeding in the territory they invade, a record of the time of arrival of even a single insect may enable its origin and track to be determined.

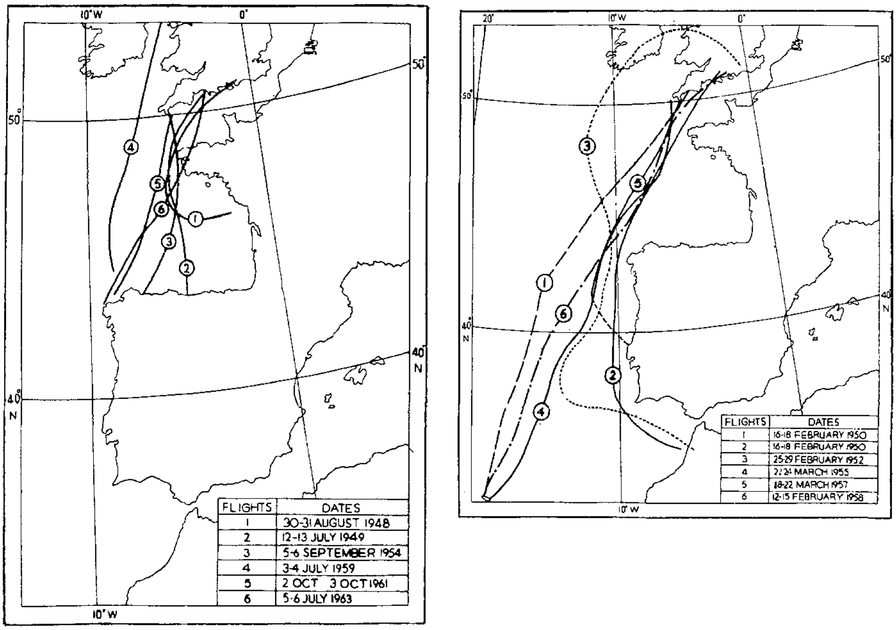
In Britain we have many amateur entomologists who, for years, have sent records of immigrant Lepidoptera to Mr. R. A. French at Rothamsted. Mr. G. Hurst of the Meteorological Office has associated many of these records with the current synoptic weather and has back-tracked the winds associated with the moths' arrival, so showing the probable track and origin of the moths.

The Lesser Army Worm, *Laphygma (Spodoptera) exigua*, (a sturdy moth about 3 cm across) does not overwinter in Britain but is a serious pest in N. Africa, Spain and the northern Mediterranean area of Europe which is about the northern limit for its continuous survival. On May 6, 1962, it invaded the south coast of England on an unprecedented scale, though only a few hundred were seen and the invasion was minute compared with that of *P. maculipennis*. A back-track of the surface and upper winds showed an 80% probability that a southerly air-stream carried the moths from an area about 320 km radius in the Atlantic west of Gibraltar, starting about 1800 hr on May 4. On May 2 (but not on May 1), temperature in Morocco north of Rabat reached 25°C with convection to about 1500 m, with 5–10 knot E. and N.E. winds, which could have brought the moths into the Atlantic before they caught the southerly wind that brought them to England by May 6 and to Holland by May 7 and 8. The moths must, it seems, have flown continuously day and night for four to six days while traversing 2400–3200 km over the sea. Gliding and resting cannot be assumed to account for this kind of travel, for the southerly air-stream had little upward component to keep moths aloft passively and most of the flight was made below 1200 m.

Many such records for this species dating back to 1947 have now been analysed, sometimes when only one or two moths were caught. The moths that arrived in February or March were always back-tracked to a subtropical source beyond Spain, usually to Morocco, to the Azores or Madeira. From May onwards most tracks originated in N. Spain and moths from there probably were progeny of earlier immigrants from North Africa (Fig. 2).

The synoptic weather systems allowing this travel have been estimated to occur once or twice every three months from January to October.

We have now established many such tracks: for *Agrotis ypsilon*, *Plusia gamma*, *Nomophila noctuella*, *Utetheisa pulchella*, from beyond Spain, probably Morocco; the hawk moth, *Hippotion celerio*, from the Azores, *Itame brunneata*



FLIGHTS	DATES
1	30-31 AUGUST 1948
2	12-13 JULY 1949
3	5-6 SEPTEMBER 1954
4	3-4 JULY 1959
5	2 OCT 3 OCT 1961
6	5-6 JULY 1963

FLIGHTS	DATES
1	16-18 FEBRUARY 1950
2	16-18 FEBRUARY 1950
3	25-29 FEBRUARY 1952
4	22-24 MARCH 1955
5	18-22 MARCH 1957
6	12-15 FEBRUARY 1958

FIG. 2. *Spodoptera (Laphygma) exigua.* Back-tracks of wind from the United Kingdom to probable sources in a. Spain, b. Morocco, Madeira.

Spodoptera (Laphygma) exigua. *Windbanen langs de waarschijnlijke gebieden van herkomst in a. Spanje, b. Marokko en Madeira, naar het Verenigde Koninkrijk.*

From HURST, 1965.

from Westphalia and the continental form of *Eurois occulta* from Scandinavia. Single specimens of a North American moth, *Phytometra biloba*, were captured in 1954 and 1958, coincident with winds blowing across the Atlantic, and in 1958, with the arrival in the same area of North American birds, namely the Baltimore Oriole and the Northern Water-thrush (FRENCH & HURST, unpublished; HURST, 1964, 1965).

Thus the area from about Iceland and Finland to North Africa and possibly the eastern Mediterranean is continually traversed by many species in one flight, and this can be detected even with very few insects, provided the recording system is continuous and the insects invade an area where there are no adults of the same species. Tracking insects becomes extremely difficult within an area of continuous breeding. This difficulty is well illustrated by aphids and, though we know more about their flight than for almost any other insect except locusts, paradoxically we know very little about their spread over long distances.

THE LONG-DISTANCE DISPERSAL OF APHIDS

Our notions about the distances aphids fly rest on extremely few observations of distances flown, backed by what can be inferred from their flight behaviour and physiology and their vertical distribution. In Europe the best record of a long-distance flight is still that of the Spruce aphid, *Cinara picea*, found on the

Spitzbergen Ice Cap 1300 km from the nearest land at the Kola Peninsula and carried, it seems, by gale-force winds in 12–24 hr (ELTON, 1925). The few other well-established records of long-distance flights are as follows: *Tuberolachnus salignus* was found on the snowfield 180 km north of Spitzbergen by PARRY in 1827 (HILLE RIS LAMBERS, 1947); many different species were caught 200–250 km out over the North Sea (HARDY & MILNE, 1937); BÖRNER (1922) recorded aphids annually invading Heligoland 55 km from the mainland. HILLE RIS LAMBERS (1957) found a single specimen of *Baizongia pistaciae* in Holland from a *Pistacia* gall, which apparently involved a flight of the order of at least 900 km; for provisional back-tracks show a track possibly along the Adriatic and thence across Europe. *Pistacia* occurs in Jugoslavia and abundantly in the south of France. Good examples occur in other parts of the world. *Aphis craccivora* invades, sometimes massively, the coastal region near Sydney in S. Australia, on NW winds from semi-desert breeding areas 320–480 km away, and beyond a mountain range 600–1500 m high. One such journey was estimated to take less than 24 hr (probably 10–15 hr) on winds of about 20 knots at about 900 m (B. JOHNSON, 1957). Populations of the grain aphid *Schizaphis graminum* annually invade the northern regions of the United States from the south and north central States travelling between 320 and 1600 km (WADLEY, 1931; MEDLER & SMITH, 1960), and DICKSON (1959) recorded aphids in the California deserts over 130 km from their breeding sites. These remarkably few observations are supplemented by much knowledge of potential flight duration found in the laboratory for two species, *Aphis fabae* and *Myzus persicae*. There are also innumerable records to show that mass flights of aphids occur in many parts of the world; also there is much information on the distribution of aphids in the air up to several hundreds of metres. Untold millions of these insects are known to fly and drift continually over land and sea, but it is difficult to know how far such populations travel on different occasions. No specific long-distance flights have been satisfactorily associated with adequate knowledge of flight potentials by the particular aphids concerned.

MECHANISMS OF APHID DISPLACEMENT AND INFERENCES ABOUT DISTANCES FLOWN

The intrinsic duration of flight of aphids depends on the amount of stored fat that can be used as fuel. Wild individuals of *A. fabae* can make non-stop, tethered flights for 6–12 hours until their available fuel is exhausted. Approximately the first 45 mins of flight is made with glycogen as fuel, before the fat is used (COCKBAIN, 1961a).

In free flight in nature, however, aphids rarely fly till fuel is exhausted, at least in single flights, and the duration of single flights is determined not by fuel but by the changing "mood" which is a neurophysiological effect. Flown freely in a flight chamber, laboratory-bred *A. fabae* fly, on average, for about 80 mins, and at most about 200 mins, before alighting. With successive alightings the flights become shorter and shorter totalling, on average, about 105 mins (KENNEDY & BOOTH, 1963a, b). Similarly *M. persicae* flew 40–70 mins in single flights (LEGGE, 1962). Most flights in the field are also relatively short, compared with the potential duration; this is shown by changes in the vertical distribution of the mixture of aphid species in the air, at least up to 300 m and probably to about 1500 m, though little is known about the distribution and flight above this height.

In northern Europe flight periodicity near a breeding source typically has two waves, one in the morning and one in the afternoon, as new aphids take-off to migrate. These aphids are positively phototactic; this with convection, takes them high into the air with a gradually diminishing density whose logarithm is approximately linearly related to the logarithm of the height. Aphids do not usually fly at night and so flight duration is usually limited also by the period of daylight. By integrating the vertical profile, the total number of aphids in the air to any height can be calculated.

If the duration of flight averages 1 hr (the trapping period) then the curves for density at ground level, near sources, and the integrated total would coincide in time. If most flights lasted much longer, the curve for the integrated total would be displaced correspondingly and prolonged throughout the day. So far this has not been observed and the two curves usually coincide fairly well (Fig. 3) indicating that the average duration of flight is of the order of 1–2 hr though a small proportion of aphids may fly from the start to the finish of the flight period (JOHNSON, 1957). Indeed it is possible that during the shorter flights of 1–2 hr the fat is scarcely used, much of the flight probably being made on the small store of glycogen.

Such average flights on calm days would take the insects no more than a kilometer. On warm, breezy, sunny days winds of about 40 km/hr at 600–1200 m would take aphids up to about 80 km or a small proportion perhaps more than twice that distance or even further. Two questions therefore arise. How often can any individual do this? How are journeys of 300–1600 km made?

Flight chamber experiments show that with successive flights on one day, total duration rarely reached 2 hr (KENNEDY & BOOTH, 1963a, b) and COCKBAIN, GIBBS & HEATHCOTE (1963) found that 1 hr of tethered flight caused 100% of *A. fabae* to settle permanently on beans, but only 18% on sugar beet, till flight muscles autolysed. With *M. persicae* 65–90% stayed for 1 hr and none permanently. After a flight of 8–12 hrs most of the *A. fabae* could not refuel before muscle autolysis stopped all flight, but 28% took off again on the second day after flying about 6 hr the day before and then the longest second flight was

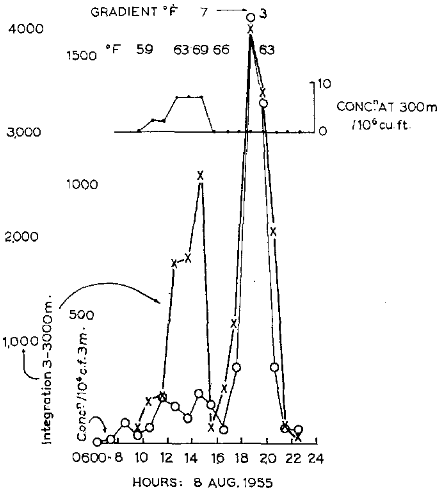


FIG. 3. Flight curves for the mixture of aphid species in the air at 3 m, 300 m and the integrated curve for total aphids between 3 and 3000 m.
Curves at 3 m and integrated total coincide for an inversion in the afternoon kept aphids below 300 m.

Vluchtkrommen voor de bladluizen (de soorten niet gespecificeerd) op 3 m, 300 m en voor alle bladluizen tussen 3 en 3000 m.
De krommen van 3 m en van alle bladluizen tussen 3 en 3000 m stemmen met elkaar overeen. Een inversie in de namiddag hield de bladluizen beneden 300 m.

After C. G. JOHNSON, 1957.

4.3 hr (Cockbain, 1961b). Flight duration in relation to settling has, so far, not been closely studied for any other species of aphids and our detailed knowledge is about these two only, supplemented by changes in vertical distribution of all the aphids in the air on certain days.

Thus there is uncertainty about how many individuals of different species make long flights repeatedly, but the total duration seems limited by the inability to refuel before the flight muscles autolyse. The maximum possible duration of one or a total of several flights would, therefore, seem to be about 12 hr (16 hr has been recorded for *M. persicae* by Cockbain (in lit.)), or the equivalent of a long summer day in temperate latitudes. Winds of 40 km/hr might thus take the small proportion of exceptional aphids 600 km, which is rather more than the observed distance flown by *A. craccivora* in New South Wales; even the 1300 km travelled to Spitzbergen comes within the expected limit for flight duration, for the journey was estimated to take about 12 hr, winds being exceptionnally strong, and there would be no darkness to inhibit flight in the northern latitudes. No doubt these aphids were the small proportion at the limit of flight

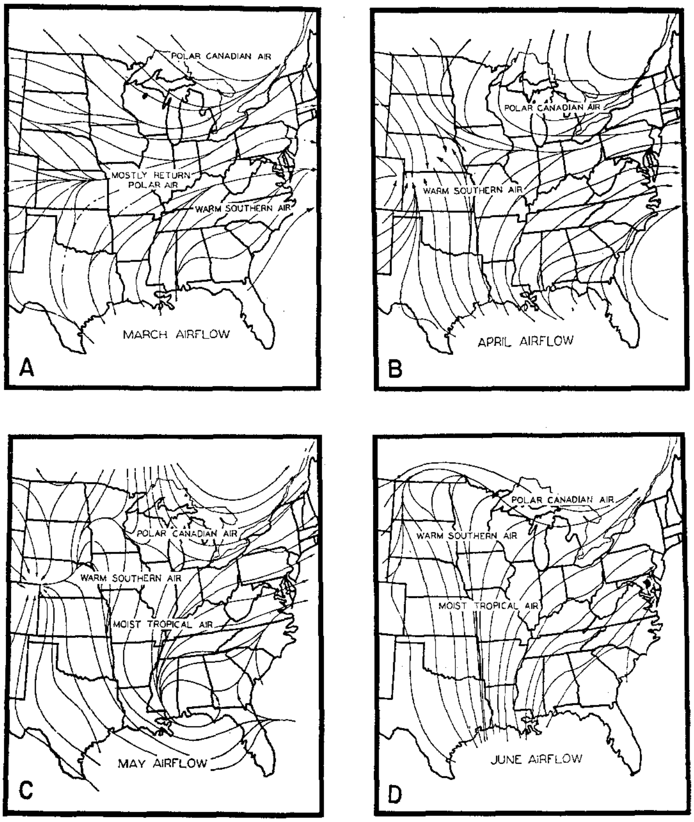


Fig. 4. Average surface resultant winds in the Central United States, March to June.
Gemiddelde windrichtingen van maart tot juni in het midden van de Verenigde Staten van Noord-Amerika.
From Medler, 1962.

duration; for the aphids on the snow there averaged about 600 per sq. km, and could have been produced from the equivalent of only a single tree in a large forest. It can only be imagined what numbers were scattered in the sea and might have been scattered over land.

In the U.S.A. the situation seems to be radically different from that in Europe. There, the synoptic weather follows a more definite pattern over a very large area for fairly long periods and prevailing winds have definite seasonal patterns (Fig. 4). In the southern and central States there are also the so-called low-level jet streams that blow from time to time. These are laminar-flow winds at between 300 m and 1000 m blowing at 90–110 km/hr and, from one place to another, lasting perhaps for a total of 2–3 days. Associated particularly with nocturnal inversions these jet-streams occur when the air nearer the ground is relatively calm (BLACKADAR, 1957), and it is supposed that *Schizaphis graminum* might travel in them, accomplishing 800 km in 10 hr and 1600 km perhaps in about a day.

Most of the above-mentioned examples are for extreme distances flown by a small proportion of a population. Such insects presumably fly till fuel is exhausted, perhaps because they are high in the air or, if over the sea, perhaps lack the change in phototaxis that brings them close to green vegetation and precedes normal landing. They can be regarded at present as the tail-ends of dispersing populations of which many thousands or millions of insects are scattered across the intervening territory; but there is no information to measure this scatter. Moreover, the extreme calculated distances for aphids may still be too small. For example, desert locusts, *Schistocerca gregaria,* sometimes land in England from North Africa having flown for about 60 hr, or about three times the duration of tethered flights in the laboratory by individuals with maximum fuel-loads (WEIS-FOGH, 1952a, b). It seems that nature is better than scientists at providing examples of extreme performances for she has so many millions of insects at her disposal.

PASSIVE TRANSPORT

At the end of the flight insects might be blown passively after all their fuel is used and wings cease to beat. This cannot, however, explain either the transport of *Spodoptera* by wind from Africa to England, or transport in low-level jet-streams, for these winds lack the upward component needed to keep non-flying insects aloft. In turbulent air and at high altitudes, however, small insects like thrips (or even aphids) might be kept airborne for a long time after actual flight had ceased. Dust particles up to 0.1 mm diameter fall at 0.65 m/sec (CHEPIL, 1951) and can be carried a long way, and the falling speed of an inert aphid in still air is only about 1.7 m/sec (TAYLOR, 1959). TAYLOR (1965) points out that the vertical density gradient for aphids and dust can be very similar and WAGGONER & BINGHAM (1961) found that the logarithm of the amount of loess deposited per unit area is linearly related to the logarithm of distance travelled up to about 100 km. At present one may guess that such passive transport occurs only with a very small proportion of any population and is probably of little importance for very long-distance displacement (at least with large insects like moths, and especially over the sea). Nevertheless, a theoretical consideration of the dispersal of small inert insects in similar terms to the turbulent diffusion of small inert particles is needed, and might be done when more is known of the build-up and decay of vertical density profiles of insects in relation to weather.

LONG DISTANCE TRANSPORT OF VIRUSES

Many important viruses, like their vectors, are widespread, and there seem to to be few data on their long-distance transport in relation to the movements of vectors. Only for one virus (Aster yellows), it seems, has such transport been proven and documented. It is difficult to distinguish natural from artificial spread; also alternative hosts of viruses are often widespread and many infected plants may be symptomless or their symptoms assigned to other causes. The picture of international virus spread is very blurred.

There are few viruses whose spread from a defined source has been traced and none, I think, associated closely with corresponding movements of the vectors. Phony disease of peach, first seen in an orchard in Georgia, U.S.A., in the 1890s, later spread rapidly and in 1933 it had destroyed over a million trees in Georgia alone and invaded at least 12 other States (HUTCHINS, 1933), but its relation to the movements of its cicadellid vectors (TURNER, 1949; TURNER & POLLARD, 1955) seems to be obscure. Maize dwarf mosaic, first recognised in the U.S.A. only in 1963 was, however, soon widespread in Ohio though mostly in the south; but at the same time it was reported from Arkansas and in 1965 from California, Illinois, Iowa and Virginia and in 1966 in Kansas (ELLET, JANSON & WILLIAMS, 1965; SILL, 1966). This virus is transmitted by the aphid *Rhopalosiphon maidis*, and has many alternative hosts among *Sorghum* species; there seems little chance of telling how it arose or spread. Subterranean clover stunt, a virus disease in *Trifolium subterraneum* in New South Wales, with *A. craccivora* and *M. persicae* as vectors, was detected in 1955 and by 1957 more than 20 million acres were infected. The disease was widespread when it appeared and there seems to be no knowledge of its spread (GRYLLS & BUTLER, 1959).

Potato veinal necrosis (a strain of Potato virus Y) increased in ratio to virus Y from 0.1 in 1953 to equal proportions in different places in W. Germany from 1953 to 1957 and later spread to Holland, Belgium, England and Finland (ROSS, 1959) but it has not been associated with movements of vectors. The rapid spread of Sugar beet leaf crinkle in W. Germany from a small source in 1945, was correlated with the local abundance of the vector, *Piesma quadrata*, but not it seems, with its flight (LASSACK, 1956; OSSIANILSSON, 1966).

The difficulties of associating the transport of a virus with movements of the vector is illustrated by events in England in 1947. Not only was *M. persicae* more abundant then than it has ever been since, but it was also associated with an unusually large spread of Potato leaf roll virus. At Cardington enormous numbers of *M. persicae* were suddenly trapped at six heights up to 650 m on July 15, 29 and 30. Analysis for July 15 showed winds up to 650 m were mainly from the east, and back-tracks suggest that had the insects become airborne during the morning in the Pas de Calais/south Belgium area (where there was convection to 1300 m) they could have been carried WNW in time to be trapped in our nets at Cardington, taking about 8–16 hr to do a journey of 200–320 km at 650 m. This was the only time during that part of July when this could have happened and it coincided with a sudden and enormous catch. On 28 and 30 July much the same thing happened again, the catch on 30 July being exceptionally large: tolerable back-tracks were again obtained to the continent where the weather was hot (JOHNSON, HURST, unpublished). These events coincided also with a sudden increase in *M. persicae* on potatoes in the east and central midlands of England where there were only small populations previously. The migrants apparently introduced leaf-roll into potato crops, where it was randomly distributed without apparent gradients, suggesting it came from a far distant source, (BROADBENT, 1948, 1950; BROADBENT & TINSLEY, 1951; BROADBENT *et al.*, 1952; BROADBENT & HEATHCOTE, 1961). Nevertheless, the insects and virus may have come from early potatoes in east England and its origin cannot now be determined.

The migration of *Schizaphis graminum* up through the states of Texas and Oklahoma into Minnesota and Wisconsin is well known and, as already mentioned, it is possible that a sequence of relatively short, northerly migrations of 50 to 100 miles by successive generations are supplemented by long-distance flights of several hundred miles. *S. graminum* along with several other species is also an efficient vector of Barley yellow-dwarf virus. The evidence suggests that some of the early outbreaks of Barley yellow dwarf in the northern states may be the direct result of such long-range flights of *S. graminum*. However, this is by no means proven and the evidence is largely circumstantial.

For example, BRUEHL (1961) states "An evaluation of these major greenbug and corn-leaf aphid migrations in relation to BYD[1] is difficult at present". Some of the reasons which make this so are because *S. graminum* is not always a vector in some states and because the toxic effects of the aphids' feeding are often confused with symptoms of Barley yellow dwarf and this makes evaluation of the virus disease difficult. It is also often difficult to assess the relative importance of immigrant species of aphids (such as *S. graminum*), compared with that of other vectors that overwinter in the northern states and are already there to distribute virus from local graminaceous plants.

Notable insect virus-vectors that migrate long distances in North America, are the leafhoppers, *Macrosteles fascifrons* transmitting Aster yellows virus to many kinds of plants and crops, and *Circulifer tenellus*, the vector of Curly top virus of sugar beet. Both are believed to fly annually for over a thousand miles into the northern states of the Union from breeding places in Louisiana and Texas and in Texas and New Mexico respectively. *M. fascifrons*, at least, even reaches Ontario, Manitoba and Alberta in May and June by journeys of 2–3 days or even less, though it is still uncertain how many of the migrants invading the northern states of the Union or the southern states of Canada come from breeding grounds in the deep south or from places further north (CHIYKOWSKI & CHAPMAN, 1953; WESTDAL *et al.*, 1961; WALLIS, 1961; MEDLER, 1962). The spring migrants of *M. fascifrons* flying into Winnipeg from 1954 to 1965 have been related to the synoptic weather by NICHIPORICK (1965) who showed that they probably originated from sources up to 900 miles away, especially from S. Dakota, Kansas and Nebraska making non-stop flights perhaps of 20–30 hours.

Quantitative data about the long-distance transport of these leafhoppers and of the viruses they carry are not easy to find. The results of many years of cooperative study in the U.S.A. and Canada seem never to have been published adequately or in a way that makes them generally available. Those which have been

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[1] This abbreviation refers to Barley yellow dwarf.

published are scattered, or in obscure journals and it would be a major task to find and collate them. Summary papers are often ambiguous; thus, MEDLER (1962) and CHIYKOWSKI & CHAPMAN (1953) state that migrant *M. fascifrons* entering Wisconsin from the south were viruliferous, but gave no data and did not discuss the possibility that the virus had been acquired locally. WESTDAL *et al* (1961) mention the possibility that viruliferous migrants in Manitoba late in June could have become infected after they arrived but imply that those arriving earlier were infected on entry; in most years the proportion of infected immigrants of *M. fascifrons* is small but that in 1957, when an explosive and widespread outbreak of Aster yellows occurred, 14% of the incoming migrants were infected (SACKSTON, 1958).

The strain of Aster yellows in Saskatchewan and Manitoba, differs from that in Alberta and the migrant leafhoppers carrying it may also come from a different source (SACKSTON, 1959). The spread of Sugar beet curly top into the eastern states of the Union from the southern states, often ahead of detectable migrants, is discussed by DOUGLASS (1954), GIDDINGS (1954), SCHNEIDER (1959) and HEGGESTAD & MOORE (1959). But the evidence relating leafhopper migrations to virus spread seems mainly circumstantial rather than direct. Leafhoppers can remain infective for life and can migrate for periods of several days. There is no doubt that they carry Aster yellows and Beet curly top virus rapidly over hundreds of miles. But most of the data seem to be available only to local specialists.

BJORLING & MOLLERSTROM (1960) (in OSSIANILSSON, 1966) describe how in 1959 in southern Sweden clamps and seed crops were almost free from Sugar beet yellows but the root crop suffered greatly in August and included two continental strains of the virus hitherto not seen in Sweden. Gotland and Finland also received Sugar beet yellows for the first time. Large swarms of winged aphids had appeared in July, seemingly from the European Continent in steady, south winds of 18–36 km/hr. According to BONNEMAISON (1958) the relative freedom of the maritime areas of north and north-west France (compared with central and eastern areas) from potato virus diseases is because the winds are most frequent from the west during spring and summer. RIBBANDS (1963) quotes the relative freedom of north and north-west England from Sugar beet yellows compared with East Anglia about 200 km to the south-south-east, as a reassuring fact indicating the improbability of frequent invasions of England from the European Continent, which is about the same distance away.

There is also the problem of persistence of infectivity by insect vectors during long flights. The persistence of virus in vectors has been studied mostly with apterae, but recent work shows that starving apterae and flying alatae lose infectivity at about the same rate (COCKBAIN, GIBBS & HEATHCOTE, 1963; COCKBAIN & HEATHCOTE, 1965). Thus aphids with the persistent Beet mild yellows virus and Bean leaf roll virus remain infective for many days and do not lose infectivity during a flight or starvation of several hours. Alate *M. persicae* infected with semi-persistent Beet yellows virus, and Cauliflower mosaic virus showed no significant lessening of infectivity after tethered flights of up to 4 hr. Even with non-persistent Beet mosaic virus, Potato virus Y, Pea mosaic virus and Cabbage black ring spot virus, though aphids on plants remained infective often less than 1 hr, flying or starving alatae were infective for much longer. Some *M. persicae* were infective with Beet mosaic virus after a 4-hr flight and possibly after 6 hr which is the time for starving apterae. Thus it seems these non-persistent viruses could be transported at least 60 km and perhaps for two or three times that distance on a non-stop flight.

THE COLORADO BEETLE, LEPTINOTARSA DECEMLINEATA, AN EXAMPLE OF SOME OTHER PROBLEMS

The Colorado beetle illustrates several points of general interest in the international spread of pests, especially the factors that cause the prolonged flights which are so dangerous internationally. Like many other pests it contrasts with most aphids in that large populations may be produced that sometimes migrate and sometimes do not – the so-called mystery of migration. It contrasts with aphids also in that much more is known about its international spread (which occurred from well-defined sources) though very little is known about its flight. In contrast to aphids it seems to be a poor flier; nevertheless, it has spread rapidly and successfully to many countries.

Back in 1906, TOWER's monumental paper described the spread of the Colorado beetle across the U.S.A. This insect is not usually accepted as part of the "aerial plankton", yet in the same way that winds carried the grain aphid, *Schizaphis graminum*, the sugar beet leaf hoppers and other pests up through the southern, central and eastern States so they also helped to spread the Colorado beetle. With the Colorado beetle progress with the prevailing wind towards the east coast was rapid, but it spread also against the direction of the prevailing winds down the Mississippi Valley though much more slowly, contrasting with the journeys of the grain aphids and leaf hoppers which go in the opposite direction (Fig. 5). This does not mean that Colorado beetles were not also blown north up the Mississippi watershed, but that others also went south. This progress against the pattern of prevailing winds, but not necessarily against the wind itself, illustrates the dangers of relying too much on prevailing winds to explain spread, and neglecting the effects of local variations in wind-speed and direction. In this respect such generalized diagrams as in Fig. 4 are of little use.

The Colorado beetle took the years from 1860 to 1880 to travel 2000 km

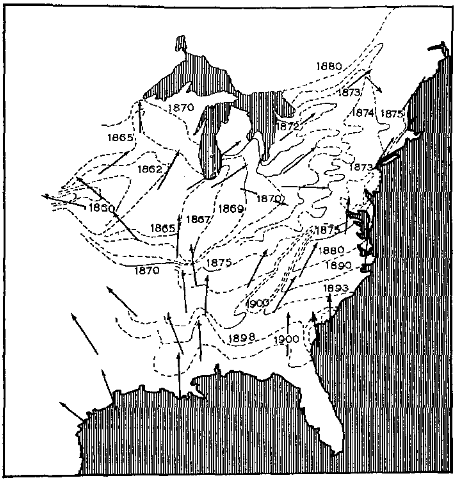


FIG. 5. Spread of Colorado beetle in North America.
Dotted lines denote spread. Arrows denote prevailing uinds.
Verspreiding van de Coloradokever in Noord-Amerika.
After TOWER, 1906.

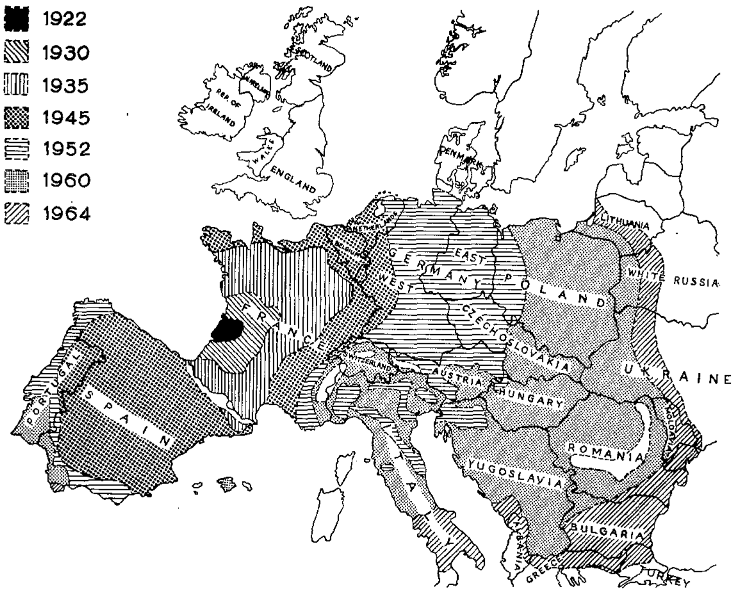


FIG. 6. Spread of the Colorado beetle in Europe. Data from Reports of European and Mediterranean Plant Protection Organisation.

Verspreiding van de Coloradokever in Europa. Gegevens van E & MPPO.

across the U.S.A. averaging about 100 km a year. In Europe, where winds and weather are much more changeable, it took 40 years to go about the same distance and achieve its present distribution; it averaged about 50 km per year (Fig. 6), but in places spread much faster than this. In 1954 in Poland it extended 120–140 km, and in the worst year, 1950, about 350 km; in central Spain in 1950 it travelled hundreds of kilometers, and in both countries mostly by natural spread (WEGOREK, 1959; EPPO, 1951). Natural spread can, however, be closely associated with artificial transport. DE WILDE (1962) mentions that dispersal flights may be directed towards docks and ships and that "one-sided attention usually paid to agricultural imports seems to need revision". This is strikingly illustrated in the transport of beetles into the United Kingdom on ships between 1947 and 1957 (JACOB & JANSON, 1958).

The beetles on vegetable produce began to be intercepted in January, reached a maximum in March and April and declined throughout the autumn. By contrast, the number of beetles not associated with vegetables but crossing the Channel mainly in the ferry boats, increased very suddenly to a larger maximum in June (Fig. 7); the invasions coincided with post-diapause flights and lasted a shorter time. Most "ship" beetles were intercepted in 1948 (279 out of a 487 in 5 years) on 18 May and in early June, following periods of very hot weather in northern France, which would favour flight. Similarly large invasions occurred in July and August, 1953–57. Flight is, therefore, extremely important even where spread is helped by other agencies.

Comparatively little work has been done on the flight of the Colorado beetle, except, it seems, mainly on temperature thresholds for flight (LE BERRE, 1950,

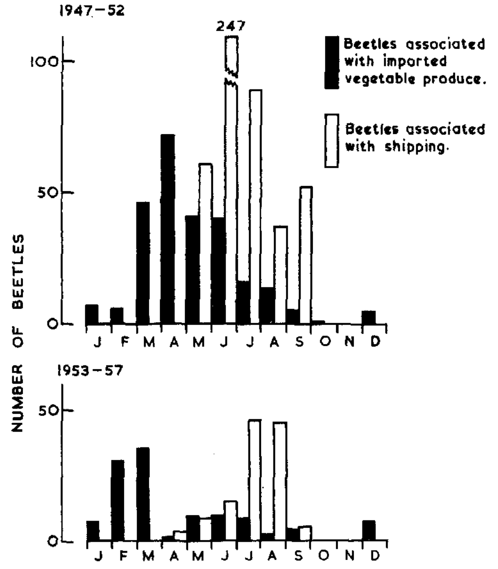


FIG. 7. Numbers of Colorado beetle invading the United Kingdom on shipping, associated and not associated with plant material.

Aantallen Coloradokevers die het Verenigde Koninkrijk per schip, al of niet met plantenmateriaal, binnenkwamen.

From JACOB & JANSON, 1958.

1952, 1962). Entomologists have tended to take flight and its variations for granted with insects that have wings, much as walking is taken for granted for animals that have legs. The reasons why flight performance varies so much have not been closely analysed.

Colorado beetles are considered to be sluggish fliers and they are blown off-course by winds of 10–14 km/hr (TOWER, 1906); yet they have been caught 20 km out to sea (EPPO, 1951; E & MPPO, 1957), and MAYNÉ (1939) reported beetles travelling at least 150 km on strong winds though it is uncertain whether by one or several flights. There is also controversy about whether flights occur before and after diapause. Conditions of warmth and intense insolation are needed to warm the body to its flight threshold (LE BERRE, 1950, 1952, 1962) and this can be associated with storms that are known to transport beetles, as reported in Belgium, Germany (EPPO, 1951; E & MPPO 1956), Poland (E & MPPO, 1958; WEGOREK, 1959) and elsewhere. The beetles may be swept to high altitudes, for they have been caught on mountains up to 2000 m (E & MPPO, 1956; WEGOREK, 1959) and many species of Chrysomelidae have been caught up to 300 m and some up to 1500 m in the air (GLICK, 1939).

As with other migrants that spread long distances *L. decemlineata* is, no doubt most affected by wind when flights are prolonged. Prolongation of flight, and the physiological reasons for it are, therefore, very important in the long-distance spread of all pests. The position with *L. decemlineata* briefly summed up by WEGOREK (1959), applies to all long-distance migrant insects. He writes "The reasons for the macromigrations have hardly been investigated. Attempts to explain the macromigrations on the basis of the physiology of the beetles failed on account, perhaps, of the paucity of the material investigated and the choice of unsuitable physiological indicators. It seems beyond question that climatic conditions such as temperature and wind play an important role with mass flights of beetles over great distances. Nevertheless the physiological conditions which predispose the beetles to take wing cannot be disregarded. Research into this aspect of the problem seems to be necessary".

New hypotheses of insect migration suggest a possible way to study the physiology of migration and it is appropriate to see how they relate to *Leptinotarsa decemlineata.* At the same time this presents the possible physiological basis of long-distance flight (JOHNSON, 1963, 1966).

It was commonly thought that insects migrate in response to currently adverse conditions, much as a man might leave an unfavourable place. It was also thought that insects are blown by wind merely as an accident. However, recent work especially with aphids and locusts, but now also with other insects, shows that migratory behaviour is often geared to the life cycle so that travel on the wind is a regular event and part of the adaptive system enabling insect populations to change habitats periodically. Locusts, for example, travel on convergent wind systems across the Sahara so that they inevitably end up in a zone where opposing winds meet and hence into a rainy area where survival is ensured (e.g. RAINEY, 1951).

It is an advantage for all insects living in temporary habitats (e.g. annual crops) to move periodically, as populations, to other temporary breeding places as a regular, inborn process, not as a behavioural response to currently adverse factors in the environment such as overcrowding or too little food. Insects also survive adverse seasons by migrating elsewhere as a regular process often on seasonal winds, or by dormancy (diapause) or by both. Indeed migration and diapause are often associated and, it seems, both are symptoms of the same endocrine deficiency syndrome. Diapause in the Colorado beetle has been studied intensively with this approach by DE WILDE (1962) and his colleagues. But so far migratory flight has not been closely studied as the concomitant symptom it seems to be in this insect. The Colorado beetle seems admirable for such a study.

Three main factors affect normal flight. The body (as affected by ambient air temperature or by insolation) must be warm enough to allow the flight muscles to work efficiently, there must be enough fuel stored as fat or carbohydrate, and the "mood" must predispose the insect to fly rather than to rest (KENNEDY & BOOTH, 1963a, b). Migratory flight is merely a particularly prolonged flight which, it seems, is ontogenetically controlled and adapted to occur at a certain stage in adult development. It is the factor causing prolonged flight that is important in long-distance displacement, rather than those causing takeoff.

The two first factors, namely the temperature thresholds for take-off and the accumulation of fuel in the form of fat and glycogen have been studied for the Colorado beetle (LE BERRE, 1962; GRISON & LE BERRE, 1953), but not flight duration and the factors that encourage prolonged rather than short flight.

A thorough survey of the literature on insect migration shows that the females of most migratory insects (there are exceptions) make their longest flights during the pre-oviposition period before they become gravid. Indeed, migration often ceases when the ovaries are ripe, and the capacity of many species to migrate seems to be associated with varying degrees of sexual immaturity during the pre-oviposition period. This is not merely a matter of fuel but of the relatively high neural response threshold for settling compared with the relatively low threshold for flight. Factors that normally induce settling therefore have no effect and this is associated with sexual immaturity in females and probably affected by endocrines (Johnson, 1963, 1966). Colorado beetles, like many other insects, become sluggish when gravid; Tower (1906) thought this was possibly caused by their increased weight and Le Berre (1962) suggested that the flight muscles are compressed by the ovaries, though this is an unlikely cause. Tower was the first to stress the importance of the pre-reproductive period in insects and considered that most flight was made by Colorado beetle females when they had unripe ovaries, and that this was why the autumn generation in the U.S.A. made most migration before diapause and migrated more than the first summer brood. I suggest that the duration of tethered flights at different stages during the pre-oviposition period would well repay study, not only for its importance to this particular pest but because of its general significance.

The length of the pre-oviposition period is governed partly by temperature, partly by feeding, partly by day-length; all of these control ovary development. It is interesting therefore to speculate about how it might affect long-distance flights.

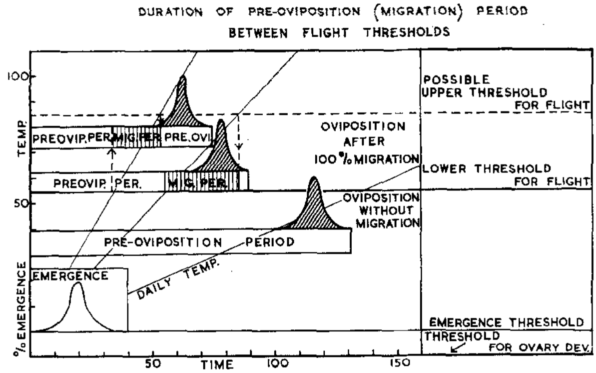


Fig. 8. Hypothetical relation between duration of pre-oviposition period and migration between upper and lower flight thresholds.

Hypothetisch verband tussen de duur van de preovipositieperiode en de migratie tussen de bovenste en de benedenste temperatuurslimiet voor de vlucht.

Two aspects must be distinguished: 1. the duration and frequency of flight by individual insects; 2. the duration of the pre-oviposition period in relation to temperature. If the second is known, it should be easy to calculate (by thermal summation) the pre-oviposition period of any brood, within which individual flights occur, for a particular temperature regime.

Assuming only temperature to be the limiting factor, that food is plentiful and daylight controls only the onset of ovary development, then it is to be expected that the migratory period for the brood, and probably the duration of flight of individuals, would be controlled partly by a gradual maturation of ovaries and partly by a triggering of flight when body temperature rises above the threshold for flight. This is illustrated very simply and hypothetically in Fig. 8, though it is impossible to do more than indicate possibilities with the few existing data. If the brood emerges from hibernation with a proportion of insects already gravid, or partly gravid, the duration of the migratory period would not be curtailed, but probably fewer would migrate a long distance.

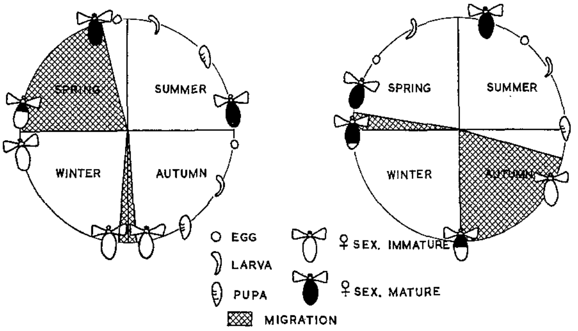
If the above hypothesis is valid it may also explain why some broods migrate and others do not, or why migration occurs after diapause in northern Europe and before diapause in other parts of Europe and in the U.S.A. (Tower, 1906; de Wilde, 1962). For, whether large numbers migrate actively for a long dis-

FIG. 9. Hypothetical relation between amount of seasonal migration, diapause and ovary development.

The left-hand diagram supposes that insects emerge from hibernation with relatively undeveloped ovaries and therefore spend a long period in the spring migrating; adults of the autumn generation are overtaken by winter before they can migrate very far. The right-hand diagram supposes that adults of the autumn generation emerge early and immature, and spend a long time migrating before ovaries become well-developed; after emergence in the spring from hibernation ovary-development is rapid, leaving little time for migration.

Hypothetisch verband tussen de omvang van de seizoenmigratie, de diapauze en de ontwikkeling van de ovaria.

In het linkse diagram wordt het geval weergegeven van insekten die vlak na de overwintering betrekkelijk onontwikkelde ovaria hebben, waardoor de voorjaarsmigratie over een lange periode plaatsvindt; imagines van de herfstgeneratie worden door de winter verrast zodat ze niet ver kunnen migreren. In het rechtse diagram wordt het geval aangeduid van insekten waarvan de imagines in de herfst vroegtijdig verschijnen met nog niet ontwikkelde ovaria, welke een lange tijd voor hun ontwikkeling nodig hebben (gedurende deze tijd vindt migratie plaats); na de overwintering ontwikkelen de ovaria zich snel, zodat er weinig tijd voor de migratie in het voorjaar overblijft.



tance before or after hibernation might be linked with the state of the ovaries when hibernation began and when it ended (Fig. 9).

These are tentative suggestions; they are undoubtedly crude and the process will be complicated particularly by feeding, temperature, light, the proportion of different-aged beetles in any brood and the time spent above the temperature threshold. But a study of how these factors are combined along the lines indicated seems to be the only reasonable hypothesis at present on which to investigate the occurrence of various amounts of migration at different seasons and, therefore, of the danger of international spread. It is of general significance.

CONCLUSIONS

Examples given show how the direction and distances of long flights are determined by the synoptic weather and by the flight duration of the insects, both with small, weak fliers and large, strong ones. Many insects, including pests previously thought to fly only locally near crops, are now known to travel high in the air as a normal habit. This happens, not merely occasionally to a few exceptional individuals, but to large populations continually. It is often an adaptive, not an accidental process, for many insects are positively phototactic at take-off and this enhances wind-borne transport: much of the aerial "plankton" is there actively and has not been "picked up" from the ground or vegetation by strong winds.

Attention has been focused on long journeys made in single flights. But not all international spread is done this way, for some insects can make many long flights before they finish migrating. For example the frit fly *(Oscinella frit)*, like aphids, is positively phototactic at take-off and on a warm summer day the mean height of flight of populations tends to be above 300 m. Like aphids the duration of single flights is, on average, of the order of an hour (JOHNSON *et al.*, 1962). Unlike aphids, however, frit fly can continue to make such flights, at least when tethered, for about two weeks and can also probably do so in nature (SOUTHWOOD *et al.*, 1961; RYGG, 1966). Distances traversed could then be very great though nothing is known about them.

Drosophila behaves like frit-fly in tethered flight though its crepuscular flight in nature tends to keep it fairly close to the habitat (WILLIAMS *et al.*, 1963). But it would be interesting to know how fruit flies, especially the Trypetidae behave, for these are day-fliers, travel on the wind and have a long pre-oviposition period of many days (CHRISTENSON & FOOTE, 1960) during which much migration might be expected. We know little about the flight of these important pests. For example the Mediterranean fruit fly, *Ceratitis capitata*, is thought to avoid strong winds by keeping shelter, which is contrary to other observations, but this paradox existed also for aphids and frit fly until it was shown that at certain times in their life they travel on the wind adaptively. The long-distance spread of *Ceratitis capitata* in Europe is generally considered to be caused artificially, but the chances of its natural spread may not yet be fully appreciated. The fly dies out annually in northern Europe (FERON, 1963), though not in more southerly parts (e.g. Austria; BOHM, 1963). GRUNDBERG (1963) called attention to the spread of *Dacus (Strumeta) tyroni*, the Queensland fruit fly which, in less than 100 years, spread naturally and became established over 2000 km from its tropical source in Queensland south to New South Wales and Victoria, apparently becoming progressively adapted to the cooler climate. It has been suggested that *Ceratitis capitata* might develop cold-resistant strains in Europe and that these might again spread south where such strains, unlike the present ones, might remain active all the year round. The capacity of fruit flies to spread naturally might be better understood by studying flight durations and take-off behaviour, than by the radio-active marking and recovery only over short distances which seems to be the fashion.

There is concern about the possibility of Tristeza disease becoming established in Mediterranean countries and the possibility of introducing its principal aphid vector, *Toxoptera citricidus* into the area, possibly on plant material from Spanish and Portugese overseas territories (REICHERT, 1959). Other aphid vectors exist there, however, and aphids can move a long way on their own power. It seems that it might be easier to keep out infected plants by quarantine than to keep out the vectors.

Increased acreages of barley in many parts of Europe emphasise the importance of cereal viruses and the aphids that transmit them, and the increase in other crops, e.g. sugar beet in Greece focuses attention on the migration of such pests as *Laphygma exigua* across the Mediterranean. A new oil plant *Camilina sativa* introduced into Poland has attracted the beetle *Ceutorrhychus erysimi* from the weed *Capsella bursa-pastoris* and given it pest status. Such changes in breeding tend to increase populations at the source and thus increase the chances of long-distance spread.

What then may be done to study this ever-changing process of the spread of old and new pests? First the concept that a few insects spread a long way only occasionally needs abandoning. Populations over very large areas constantly mix and travel very far. Yet the concept that pest populations need sampling and studying only on a micro- or meso-scale, as if neighbouring fields were the normal limits, is still current, in spite of much international cooperation in reporting pests spreading to different countries. It seems that we need an entirely new approach following the full realisation that large populations are moving over long distances every year.

To monitor the movements of present pests, as well as possible future ones, we need to sample continuously and quantitatively in a standardized way over a very wide area. Continuous sampling is essential, for migrations in any particular direction often last for less than a day and are unpredictable. The most feasible way to do this, at least with the smaller-sized insects and with some of the larger ones, is by sampling the flying population. To do this on a national or international scale may be less difficult than seems at first.

At Rothamsted Dr. L. R. TAYLOR and Mr. FRENCH have developed a system for continuously recording flying insects with suction traps 40-ft high which sample the general (aerial) population; and light traps of standard pattern sample the larger, less common, night-flying insects. We are testing this out on a national scale with six suction traps at different places from Scotland to the south coast of England and light traps all over the country. Our experience, so far, suggests that, over the season, each suction trap indicates the size of the drifting population of aphids, thrips, small Diptera and Coleoptera and other insects with slow flight over a radius of about 90 kilometers. This is so, it seems, because of the rapid and wide-scale mixing and movement of aerial populations. Indeed it is this process that makes it possible to conceive of sampling over such a wide area, with so few traps.

Parallel to this system in Britain, Dr. TAYLOR, in conjunction with Kansas State University, also has a line of similar suction traps from Texas up to the Canadian border, to monitor the movements of the grain aphid *Schizaphis graminum* and possibly other insects. We hope and expect that such relatively few high traps, spread over a long distance, will not merely monitor changes in the size of populations over a very wide area, but also detect movements of populations from place to place, for example when sudden large catches occur in particular places in association with certain winds, or if we learn to distinguish differences between local races of insects, as I think may be possible. These traps also seem to be very sensitive indicators of the early appearance of flying insects and promise to be useful in warning about pests over a wide area. I hope that we shall soon prove the worth of this system and that then, perhaps, it may be extended into Europe.

ACKNOWLEDGEMENTS

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SUMMARY

Insects can travel, by a single flight, over distances ranging from a few metres to more than 3000 km. The distances and directions flown by long-distance migrants are determined mainly by the duration of active flight and the speed and direction of wind, within synoptic weather systems. This is illustrated by back-tracks of wind trajectories associated with the arrival of immigrant insects into Britain from Scandinavia, possibly east Russia, Germany, Morocco, the Azores, Spain and the U.S.A. The long-distance movements of aphids are discussed in the light of records and laboratory and field work on flight and aerial distribution. Difficulties of associating the international spread of insect-borne viruses with movements of vectors are discussed.

As an example of another type of migrant, the Colorado beetle is contrasted with aphids and illustrates some unsolved problems of insect migration especially the relation of prolonged flight duration to sexual development. A hypothesis for the Colorado beetle in general line with recent work on migration is suggested.

The spread of some old pests and diseases in Europe and the possibility of new ones are mentioned, and a system of sampling that might monitor them is described.

SAMENVATTING

Insekten kunnen zich in een niet onderbroken vlucht over afstanden van meer dan 3000 km verplaatsen. De afstand en de richting van de lange-afstandvliegers worden hoofdzakelijk door de duur van de actieve vlucht en de snelheid en de richting van de wind bepaald. Dit wordt duidelijk gemaakt aan het verband tussen het binnenvliegen van insekten in Engeland vanuit Scandinavië en misschien ook vanuit Oost-Rusland, Duitsland, Marokko, de Azoren, Spanje en de Verenigde Staten van Noord-Amerika en de in de bewuste periodes heersende wind.

De lange-afstandsverplaatsingen van bladluizen worden besproken in het licht van waarnemingen elders en van laboratorium- en veldwerk over de vlucht en de verspreiding in de lucht. Moeilijkheden om de internationale verspreiding van door insekten overgebrachte virussen met de verplaatsing van de overbrengers te correleren, worden besproken.

Als voorbeeld van een ander type migrerend insekt wordt de Coloradokever tegenover de bladluizen gesteld. De Coloradokever werpt enkele onopgeloste problemen van insektenmigratie op, in het bijzonder het verband tussen een langdurige vlucht en de geslachtelijke ontwikkeling. Er wordt voor de Coloradokever een hypothese opgesteld in verband met het huidige werk over migratie.

Tenslotte wordt de verspreiding van enkele oude ziekten en plagen in Europa vermeld en de mogelijkheid van het optreden van nieuwe. Er wordt een bemonsteringssysteem beschreven, dat hiertegen tijdig zou kunnen waarschuwen.

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