Long-Range Aerial Dispersal of Cereal Aphids as Virus Vectors in North America [and Discussion]

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Long-range aerial dispersal of cereal aphids as virus vectors in North America

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Cereal aphids are important as direct pests of crops and as virus vectors. Several species, including the corn-leaf aphid (*Rhopalosiphum maidis*) and the green bug (*Schizaphis graminum*), persist and reproduce parthenogenetically throughout the year in the southern areas of the United States. They persist less readily or not at all in the northern states and Canada where winters are cold and these areas are reinvaded annually by migrants from the south, some of which are likely to be viruliferous.

This paper reviews studies on the reinvasion phenomenon including the recent 'Pests and Weather' project in Illinois (1983–1985) in which radar and traps mounted on a helicopter were used to detect cereal aphids in flight at altitudes of up to 1100 m. A new back-tracking procedure, electrophoretic analyses and fuel utilization studies were used to determine possible sources of the aphids caught.

The studies on cereal aphid vectors in North America and the various difficulties encountered are discussed in a wider geographic context and in relation to studies on other types of vectors. It is concluded that long-range dispersal has received inadequate attention in relation to its biological and economic importance.

Introduction

Detailed epidemiological information is required to develop truly effective disease control strategies. It is particularly important to determine the main sources of infection from which spread occurs. The ease with which this can be done depends in part on the complexity of the pathosystem being considered and the distances over which spread occurs. Plant viruses are transmitted by contact, pollen, seed, or vectors. Much spread is circumscribed and over distances not exceeding tens or hundreds of metres (Thresh 1976, 1985). Thus it is usually possible to locate sources of infection within plantings or nearby, or to infer that such sources exist and that more distant ones are relatively unimportant. This feature of many plant virus diseases greatly facilitates control by isolation and other forms of sanitation (Vanderplank 1948). However, some virus disease outbreaks develop far from any known sources of infection or of vectors and in circumstances suggesting spread from afar.

Johnson (1967) and Thresh (1983) reviewed the available evidence on the long-range dispersal of plant viruses by insect vectors. Sellers (1980, 1983) made similar assessments of vector-borne viruses of vertebrate hosts. Our paper reviews the long history of studies in North America on cereal aphids and the viruses they transmit and discusses the biological importance of long-range dispersal.

The green bug *Schizaphis graminum* and corn-leaf aphid *Rhopalosiphum maidis*

Two of the many aphid species that infest cereals and grasses in North America have received considerable attention in studies of long-range dispersal: the green bug, *Schizaphis graminum* (formerly *Toxoptera graminum*) and the corn-leaf aphid, *Rhopalosiphum maidis*.

S. graminum infests barley, wheat, sorghum, maize and many grass species. Populations of apterae multiply parthenogenetically on these hosts and can cause considerable damage. Eggs are produced by sexuales in the autumn and laid mainly on *Poa pratensis*. However, in the U.S.A. and Canada reproduction seems to be mainly or entirely parthenogenetic, hence the need for a suitable succession of actively growing host plants for colonization and reproduction throughout the year.

Populations persist in regions where wild or cultivated hosts grow in continuous overlapping sequence. Survival in this way is not possible in areas where there are prolonged periods of drought or extreme cold. This explains why populations occur throughout the year in parts of Texas and Oklahoma, whereas they usually perish each winter in the northern states and Canada where temperatures are much lower.

R. maidis has no known sexual phase in North America and does not produce eggs. Otherwise it behaves very like *S. graminum*, infesting a wide range of cereals and grasses. Populations persist and reproduce parthenogenetically throughout the year in the southern states. They do not survive the winter in the northern states or Canada but reappear each year in late spring or early summer and persist until autumn.

The need for a satisfactory explanation of this important feature of the biology of both *R. maidis* and *S. graminum* has long been apparent. Davis (1909) suggested that *R. maidis* 'may hibernate as adults in warmer states or even in southern Illinois, and, as the season progresses,

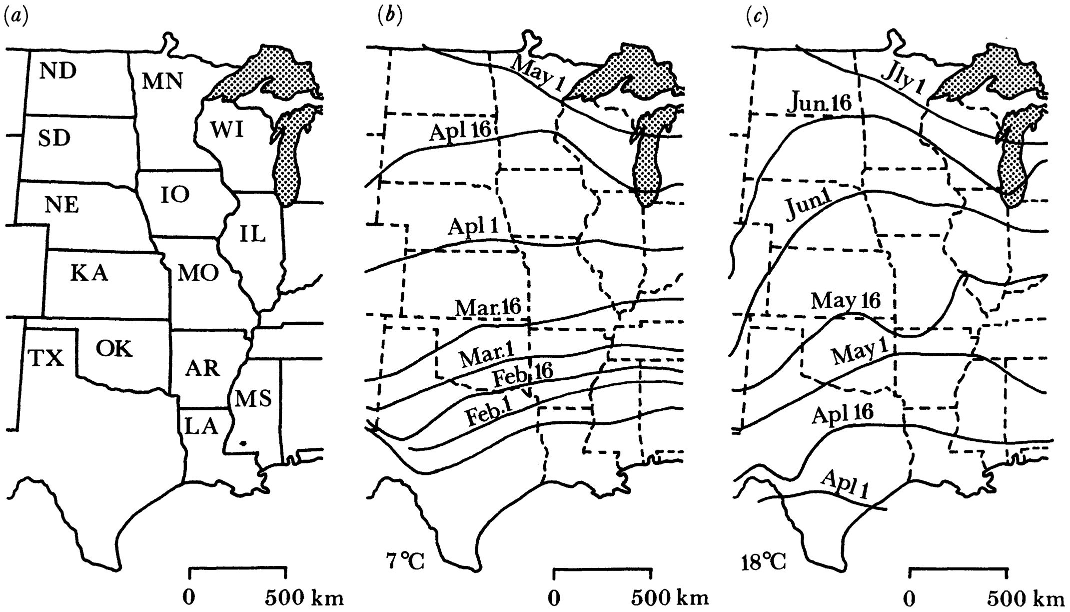

FIGURE 1. Sketch maps of the central United States including state boundaries (*a*) and isotherm lines showing the average dates when the daily mean temperatures reach (*b*) 7 °C and (*c*) 18 °C.

gradually diffuse themselves to the North with the advance of the season and infest the plants in those northern states'. However, he seemed reluctant to accept this explanation on the grounds that 'aphids are probably unable to travel great distances' and suggested that there may be other hosts during the winter and spring.

No alternative hosts have been found for *R. maidis* or for *S. graminum* and it is now generally accepted that both species overwinter in the south and disperse northwards each year as temperatures rise and actively growing host plants become available. However, as discussed in the following sections, there is continuing uncertainty regarding several important aspects of the reinvasion phenomenon and in particular on the source areas from which colonization occurs, on the routes taken and distances travelled and on the many factors influencing long-range transport.

Previous studies

Early outbreaks of S. graminum

Serious outbreaks of *S. graminum* occurred in 1890, 1901, 1903 and 1907. The main features of these outbreaks and the areas and crops affected were reported by Webster & Phillips (1912). They quote graphic accounts of the damage sustained in Missouri during 1890 when 'the oat crop in the vicinity of St Louis and probably extending a hundred miles in every direction' was being completely destroyed.

The 1907 outbreak was even more damaging and crops were affected sequentially from central Texas to Saskatchewan, Canada. Aphids were seen flying in great numbers from maturing and severely damaged crops. The significance of their dispersal northwards was fully appreciated at the time as it led to the infestation of younger crops that were in a more suitable physiological condition for colonization than those abandoned. It was concluded that 'but for the viviparous reproduction in such overwhelming numbers in the south, during winter and early spring, to drift northwards with season, there would be little if any damage caused in the Northern States'.

The next major outbreak of *S. graminum* was in 1916 in Oklahoma and Texas, where 380000 ha of wheat and oats were devastated or seriously damaged (Kelly 1917). There were further graphic accounts of aphids dispersing in large numbers but no serious outbreaks occurred further north. From these and subsequent observations it became apparent that damaging infestations occur only occasionally in the south and that they do not necessarily lead to later outbreaks in the north. This emphasized the need to study the conditions influencing the build-up of populations and the nature, timing and magnitude of the 'drift northwards'.

The 1926 outbreak of S. graminum in Minnesota

A severe outbreak of *S. graminum* occurred in Minnesota in 1926 after several years of little or no serious damage. This led to a detailed consideration of the biology of the species and to an assessment of the frequency with which damaging outbreaks are likely due to invasion from the south (Wadley 1931). Invasions in April and May during the early part of the growing season were considered to be of particular importance because they occur when crops are most vulnerable and there is adequate time for damaging infestations to develop. However, it was also concluded from the weather records for 1919–27 that winds during April and May are usually sustained for a sufficiently long time to introduce aphids from states bordering southern Minnesota but not from areas as remote as Texas or Oklahoma. Hence the supposition that crops are normally colonized sequentially from south to north over a period of weeks or months and that Minnesota is usually invaded too late to cause serious damage.

Direct colonization early in the growing season from areas far to the south was considered to be an unusual event that occurred only when weather conditions were extremely favourable. Such conditions occurred in April and May 1926 when sustained southerly winds extended from Texas or Oklahoma to Minnesota and into southern Canada. Conditions in the worst-affected parts of Minnesota were unusually dry in April, May and early June 1926 and this seems to have facilitated the establishment and build-up of aphids. A combination of suitable winds followed by a dry period was considered unlikely to occur more frequently than once in every 20 years. Moreover, even if suitable conditions occur, large infestations do not always develop in the south. Overall, Wadley concluded that *S. graminum* 'will seldom be generally injurious in Minnesota'.

R. maidis and S. graminum as virus vectors

Both *R. maidis* and *S. graminum* were studied originally as direct pests of cereals, although the former has long been known as a vector of sugarcane mosaic potyvirus. The situation changed greatly in 1951, when barley yellow dwarf luteovirus was first reported (Oswald & Houston 1951). *R. maidis* was used in some of the first successful transmission experiments with this virus and *S. graminum* was shown later to be a vector of some strains. These findings, and the mounting evidence that barley yellow dwarf virus causes serious and prevalent diseases of cereals and grasses, necessitated a complete reappraisal of the economic importance of *S. graminum*, *R. maidis* and other grass/cereal aphids (Bruehl 1961). Indeed, it was suggested that some of the damage and discolouration previously attributed to *S. graminum* was due to barley yellow dwarf virus and not solely to direct feeding. There can be no certainty about such retrospective interpretations but the importance of *R. maidis* and *S. graminum* as vectors of barley yellow dwarf virus has been recognized since the 1950s and further emphasized the need to study long-range dispersal.

Such studies became even more important with the first reports of maize dwarf mosaic disease in 1961 (Janson & Ellett 1963). This is caused by a potyvirus that is transmitted by many species of aphid, including *S. graminum* and *R. maidis*. Maize dwarf mosaic virus was first reported in Ohio but it is now known to infect maize, sweet-corn and sorghum in many parts of the United States. Infection is most prevalent in southern areas where winters are mild and Johnson grass (*Sorghum halepense*) thrives as an overwintering host of the virus and its vectors. However, infection can also occur elsewhere, as in Minnesota in 1977, in circumstances suggesting spread from afar.

The 1959 *infestation of S. graminum in Minnesota and Wisconsin*

Exceptionally severe infestations of *S. graminum* occurred in Wisconsin and Minnesota in 1959 at the time barley yellow dwarf virus became prevalent in many parts of the United States and Canada. The infestation of small-grain crops in Minnesota was first reported on 18 May, when aphids were already abundant in some areas and causing conspicuous damage (Hodson & Cook 1960). As *S. graminum* does not readily overwinter in Minnesota it was assumed to have spread from areas to the south some time earlier. Suitable conditions for dispersal occurred on 4 May when the harlequin bug, *Murgantia histrionica*, was seen alighting in large numbers in central Minnesota, even though it had never been seen previously in the state.

M. histrionica, a common pest south of latitude 40° N, was abundant in Oklahoma and Texas during the week ending 8 May at the same time that *S. graminum* arrived in Minnesota in large numbers. These observations suggested that the northward flights of both *S. graminum* and *M. histrionica* had been influenced by the same weather pattern and they may have originated from the same area. Conditions for long-range flight were favourable during the four days preceding 4 May, when sustained southwesterly winds advected warm humid air across Texas and Oklahoma into Minnesota and Wisconsin. The winds were consistent in direction from the surface to an altitude of 1700 m and were associated with a cold frontal system to the northwest. Wind speeds declined in Minnesota during the afternoon of 4 May when the first *M. histrionica* was found.

S. graminum entered the adjacent state of Wisconsin at the same time as the influx into Minnesota (Medler & Smith 1960). Alate aphids were trapped for 12 days, beginning 1 May, and severe infestations were recorded on young crops of oats in many parts of Wisconsin during early June. The first symptoms of barley yellow dwarf virus were recorded on 23 May and infection became more prevalent than for several years.

Association of long-range dispersal with low-level jet winds: 1963–1969

Low-level jet winds have received considerable attention because of their potential importance in facilitating the long-range dispersal of aphids (Jensen & Wallin 1965). These winds blow strongly from the southern states at speeds of up to 80 km h^{-1} and extend from ground level to *ca.* 900 m. They are best developed at night and have been associated with the following conditions: clear skies, strong afternoon insolation, a high-pressure area over the eastern or southeastern states, a low-pressure area located over or just east of the central or southern Rockies, and a stationary or near stationary front extending to the northeast for 800–1600 km from the low pressure area (Hoecker 1965).

Associations between low-level jet winds and the first reports of cereal aphids and yellow dwarf virus were studied in Iowa during 1965 (Wallin *et al.* 1967). The observations were made when populations of *S. graminum* were known to be high in Oklahoma and Missouri, but not in the adjoining state of Kansas. The first reports of *S. graminum* in Iowa were in April or May at the time of or soon after jet winds; barley yellow dwarf virus was recorded 24 days later.

In each of five years there were low-level southerly jet winds on at least nine days during the months of March, April and May, when spring-sown cereals were most vulnerable to infection (Wallin & Loonan 1971). Nevertheless, there were big differences between years in the final incidence of barley yellow dwarf virus. Spread was greatest in seasons when temperatures exceeded 19 °C in the days immediately after influxes occurred.

Similar studies were made by Kieckhefer *et al.* (1974) in South Dakota where low-level jet stream winds occurred on at least seven days in April and May every year from 1963 to 1969. Many of the cereal aphids caught at 12 m were taken on days with low-level jet winds, but some occurred on other occasions. This suggests that jet winds were not essential for an influx of aphids and that these winds sometimes occurred over areas where alates were not numerous or did not become airborne.

Aircraft trapping over Kansas: 1965 *and* 1966

Flights were made over Kansas in July 1965 and from May to July 1966 to determine whether aphids remained airborne after dusk (Berry & Taylor 1968). This was a point of great importance in relation to the distances aphids can disperse. Previous workers in North America suggested that aphids are transported far during prolonged overnight flights, whereas studies in England established that few aphids remain airborne after dusk and that they are unlikely to take off again after a long daytime flight.

R. maidis, *S. graminum* and other aphid species were caught in substantial numbers between 01h00 and 04h00 Local Summer Time in flights over Kansas at an altitude of 610 m. The nocturnal density averaged 34% of that during the previous afternoon, compared with only 4% over England as determined from previous studies that used traps suspended at 300 m from a tethered balloon (Johnson & Taylor 1955*a*, *b*). The big difference in aphid behaviour was attributed to the very different air temperatures of the two regions. Temperatures in Kansas usually exceeded 20 °C and no nocturnal flight was detected below 17 °C, whereas temperatures over England were usually below 15 °C. Aphids were caught in Kansas when strong low-level jet winds occurred and also at other times, confirming that jet winds are not essential for sustained overnight flight.

The 1977 *epidemic of maize dwarf mosaic virus in Minnesota*

Maize dwarf mosaic potyvirus became prevalent in sweet corn in 1977 in large areas of Minnesota where the virus had not previously caused serious problems. Infection was also reported for the first time in the adjacent states of North Dakota and Wisconsin and in Ontario, Canada (Zeyen *et al.* 1987). A feature of the epidemic was the sudden onset of disease in mid-July when whole fields were affected and there was no evidence of spread from seed-borne inoculum or from initial foci within or near affected crops. This led to the view that inoculum had been introduced by viruliferous aphid vectors from earlier plantings far to the south.

There was no direct evidence of spread in this way. However, an examination of weather records showed that conditions were favourable for the build-up of populations of *S. graminum* and other aphid vectors in possible source areas to the south, for their subsequent dispersal northwards and for deposition in certain parts of Minnesota and adjoining states.

Conditions during the spring of 1977 were very favourable for the build-up of aphid populations on cereals in the southern states. Temperatures were unseasonably high, soil conditions were adequate for plant growth and sowing was completed 2–4 weeks earlier than the long-term average. By 7 May some districts were experiencing drought which became severe in Oklahoma and neighbouring states (figure 2). Crops began to deteriorate and this may have led to the development and subsequent exodus of alates, which often become numerous under such conditions.

On 2 July, strong southerly geostrophic winds of *ca.* 80 km h^{-1} at 300–500 m above ground level extended from Texas into the Great Plains area. The two major influences were a low-pressure area near Lake Winnipeg, Canada, and a high-pressure area over West Virginia. In the late evening of 2 July and the early morning of 3 July the southerly winds were interrupted by a cold front and associated thunderstorms.

Correlations were established between amounts of rainfall and the incidence of maize dwarf mosaic. Areas south of the cold front that received more than 44 mm of rain had no diseased fields, whereas those most severely affected were in areas receiving less than 9 mm. These findings are explicable if airborne vectors had been forced to alight because of the decrease in temperature and down-draughts of air associated with the cold front and if the colonization of host plants was reduced by subsequent periods of driving rain.

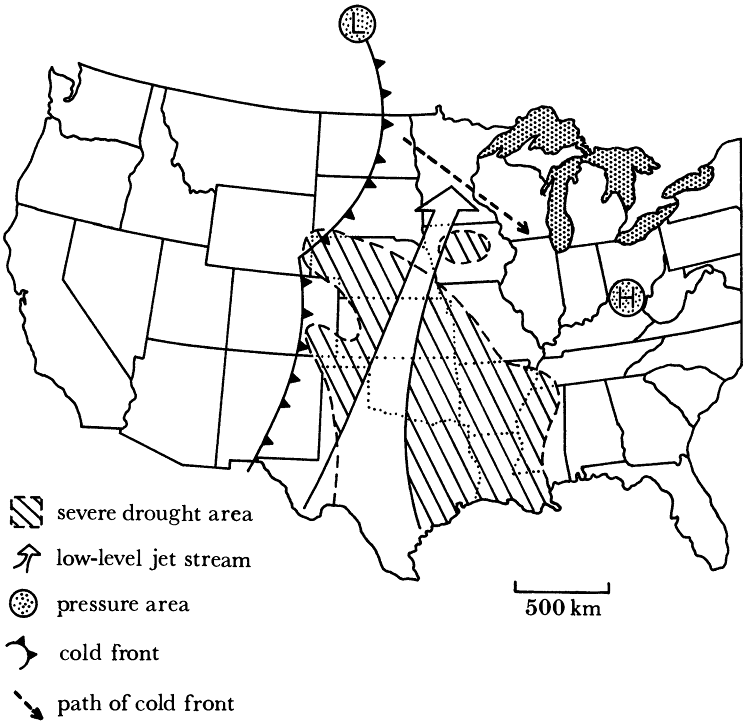

FIGURE 2. Sketch map of the continental United States showing areas affected by severe drought during May and June 1977. The large arrow indicates the path of low-level jet winds into Minnesota on 2 July 1977 and the small arrow shows the path of a cold front associated with thunderstorm activity. Adapted from Zeyen *et al.* (1987).

The Minnesota observations provided circumstantial evidence of long-range virus dispersal that could have occurred over distances exceeding 1000 km if aphids stayed airborne for *ca.* 12 h and remained infective. However, this assumption seemed unwarranted at the time because maize dwarf mosaic virus is transmitted in the non-persistent manner and in previous studies it was not retained by aphids for longer than six hours (Tosic & Sutic 1968). Retention times are usually considerably less, especially when aphids feed or probe plant tissues. This implies that maize dwarf mosaic is unlikely to be transported over great distances by aphids in flight. Such a conclusion is consistent with the many steep gradients of infection observed and there is little evidence that non-persistent viruses are spread far by vectors (Thresh 1976, 1985).

The apparent inconsistency between field observations and transmission studies was resolved by the subsequent findings of Berger *et al.* (1987). In experiments with many aphids, virus was retained for up to 21 h by alate *S. graminum* held in glass petri dishes at 25 °C. This greatly exceeded previous estimates, and retention may be even longer in air-borne aphids because of the cooler temperatures encountered aloft and the inability of flying aphids to probe plants and thereby decrease the charge of virus being carried. Thus retention for up to 21 h, even in only a small proportion of the airborne aphids, would permit spread to Minnesota by alates originating from areas as far south as central Texas. This assumes that the aphids are infectious on take-off and remain airborne for a sufficiently long period in winds of the speeds recorded in 1977.

The foregoing evidence is sufficiently strong to suggest that maize dwarf mosaic may sometimes spread far and other non-persistent viruses may behave similarly. However, the maize–virus pathosystem in the United States is unusual, if not unique, because of the huge areas of susceptible crops grown in warm areas during the winter and spring and at higher latitudes during the summer and autumn. Large source and catchment areas, sequential planting, interconnecting air streams, and enormous populations of cereal aphids greatly facilitate long-range virus spread. Moreover, this can occur even when there is great mortality *en route* or when only a small proportion of aphids is infectious on take-off and remain infectious throughout prolonged flight.

There are many other non-persistent viruses, but most infect horticultural crops that are grown in small areas on a very limited scale. Two notable exceptions are soybean mosaic and sugarcane mosaic potyviruses, and these could be transported far in Asia or South America. However, both viruses are disseminated in planting material, and long-range spread by aphid vectors is likely to be much less frequent than local spread from sources within crops or in nearby plantings. Thus the main importance of long-range spread may be in disseminating novel strains of virus that are able to infect cultivars resistant to the usual strains. It may be significant that serious problems have already been encountered due to the rapid build-up of resistance-breaking strains of both sugarcane mosaic and soybean mosaic viruses (Abbott & Tippett 1966; Cho *et al.* 1977).

Observations on cereal aphids and barley yellow dwarf virus in Canada

Damaging infestations of cereal aphids and epidemics of barley yellow dwarf virus occur sporadically in Canada. Some have been associated with sudden influxes of aphids presumed to be from the south, as in Manitoba in 1969 and New Brunswick in 1970 (Gill 1970; Gill *et al.* 1971). Evidence of invasion from remote sources was that in these and some other outbreak years immigrants were scattered throughout plantings and not mainly around the boundaries, as would be expected if spread had been from grasses or other local sources. Moreover, some of the strains of virus encountered differed from those infecting nearby grasses or cereals the previous season.

This occurred in 1976 when there was a large influx of aphids to spring-sown cereals over large areas of eastern Canada. The influx occurred in late June when winds were predominantly from the south and southwest, whereas winds were much more variable in the five succeeding years when no serious outbreaks developed (Paliwal 1982*b*). Steady southwesterly winds in October 1982 coincided with a sudden influx of aphids to autumn-sown cereals in Ontario and Quebec Provinces and some fields became almost totally infected with yellow dwarf virus (Paliwal & Comeau 1984).

A more detailed analysis of wind speed and duration was undertaken by Rose *et al.* (1975) following the sudden appearance of *R. maidis* in large numbers at sites in Ontario during the night of 5–6 August 1973. Back-tracks were prepared from surface and 850 mbar† synoptic charts assuming that the aphids arrived at 01h00 Eastern Standard Time (EST) and that they had flown for *ca.* 9 h at 650 m above ground level. On these assumptions they would have originated *ca.* 400 km away in Wisconsin where heavy infestations occurred (figure 3). Even longer flights would have been possible if the aphids had flown until daylight or if they had taken off earlier or flown in stronger winds at lower altitudes.

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† 1 mbar = 10^2 Pa.

FIGURE 3. Sketch map of the Great Lakes area of the United States and Canada showing the estimated back-track of *R. maidis* from the place of arrival in southern Ontario assuming overnight flight 5–6 August 1973. A nine-hour flight ending at 01h00 EST on 6 August would have originated *ca.* 400 km away at the site marked in central Wisconsin. Adapted from Rose *et al.* (1975).

THE ILLINOIS 'PESTS AND WEATHER' PROJECT: 1983–1985

In 1983 a multidisciplinary project was begun in Illinois to obtain additional information on the dispersal of aphids into and across the state. The initial impetus for the project came in part from previous studies on the epidemiology of soybean mosaic virus (Irwin & Goodman 1981). These studies demonstrated the importance of many different aphid species as virus vectors, even though they only visit soybean crops and do not colonize or reproduce on soybean in the area. *S. graminum* plays a minor role in the spread of soybean mosaic virus and *R. maidis* a moderately important one, but both species are of great importance in the state as vectors of cereal viruses.

Particular attention was given to *R. maidis* during the Illinois project because in some years it occurs in large numbers and causes serious damage to maize, as in 1980 when over 162000 ha were treated with insecticide to control that species alone. Much smaller areas were treated in the two preceding and the two following years. This emphasized the need to develop a suitable method of forecasting the need for pesticides. *R. maidis* was also selected for study because it is easy to locate on maize and sorghum, and techniques have been developed to culture it readily in the laboratory. Moreover, landing rates of this species have been recorded routinely in experimental plantings of soybean in central Illinois for many years (Irwin & Goodman 1981). Another feature of *R. maidis* is that it does not reproduce sexually, thus facilitating the use of genetic markers to characterize populations and trace their movements.

The availability of a large multidisciplinary team and special facilities, including the Illinois State Water Survey's high-resolution radar and a helicopter belonging to the Aviation Institute, permitted a wide-ranging approach. Some of the unresolved issues raised in previous studies were addressed including the origins of immigrant aphids arriving from the south. The various techniques used in the 'Pests and Weather' project are considered in the following sections together with results of catches obtained on one particular day.

Genetic and other insect markers

Various techniques have been used to mark aphids and other insect vectors to follow their movement (Pettersson 1968). Information has been obtained in this way on the dispersal of the rice brown planthopper (*Nilaparvata lugens*) in China over distances of up to 700 km (Anon. 1981). However, the probability of recovering marked insects over such great distances is low, and so many insects have to be marked that this approach was not adopted in the Illinois project. Mineral analyses of aphids to determine their origins were also considered inappropriate and other studies on cereal aphids with the technique have not given very encouraging results (Bowden *et al.* 1985).

The inherent genetic makeup of different populations of a species forms another set of potential markers. Intrinsic genetic differences among populations can be determined by electrophoretic analyses, especially of their enzymes, to characterize 'population types' or 'electromorphs'. This approach was adopted by the Illinois team studying *R. maidis* (Steiner *et al.* 1985; Voegtlin *et al.* 1987).

Aphids were collected between western Texas and Louisiana in May 1983 and 1984, and between eastern Texas and eastern Georgia during May 1985, for comparison with specimens collected in Illinois during July and August of these years. In 1983, 8 of the 21 enzymes assayed were useful in distinguishing between *R. maidis* populations: *Hk-1*, *Idh-1*, *Ald*, *Pgi*, *Got*, *Mdh*, *Pgm* and *Pep*. Loci were scored numerically based on mobility in starch gels in relation to the most common allele present.

The 1983 collections from western Texas, Louisiana and Oklahoma were of a relatively consistent type that was distinct from the Illinois collections (Steiner *et al.* 1985). This suggested that the Illinois samples had not originated from any of the southern areas surveyed. They may have arisen further north, in Arkansas or Missouri, where *R. maidis* is likely to have overwintered successfully during the exceptionally mild winter of 1982–83.

Subsets of the enzymes that demonstrated differences between populations in 1983 were assayed in 1984 and 1985. The 1984 samples differed from those collected in 1983 even though they were from the same southern areas. The dominant allele *Hk-1* was more mobile than in 1983 and there were differences in *Mdh-S* between the southern and northern samples in 1984, but not in 1983. Even the low variation for *Mdh-F* and *Got-F* in the 1983 Texas samples was not apparent in 1984. Alleles *Hk-1* and *Pgi* were of special interest in 1984 because there were differences between the southern and northern samples, indicating that the Brinkley, Arkansas, populations could not have originated from those sampled in Texas or Oklahoma (Steiner *et al.* 1987).

In 1985, only *Hk-1* of the nine enzymes analysed showed any regional variation. The ratio of fast to slow alleles in the populations sampled between Georgia and Texas formed a cline. There were close matches between the Illinois samples and those from Louisiana and Mississippi, which suggested that the source areas may have been in these states (Steiner *et al.* 1987; Voegtlin *et al.* 1987).

Electrophoretic analyses of nine populations of *R. maidis* sampled intensively in central Illinois in the autumn of 1984 distinguished at least three distinct electromorphs (Steiner *et al.* 1987). This indicates a complex situation and there could have been influxes from different localities, on different winds, over different distances and at different times.

Although the northern and southern populations were not matched in 1983 or 1984, the results demonstrated that the electromorph approach could be useful. This was confirmed in 1985 and the three years taken together illustrate the great variation in genotype between localities and years and substantiate the existence of many naturally occurring clones.

These preliminary findings indicate how genetic markers can help determine source regions, provided that their limitations are appreciated. In any future surveys it will be important to determine chromosome numbers because recent studies on North American collections have distinguished a form of *R. maidis* with $2n = 10$ that infests barley from a $2n = 8$ form found mainly on maize and sorghum (Blackman *et al.* 1987). The development of ribosomal DNA (rDNA) probes to *R. maidis* might also provide additional genotypic information that would increase the ability to distinguish between populations. This could make characterization more precise, although it would not resolve the biological problems encountered. For example, the reason for the differences between years in the southern populations is not known, but back migration from the north probably occurs each autumn and could lead to the introduction of new morphs. Thus specific clones could be favoured by climatic events that alter the dominant genotypes from year to year. It could also be that the southern area that was sampled is not the base population from which the migrants originate, but instead represents a shifting, intermediate region that is colonized from populations further to the south, perhaps in Cuba or Mexico.

Other vectors and pathogens may enter the mainland United States in this way. For example, it has been suggested that rice hoja blanca virus is introduced to Florida and Louisiana by planthopper vectors, *Sogatodes* spp., swept northwards from Cuba by hurricane winds across the Gulf of Mexico (Everett & Lamey 1969). There is also circumstantial evidence that spores of the sugarcane rust fungus, *Puccinia melanocephala*, and blue mould of tobacco, *Perenospora tabacina*, are also blown into and across the United States from tropical and subtropical areas to the south and southwest (Davis & Main 1986; Purdy *et al.* 1985). Similar, largely circumstantial, evidence has been obtained that mosquitoes introduce several important viruses of vertebrate hosts into the mainland United States during the summer months from warmer areas to the south (Sellers 1980).

Developing back-trajectories

Back-trajectories provide evidence on the dispersal routes and source regions of vectors being translocated aerially over large distances. For trajectories to be accurate they must incorporate a substantial amount of information gathered from distinct and varied sources. Under most circumstances the flight speed of aphids and other vectors is much less than wind speed, particularly when weather conditions favour long-distance movement (Drake & Farrow 1988).

Consequently, weather conditions and, in particular, air motion strongly govern the aerial dispersal tracks. Good estimates of air speed and direction at various sites and heights from 10 to 1500 m above ground are needed to produce accurate trajectories. Information is also needed on abundancies and vertical distributions of the target species, their likely terminus, and time spent aloft.

Wind roses and general information on the direction of prevailing winds have been used previously to interpret the aerial translocation of insects. However, this can lead to large discrepancies in routes and distances travelled because they represent long-term averages or integrations at a given locality, whereas aerial translocations are usually short-term events influenced by the prevailing meteorological conditions (Scott & Achtemeier 1987). Streamlines, which are instantaneous patterns of air movement, have also been used to define aerial transport pathways. Trajectories showing the actual path of air movement are more appropriate because aerial dispersal can occur for many hours and the weather systems causing directional air flow at any instant move with time.

The numerical trajectory model developed during the Illinois Project (Scott & Achtemeier 1987) takes account of the large variability that occurs in wind direction and velocity with height above ground. It uses data from routine soundings of the upper atmosphere obtained by the National Weather Service. Soundings are made twice daily from a network of widely spaced monitoring sites and permit accurate back-tracking as wind speeds and directions can be interpolated in seven horizontal slices through the troposphere over the entire United States. Trajectories can be computed quickly and inexpensively to provide an accurate indication of the route taken by small volumes of air containing small insects in long-distance flight.

Assessing the vertical distribution of airborne vectors

One of the most important parameters required for the numerical back-trajectory model is a knowledge of how high the specimens are flying, so that calculations can be based on the most appropriate airstream. Both radar and direct sampling methods were adopted in the Illinois Project.

Radar

Radar has been used to study the aerial movement of large insects such as locusts and moths (Schaefer 1976; Riley 1980; Drake *et al.* 1981), and also smaller insects, including aphids (Schaefer *et al.* 1979), leafhoppers and planthoppers (Riley *et al.* 1987).

The Illinois project monitored aphid movement using the State Water Survey's high-power 10 cm CHILL radar with a large parabolic antenna of 8.5 m diameter (figure 4). The instrument had doppler capabilities and a maximum estimated detection range of 40–50 km for aphid concentrations. Accurate estimates of mean insect ground-speed are possible and mean flight speed can be calculated if wind-speed measurements are available. The radar can be operated in plan position indicator (PPI) or range-height indicator (RHI) modes. This allows the atmosphere to be viewed in thin near-horizontal and vertical slices. Atmospheric phenomena, such as clouds or precipitation, reflect strongly at the waveband used, potentially masking any insect echoes that may occur. Consequently, when used to resolve small insects in the atmosphere, the CHILL is restricted to times of little or no cloud cover, which is an operational limitation. Radar reflections from insects and those due to atmospheric inhomogeneities can be resolved by using the dual polarization facility of the CHILL radar (Mueller & Larkin 1985).

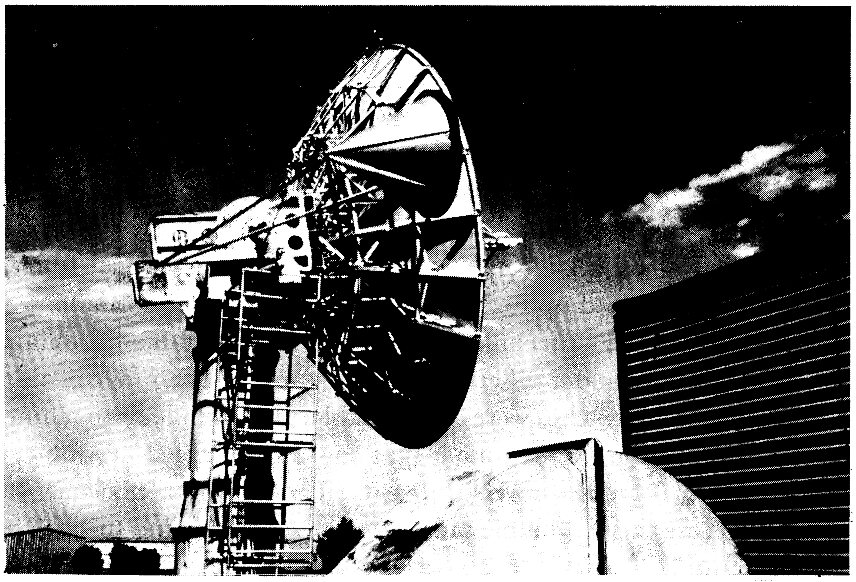

FIGURE 4. The CHILL radar at the University Airport south of Champaign, Illinois.

Because of their small reflective power (Riley 1985), individual insect vectors return very little energy to a radar and the system must be extremely sensitive to give satisfactory results. Alternatively, many insects must be present in any given pulse volume. For instance, Riley (1985) has demonstrated that the radar cross section of aphids is approximately 10^{-5} cm^2, which is five or six orders of magnitude less than that of moths and locusts.

The small cross section imparts a serious limitation to radars, but an advantage of radars is that they permit large volumes of air to be scanned quickly and over considerable distances. This is apparent from experience with another radar used in entomological studies. It scans about 2×10^{14} m^3 of air per hour, whereas two nets suspended from a kite sampled only about 5×10^4 m^3 per hour depending on the winds encountered (Farrow & Dowse 1984). Thus even such small radars, which are considerably less powerful than the CHILL, scan a volume 4×10^9 times greater than do aerial collectors in the same time period. Radars are, therefore, appropriate for scanning large portions of the atmosphere over short time intervals, making them ideal instruments for routine surveillance for large influxes of airborne insects.

The Illinois CHILL radar was used successfully to monitor aphids and other insects flying at heights between 150 and 2000 m during the summers of 1984 and 1985 (Irwin & Hendrie 1985; Hendrie *et al.* 1985; Mueller & Ackerman 1987). Data for study were analysed as both near-instantaneous PPIS and RHIS. By averaging over thin slices of space for short periods of time, profiles were obtained for direct comparison with density data from direct sampling by helicopter.

Direct sampling methods

Although remote sensing has some advantages, it cannot distinguish between, nor identify, the many vector species that may be airborne. Other methods are required to identify the insects being located and various sampling techniques were considered for use in Illinois.

Collectors attached to tall towers were used initially to sample at heights up to 30 m above ground, but suction traps at that height failed to detect aphids when they were being caught in substantial numbers at higher altitudes by tethered sampling devices or helicopters (Hendrie

& Irwin 1987). This emphasized the importance of being able to sample at considerable heights above ground and two approaches were adopted.

Tethered techniques. Tethered techniques such as sieving devices or sticky traps attached to kites, balloons or 'kitoons' have been used previously to sample insects from 100 to 400 m above ground (Johnson 1969; Farrow & Dowse 1984). These devices can provide valuable information, not only on the occurrence, phenology and numbers of airborne insects, but also on their vertical distribution in the lower atmosphere.

Early in the Illinois project, a kite-supported, tethered sieve modified from the design of Farrow & Dowse (1984) was used up to 300 m above ground in the spring and early summer of 1984 (Hendrie *et al*. 1985). The technique proved to be unsuitable for obtaining accurate information on aerial densities under differing conditions and over a range of altitudes because the integrity and timing of the catches were questionable. It was difficult to maintain a selected height, or even a constant height. Only one height could be sampled at a time, and so it was not possible to assess vertical profiles of vector density. The collection efficiency varied and was difficult to estimate because the air volume sampled changed with wind speed. The system may also have influenced the flight path of insects by attraction or repulsion. Moreover, it was usable only during certain meteorological conditions and the Federal Aviation Authority regulations limited operating heights to less than *ca*. 330 m. They also stipulated the need for a flashing light at night, and this could have been attractive to some insects. Overall, it was concluded that the kite technique had serious limitations and was not used routinely.

Aircraft sampling. Previous workers have used collectors including sticky screens and sieving devices attached to piloted or remotely operated fixed-winged aircraft or helicopters to sample arthropods, including vector species, from heights ranging from 100 m to more than 5000 m (Glick 1939; Johnson 1969; White 1970; Kreasky *et al*. 1972; Rainey 1976; Greenbank *et al*. 1980). For quantitative studies, the technique adopted should ideally provide good vertical and temporal resolution, accurate density resolution and identifiable specimens that can be used in bioassays. However, some of the aircraft used interfered with the airflow entering the collectors, whereas the efficiency of some devices was decreased because they used convergent or divergent stream tubes. Other methods damaged delicate specimens or used sticky surfaces that made the catches difficult to handle, or sampled inadequate volumes of air. Another difficulty in using aircraft is that they can seldom be operated frequently or for long periods because of the costs incurred or because they are not always available. This explains why they have been used infrequently and then only for specific projects rather than routinely.

At the outset of the Illinois project, Hendrie *et al*. (1985) collaborated with aeronautical engineers and designed a novel sampling device suitable for use on aircraft. Two identical collectors were constructed and tested in a large wind tunnel. They were then fitted, one to each skid, on a Hiller UH12D Helicopter (figure 5). Each collector was mounted with the orifice well in front of the leading nose of the cockpit to reduce disturbance of the sampled airstream. Once the helicopter attained a forward translation of more than 9 m s^{-1}, all interference with the air flow into the collectors was eliminated.

This aerial sampling technique provided absolute integrity of the sampled stream tube and air-flow intake. The likelihood of insect avoidance was minimized, and an internal expansion chamber avoided damage to delicate specimens. This facilitated further analyses of collected specimens and allowed them to be processed and identified in a more reliable and timely manner than when sticky traps or other devices are used. The helicopter facilitated accurate

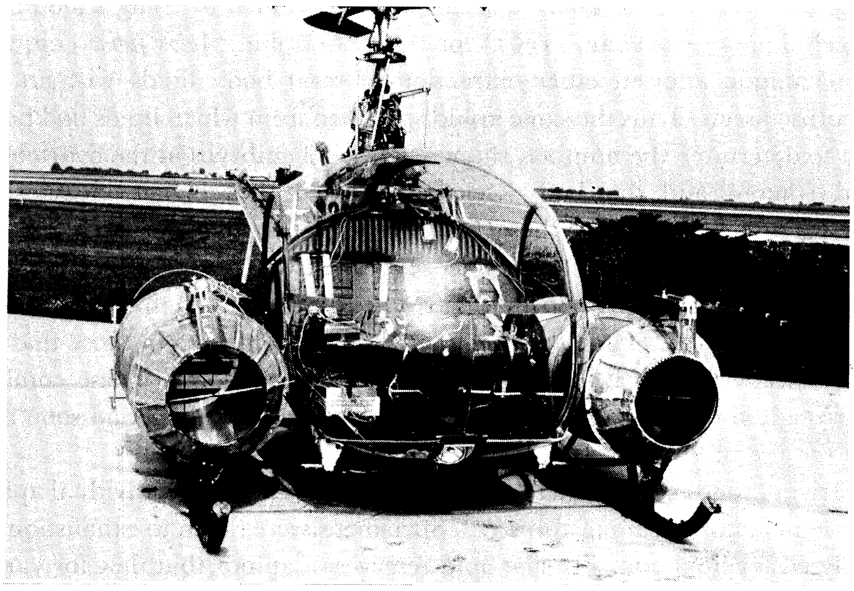

FIGURE 5. Two collectors fitted to the Hiller UH12D helicopter for aerial sampling.

assessments of the vertical distribution of airborne insects, including small and delicate specimens of taxa such as aphids, midges and mosquitoes, by aerial density and species. Results from this technique were matched with data from the CHILL radar and the two techniques are complementary.

By using the helicopter-mounted collectors, it was established that several important vectors of plant viruses, including *R. maidis*, commonly fly more than 1 km above ground level in central Illinois. Some individuals occurred at heights approaching 2 km during the 1984 and 1985 growing seasons (May–August). During early morning flights and before much air turbulence developed, *R. maidis* frequently occurred in discrete layers of variable depth at 50–300 m and at densities of up to 11.3 specimens per 1000 m^3. Supporting CHILL radar observations determined that the layers sometimes extended horizontally for many kilometres. Aerial specimens were usually associated vertically with zones of wind maxima or layers in which the temperature changed little with height. The greatest numbers of airborne aphids were found moving towards the north or northeast in advance of approaching cold fronts. They were generally associated with pre-frontal weather situation and temperature inversions or isothermal conditions. With the exception of a few species of Diptera, 12 °C appeared to be the lower threshold for insect flight activity.

Energy depletion during flight

Even small insects must maintain active flight to stay aloft for long or they tend to fall out of the atmosphere (Pedgley 1982). As with any other activity, energy is consumed during flight and the amount of fuel used as energy is directly proportional to flight duration (Fulton & Romney 1940). This provides a possible means of estimating the time insects have spent aloft. However, flight activity is not the only factor that determines the level of lipids or other possible fuels in alate aphids. Post-eclosion age, morph, reproductive status and nutrition are also important. Depletion of lipids other than for flight must be understood and taken into account when using lipids to indicate flight duration.

The total lipid content of individual *R. maidis* was determined by using a modification of the gravimetric technique of Cockbain (1961) for the bean aphid, *Aphis fabae* (Liquido & Irwin 1986). This technique allowed ether extraction of total body lipids without the need to homogenize entire insects. Thus the same aphid specimen from which lipids had been extracted could be used to determine the number, shape and size of embryos in the ovarioles. A relation between lipid content and dry body weight indicated that bigger, heavier aphids had proportionately more fat than did those that were smaller and lighter. Lipid content also decreased significantly with post-eclosion age, suggesting that young adults have the greatest flight capacity (Liquido & Irwin 1986). Other studies demonstrated that wingbeat frequencies are much higher in *R. maidis* alatae that are about one day old than in those that are younger or older (E. I. Zarkova & M. E. Irwin, unpublished observations). These combined sets of information strongly link the 'migratory urge' of *R. maidis* with the period soon after eclosion and facilitate the use of lipid levels to estimate flight duration.

Liquido & Irwin (1986) studied fuel depletion during the flight of individual aphids tethered in a wind tunnel in an air stream of 1 m $\sec^{-1}$. Specimens were flown to exhaustion, then frozen and later analysed for lipid content. The lipid reserves of aphids that flew for varying lengths of time were then compared to provide estimates of the rate of depletion. In experiments with aphids one day after eclosion, the lipid content decreased from 55 % to 20 % of dry body weight over flight periods of about six hours (figure 6). There was little further decrease in lipid content even in aphids that flew for up to eight hours longer. This suggests that some other energy source was being used in longer flights and the remaining lipids may be unavailable for flight because they are bound in developing embryos. Other researchers have demonstrated changes in fuel utilization during flight. For instance, Cockbain (1961) reported that during the onset of flight *A. fabae* used glycogen and only later switched to lipids. Lipids and glycogen are used concurrently by the brown planthopper, *Nilaparvata lugens* (Padgham 1983).

The results suggest that the lipid content of *R. maidis* in flight can be used to indicate the length of time they have flown, but only for periods not exceeding six hours. However, such estimates of flight duration have limitations, owing to the inherent biological variability in lipid

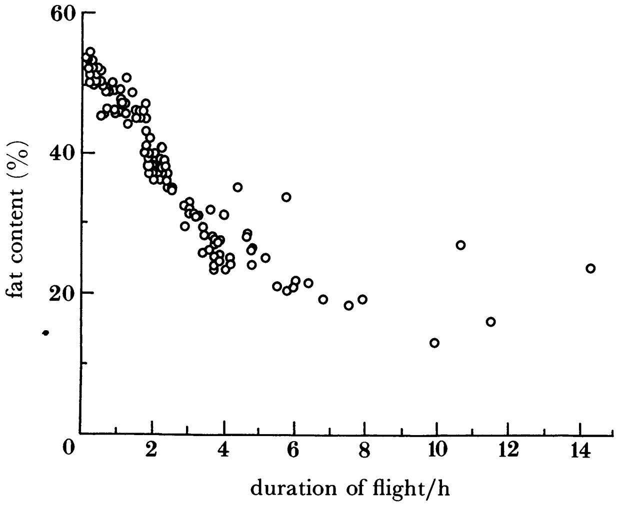

FIGURE 6. The decrease in lipid content, based on dry weight, of 0.5 to 1.0-day-old alates of *R. maidis* during sustained periods of tethered flight. Adapted from Liquido & Irwin (1986).

content among individuals and the lack of knowledge of the role non-lipid flight fuels play in long-range transport. Fuel consumption may differ between laboratory-reared specimens in tethered flight and naturally occurring specimens in free flight. Moreover, host plants may influence the amount of lipid reserves in individual specimens. These limitations can be overcome through further investigation and the technique may eventually permit more accurate estimates of flight duration than is currently possible.

9 *August* 1984*: observations and subsequent analyses*

The detailed information to be gained from a multidisciplinary approach is apparent from the observations made on 9 August 1984 (Hendrie *et al.* 1985). Weather charts indicated that a pre-frontal pattern with a moderately strong SSW flow of warm, moist air had been moving into the midwestern region for some hours preceding the observation period. CHILL radar observations at 05h37 Central Standard Time (CST) showed three strong layers of insect-like targets (figure 7*a*, *b*) that persisted until noon. The layers then weakened but could still be differentiated until 13h00 CST. The polarization of the display on the PPI indicated marked directional orientation. Helicopter-mounted collectors were used to sample at heights from 50 to 1000 m between 06h55 CST and 08h00 CST. Aphid specimens caught in the collectors were identified to species and specimens of *R. maidis* were separated and frozen for later analysis of lipid content and curation.

The uppermost layer of insects extended from *ca.* 900 to 1200 m above ground and consisted entirely of *R. maidis* at a density of 4800 individuals per 10^6 m^3. The middle layer extended from *ca.* 500 to 650 m and contained a mixture of *R. maidis*, flies and wasps at about 2000 specimens per 10^6 m^3. The lowest layer extended from the surface to *ca.* 200 m and the samples contained diverse species at up to 10000 specimens per 10^6 m^3, but not *R. maidis*.

Insect data from the helicopter-mounted collectors and the reflectivity data from the CHILL radar were plotted together (figure 7*b*), and considered in relation to vertical profiles of wind speed and direction, dry bulb temperature and dew point obtained from instruments mounted on the helicopter. There was a marked concurrence in heights and densities of layered insects as determined independently by direct sampling and radar. The temperature data indicated a strong subsidence inversion to *ca.* 600 m and an isothermal layer above 1100 m. The uppermost layer of aphids was associated with this isothermal layer and the zone of greatest wind speed. The middle layer coincided with the top of the inversion.

Mean lipid content based on dry body weight of *R. maidis* specimens was 22.7% from the upper layer and 31.8% from the middle layer. Laboratory-obtained relations comparing lipid content and flight duration (figure 6) suggest that the probable flight duration of specimens from the middle layer was 2–5.5 h and from the upper layer was 5 to more than 24 h. Suction traps at ground level and on the 30 m tower did not collect any aphid specimens during the night of 8 August, indicating little or no aphid activity near the ground and no take-off or landing during darkness. Based on this evidence and from the estimates of flight duration, it was concluded that *R. maidis* specimens from the middle layer must have begun flight after the ending of solar darkness (04h28 CST) on the morning they were caught. On these assumptions maximum possible flight duration was 2.75 h. The *R. maidis* specimens in the upper layer were likely to have begun flight between solar dawn and solar dusk the previous day, with a flight duration of 11.5 to 25.75 h, assuming that they did not fly more than one night.

The Illinois trajectory model was used to estimate the flight pathways for *R. maidis* specimens

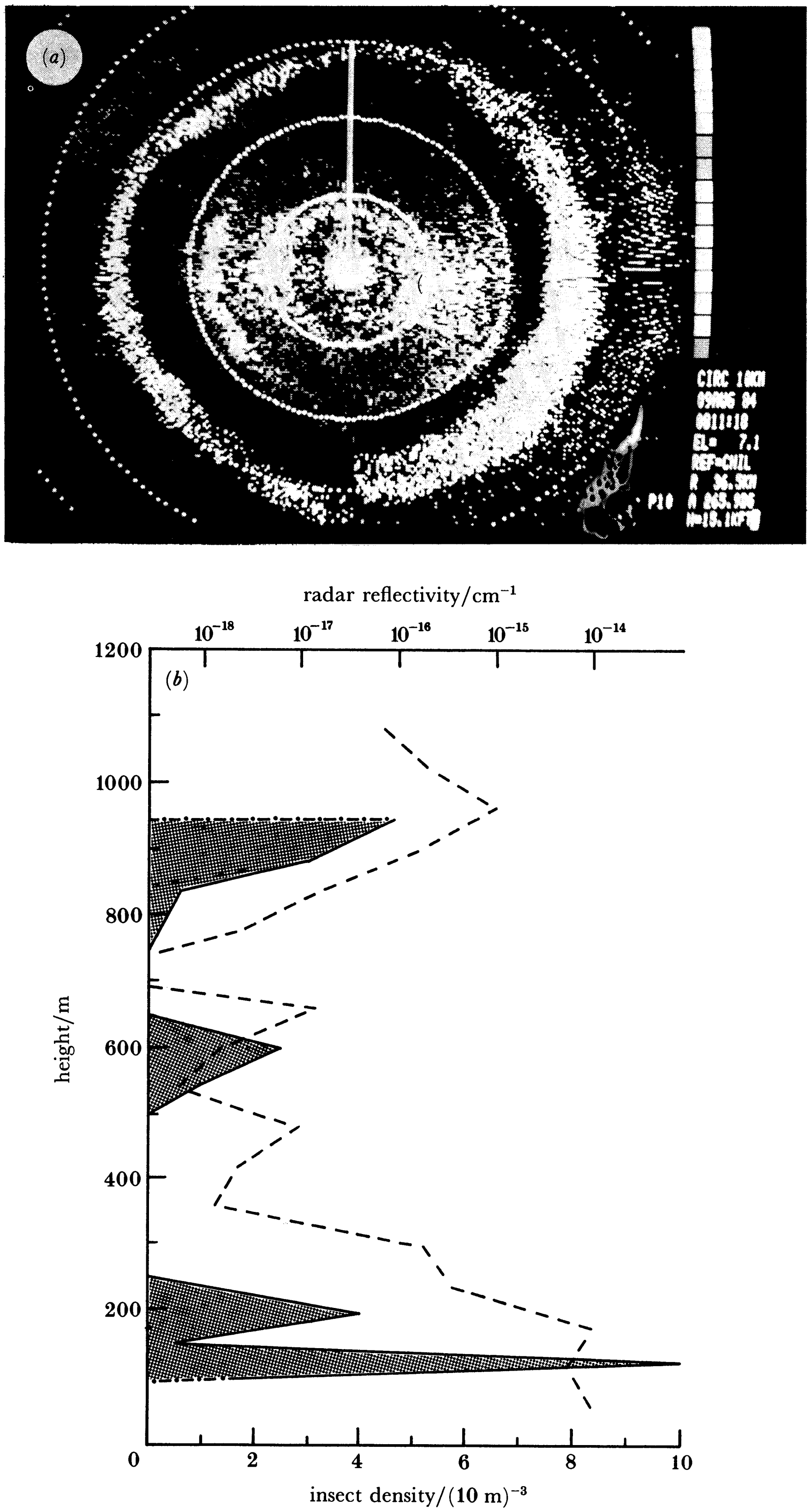

FIGURE 7. (*a*) A PPI taken from the CHILL radar on 9 August 1984 showing three distinct zones of insects. The upper zone (outermost irregular band) consisted of directionally orientated aphids. The middle zone and the one closest to the ground (inner band) contained a mixture of insects. (*b*) Vertical profile of insect density and radar reflectivity observed during flights of *R. maidis* over Champaign, Illinois at 06h35 CST on 9 August 1984. Adapted from Hendrie & Irwin (1987).

in the upper and middle layers (figure 8). Based on these calculations, the upper layer of specimens probably originated between Columbia, Missouri and Dallas, Texas, 400–1100 km SSW. The estimated source area of the middle layer of specimens was 50–80 km westward in Illinois.

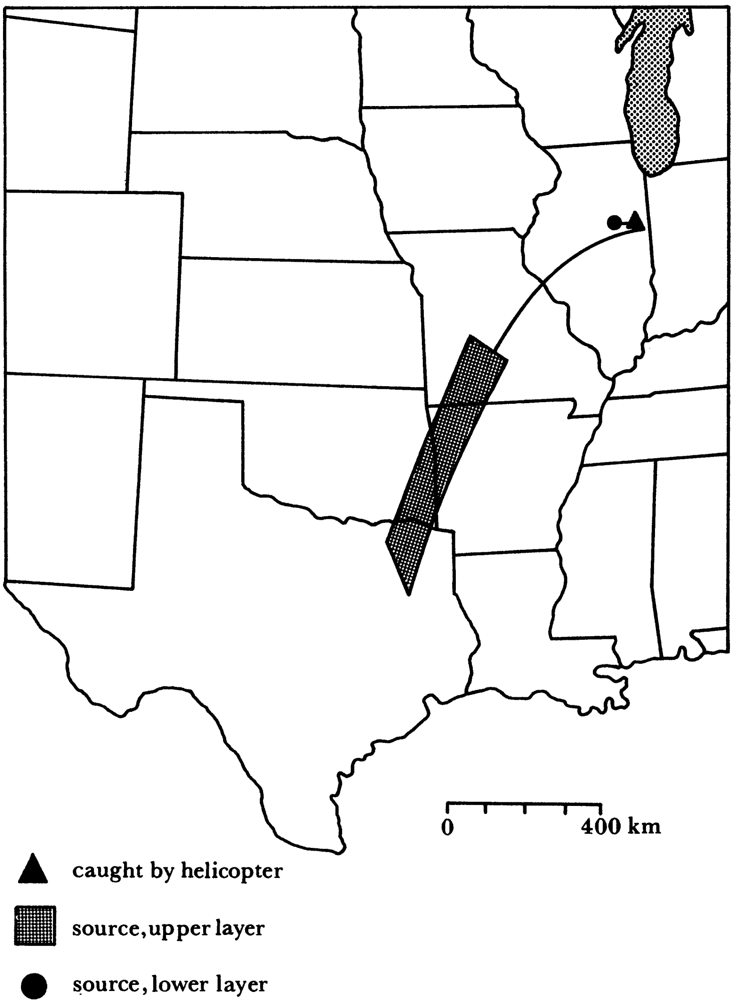

FIGURE 8. Sketch map of the central United States showing the most likely sources of the *R. maidis* specimens collected by aerial sampling on the morning of 9 August 1984. Separate sources were calculated for the upper and lower layers of aphids by back-tracking and from analyses of lipid content. Adapted from Hendrie & Irwin (1987).

The information obtained during this case study confirms the potential of a multidisciplinary team approach using diverse techniques. When all data-gathering procedures were operated simultaneously, they could produce reasonable back-trajectories. It is expected that when long-range dispersal is sufficiently well understood, the trajectory model will be able to forecast long-distance migration events.

DISCUSSION

The studies reviewed in this paper illustrate how different approaches and techniques have been used to investigate the long-distance dispersal of cereal aphids and the viruses they transmit. The studies have continued in the same region for more than 60 years and yet the phenomenon is still poorly understood. This is a surprising situation when considered in relation to the enormous area and value of the crops attacked and to the losses sustained.

There is an obvious need for methods of forecasting when and where major influxes are likely to occur and whether the immigrants are likely to be infective. However, the knowledge currently available on the long-range transport of cereal aphids in North America is so rudimentary that precise forecasting will be impossible until much additional information has been acquired. One reason for this situation is that previous studies have been intermittent and localized. Moreover, the scale of past operations has been totally inadequate in relation to the magnitude and complexity of the problem.

Much of the available information is fragmentary or incomplete because of the great difficulties encountered in collecting and collating data from a sufficient number of sites and with adequate frequency over the huge areas involved. Extensive trapping and monitoring operations, together with the personnel, transport and support facilities required, are expensive. It has also been difficult to secure and maintain the necessary momentum, funding and cooperation between different states and regions. Further difficulties have arisen because spread can be erratic and inconsistent owing to seasonal vagaries in the weather or to other factors. These difficulties, and the problems encountered in assembling and maintaining a multidisciplinary team to exploit the full range of techniques available, explain why the approaches adopted have been selective and why there have been no appropriate long-term studies.

There has also been uncertainty concerning the precise significance of long-range dispersal and whether it is a rare, occasional, or episodic phenomenon occurring only in exceptional circumstances, or whether it is a recurring feature of consistent biological and economic importance. The sudden deposition of large numbers of immigrants over a short period of time and in restricted areas is clearly exceptional and such events are likely to attract attention. However, they may simply be extreme expressions of dispersive processes that occur much more regularly and frequently but pass largely unnoticed because insects are deposited diffusely over very large areas, as for *R. maidis* in most years.

There are additional uncertainties because it may be difficult to distinguish between spread from local and distant sources and there is a tendency to attach greater importance to a few nearby sources than to more numerous ones occurring much further away. There is less ambiguity in interpreting the occurrence of pathogens or vectors where no local sources of infection or vectors exist, although their absence is often difficult to establish beyond reasonable doubt. This explains the importance of insect catches on ships or oil platforms at sea and observations at remote or isolated sites. These feature prominently in the literature on long-range dispersal and first drew attention to the phenomenon. For example, early workers on sugarbeet curly top disease in the southwestern United States observed that infection occurred suddenly and in large amounts soon after crops were heavily infested by winged adults of the beet leafhopper (*Neoaliturus tenellus*, formerly *Circulifer* (*Eutettix*) *tenellus*). This occurred even in remote, irrigated plantings within arid areas far from the nearest possible sources (Ball 1917).

The beet leafhopper was later shown to be the vector of curly top virus, which is carried regularly into plantings over distances of hundreds of kilometres by migrants from weeds and other vegetation in the winter breeding grounds within the foothills of the mountain ranges. There have since been detailed studies on the annual movements of the beet leafhopper to and from the winter breeding grounds, on the weather conditions influencing population build-up, take-off and flight, on the utilization of energy during flight, and on methods of predicting the size, timing, distance and direction of flights (see Johnson 1969; Thresh 1986).

The only other detailed studies on the long-range movements of leafhopper vectors in North America have been on *Macrosteles fascifrons*, which transmits the aster yellows mycoplasma and oat blue dwarf virus. It behaves like *S. graminum* in that major influxes of adults into the northern United States and Canada from maturing cereal crops in the south are more important and occur earlier than populations originating locally from eggs (Chapman *et al.* 1965). *M. fascifrons* disperses northwards each year at much the same time and in similar conditions as those influencing cereal aphids (Peterson *et al.* 1969). Progress has been made in forecasting the magnitude and timing of the dispersal from an assessment of weather conditions, spring surveys of source regions and tests of the infectivity of vectors (Chapman 1974). There is no such information on the behaviour of the corn leafhopper (*Dalbulus maidis*) that transmits a mycoplasma and other pathogens of maize. The origins of the populations that occur annually in the continental United States are not known although an outbreak in Florida in 1979 was associated with hurricane winds across the Caribbean (Bradfute *et al.* 1981).

Outside North America, evidence has been obtained that the grain aphid *Macrosiphum miscanthi* was swept across the Tasman Sea in 1967 from Australia to the south island of New Zealand (Close & Tomlinson 1975). There is a continuing programme of research on long-range dispersal of other insect vectors in Australia (Seymour 1982). Similarly, a network of suction traps has been operating in Britain since the 1960s to monitor aphid movement throughout the growing season (Taylor 1974). This network has been extended to seven other European countries (Robert 1987). There have also been studies on the dispersal of several aphid species, including *R. maidis*, into Sweden from countries to the south (Wiktelius 1984).

Much less information is available from tropical and subtropical areas, although there is circumstantial evidence of long-range dispersal which may be a crucial feature of the epidemiology of several important virus diseases, including maize streak and groundnut rosette, in at least some parts of Africa (Thresh 1983). There is similar uncertainty concerning the role of long-range dispersal in the epidemiology of the whitefly-borne viruses now prevalent in many countries and of the viruses causing rice tungro disease in Southeast Asia and rice hoja blanca in South America. This is a serious limitation of current management strategies, as the effective range of dispersal is not known and it is not clear whether control measures have to be adopted on a regional scale to be fully effective.

A 'regional' approach is required to the problem of the rice brown planthopper (*Nilaparvata lugens*) in Asia (International Rice Research Institute 1979). Migrants spread northwards each year into Japan, northern China and other temperate rice-growing areas where overwintering is not possible. The annual influx into Japan and the associated weather conditions have been monitored intensively to develop forecasting methods. Similar studies have also been undertaken in China where there is evidence of a back migration southwards each autumn. There has also been a supporting programme of research including the use of radar (Riley *et al.* 1987), fuel utilization (Padgham 1983) and back-tracking procedures to locate possible source areas and the heights, distances and direction of flight (Rosenberg & Magor 1983, 1987).

Similarly detailed studies are required on a much wider range of virus vectors. Long-range dispersal is not receiving the degree of attention commensurate with its economic and biological importance. Moreover, studies are required not only on the timing and routes of dispersal but also on the biotypes of vector and virus strains involved. These aspects of dispersal have been unduly neglected, yet they are of great and increasing importance with the increased use of pesticides and of cultivars selected for their resistance to viruses or vectors. The emergence and dissemination of pesticide-resistant vectors or of vector biotypes or virus strains able to overcome host-plant resistance mechanisms has profound consequences for pest and disease control strategies.

This is apparent already from observations on cereal aphids and barley yellow dwarf virus in North America. The virus is very variable and those breeding for resistance are well aware of the need for information on the strains likely to be encountered and of the difficulties arising when inoculum is introduced periodically from afar each year and not always from the same source or of the same type (Paliwal 1982*a*; Rochow 1967). There have also been reports of the sudden appearance over a wide area of pesticide-resistant biotypes of *S. graminum*. This occurred in Texas, Oklahoma and North Dakota in 1973–4 when it became difficult to achieve satisfactory control by using standard applications of insecticide (Peters *et al.* 1975). Others in the United States have reported a new and possibly introduced biotype of *S. graminum* able to infest sorghum varieties that were previously resistant (Daniels 1981). The appearance of the new biotype was associated with a big change in the seasonal pattern of flight activity. These findings emphasize the importance of monitoring changes in vector biotypes and virus strains in future studies of long-range dispersal.

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Discussion

B. D. Harrison, F.R.S. (*Scottish Crop Research Institute, Dundee, U.K.*). How successful has Dr Irwin been in applying the information on long-distance dispersal of aphids to the epidemiology of soybean mosaic virus? Superficially, the data would seem more difficult to apply to this kind of virus, which is usually retained in vector aphids for less than an hour and can be transmitted by several aphid species, than to a virus which persists in its vectors for long periods and has only one vector species. Is his approach proving to be useful for studying systems of this second type?

M. E. Irwin. Unfortunately, our research has not reached the stage where the information generated on long-distance dispersal of aphids can be used to forecast aphid arrival or rates of epidemics of soybean mosaic virus. The value of such an approach is either (*a*) to provide data on whether a given specimen has travelled a long distance or (*b*) to develop a predictive capability for the arrival of aphids from afar. The former depends on our abilities to determine the level of flight fuels and deduce whether the specimen has flown for a considerable time. This we can do to a limited extent with *R. maidis*, although many complicating factors must still be worked out. We have but begun to understand the phenomenon of long-distance dispersal and cannot yet predict the event. It is likely that the research will allow prediction of virus spread in other systems more easily than it will with soybean mosaic virus. These systems include barley yellow dwarf and maize dwarf mosaic viruses. Prediction even in these systems is years and considerable research away.

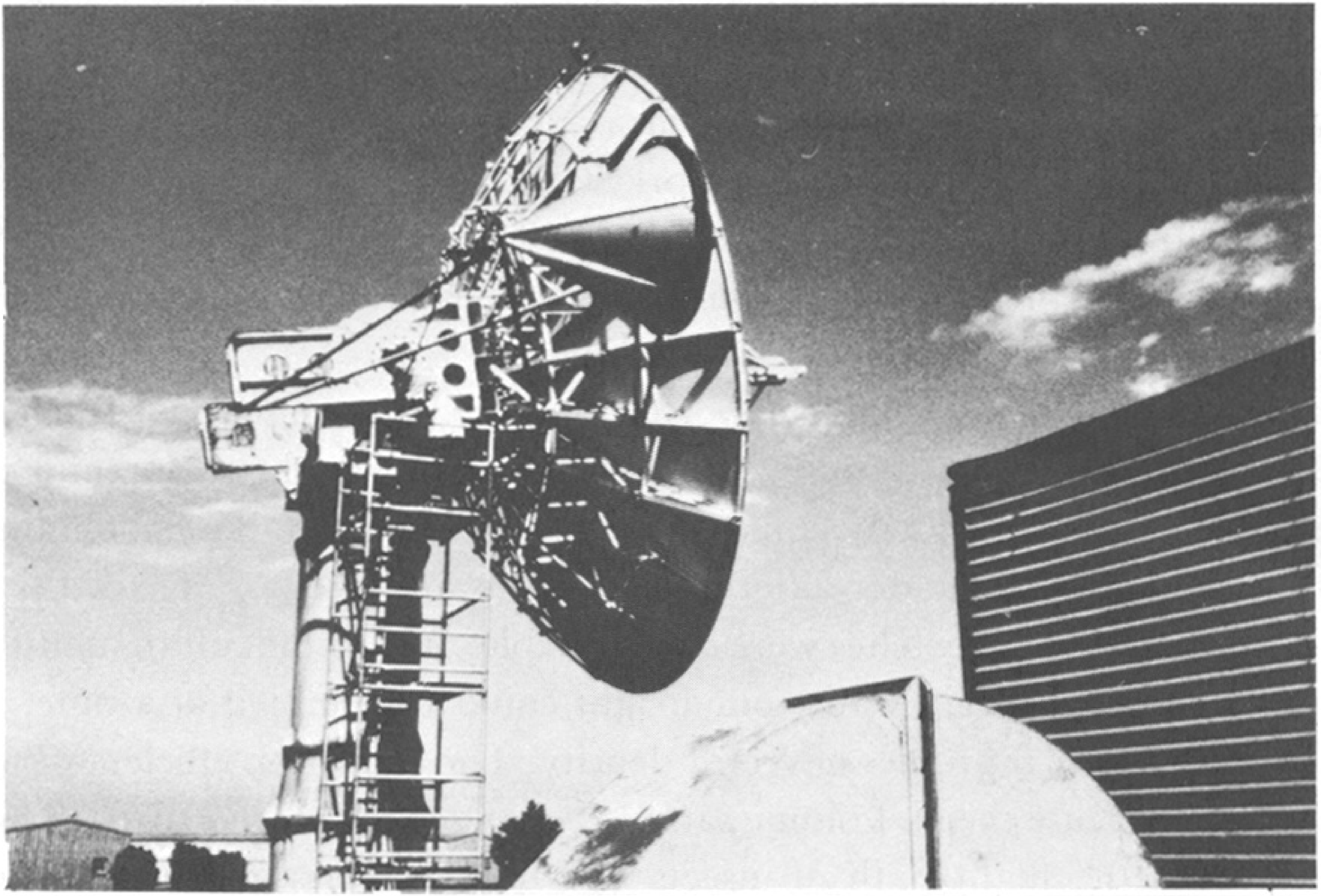

FIGURE 4. The CHILL radar at the University Airport south of Champaign, Illinois.

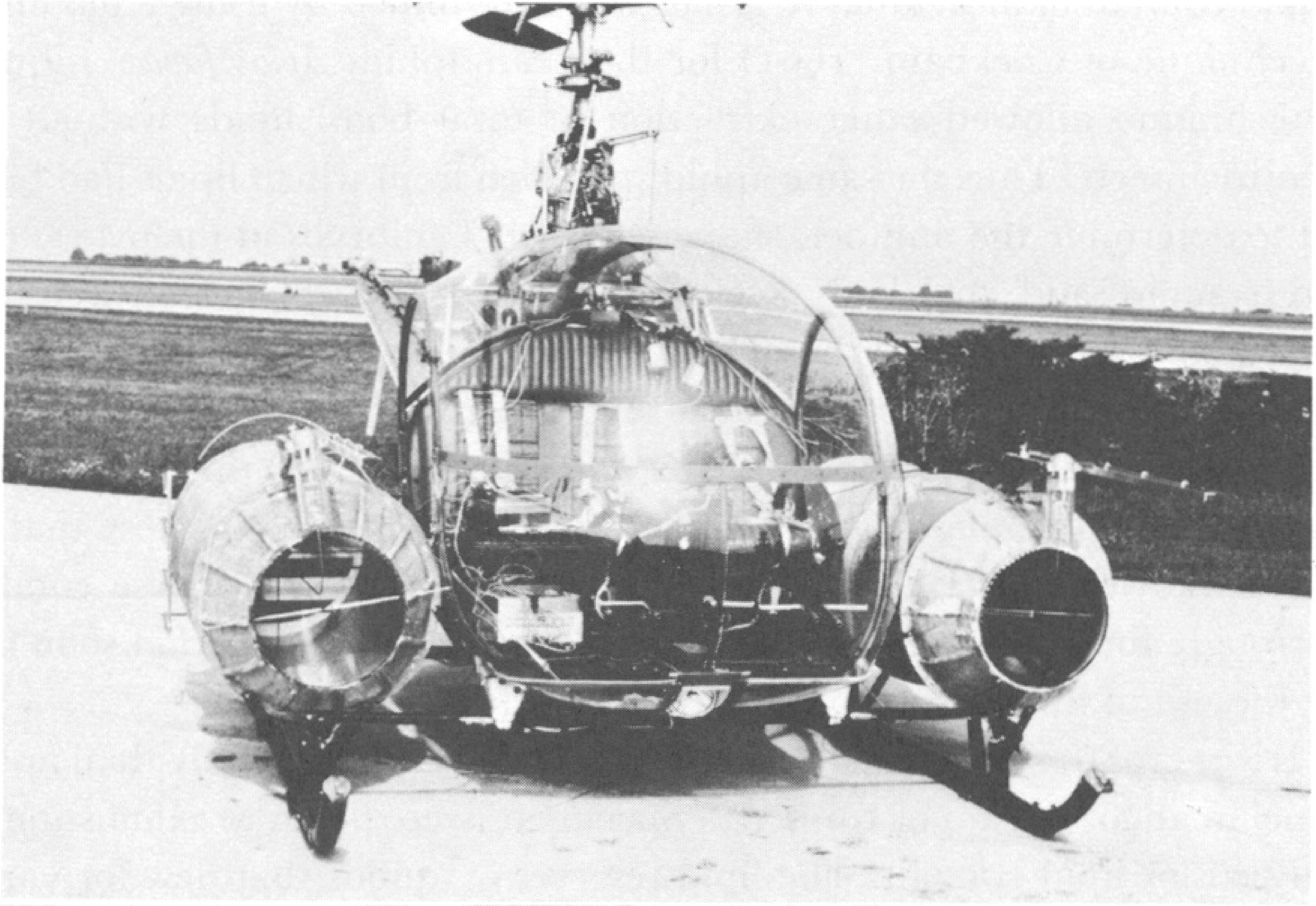

FIGURE 5. Two collectors fitted to the Hiller UH12D helicopter for aerial sampling.

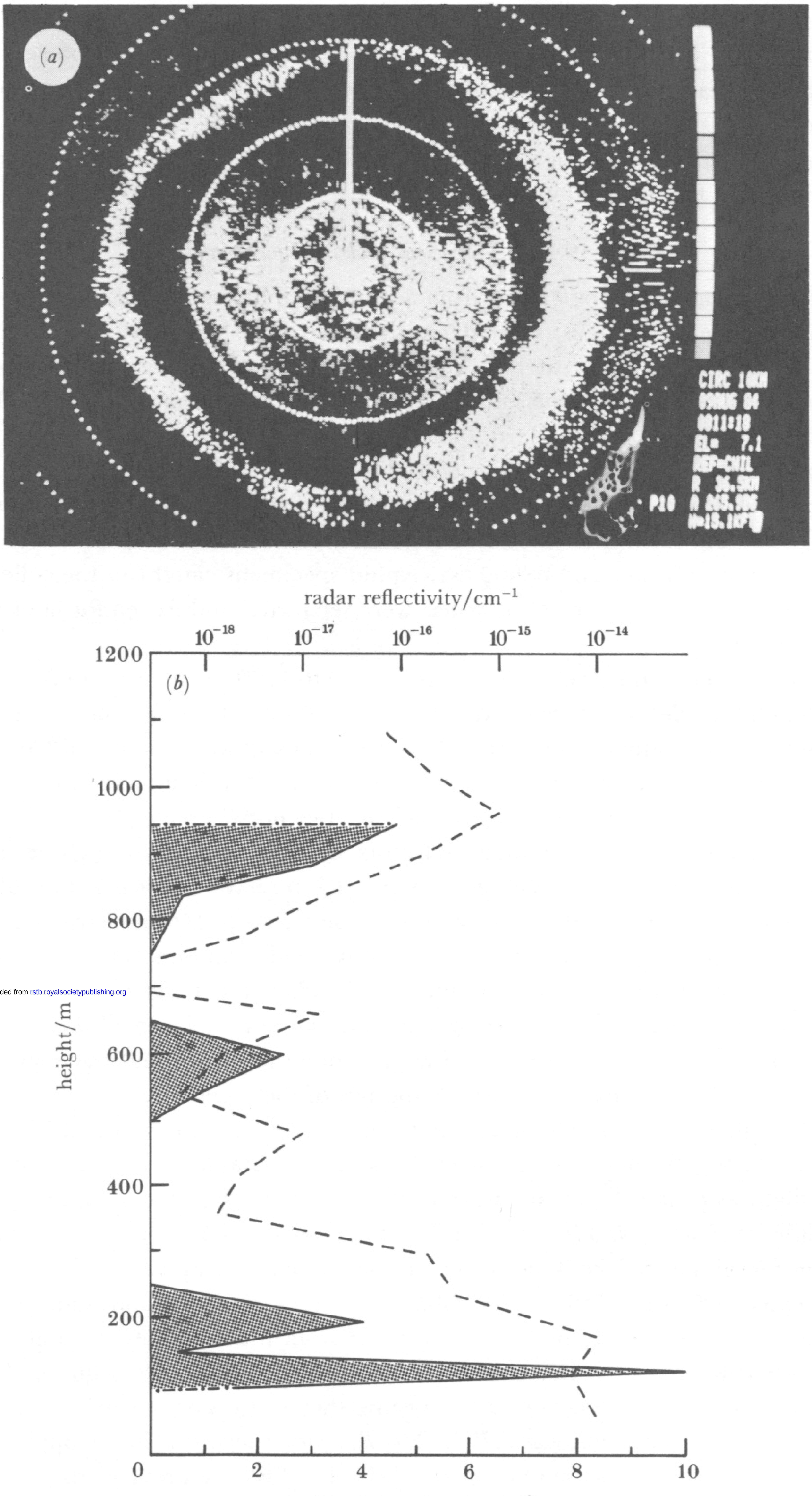

FIGURE 7. (*a*) A PPI taken from the CHILL radar on 9 August 1984 showing three distinct zones of insects. The upper zone (outermost irregular band) consisted of directionally orientated aphids. The middle zone and the one closest to the ground (inner band) contained a mixture of insects. (*b*) Vertical profile of insect density and radar reflectivity observed during flights of *R. maidis* over Champaign, Illinois at 06h35 CST on 9 August 1984. Adapted from Hendrie & Irwin (1987).