

## The Long-Range Dispersal of Plant Viruses by Arthropod Vectors [and Discussion]

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*Phil. Trans. R. Soc. Lond. B* 1983 **302**, 497-528

doi: 10.1098/rstb.1983.0071

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## The long-range dispersal of plant viruses by arthropod vectors

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Many plant viruses have winged or otherwise windborne insect or mite vectors that can fly or be blown far, suggesting that at least some of these viruses can be transported over great distances. However, this is difficult to substantiate and the evidence is largely circumstantial and mainly derived from studies on beet curly top and a few other viruses transmitted by leafhoppers, planthoppers or aphids.

This review considers the evidence for long-range dispersal of plant viruses in an overall ecological context that is also applicable to other types of host and pathogen. All the known or suspected examples are attributed to particularly active migrant forms of species that are well adapted for colonizing new habitats as the original ones deteriorate. It is concluded that distant spread occurs more frequently than is generally supposed and that it is an extreme expression of dispersive processes that occur repeatedly but over generally shorter distances. These conclusions are shown to be compatible with the view that plant viruses mainly cause 'crowd diseases' that do not spread far in any considerable amount and are amenable to control by isolation and other measures of crop hygiene.

### INTRODUCTION

Many plant viruses have arthropod vectors that can fly or otherwise be blown far. This raises the possibility that some of these viruses can sometimes be spread naturally over distances of tens or even hundreds of kilometres. The evidence for such long-range dispersal is considered in this review with particular emphasis on information obtained since previous assessments (Johnson 1967, 1969). The spread of viruses by pollen and their widespread dissemination through the extensive traffic in seed and other propagules are not discussed here; they have been reviewed recently elsewhere (Hewitt & Chiarappa 1977; Kahn 1982; Mandahar 1981).

### METHODS OF SPREAD

An effective means of spread is an essential requirement for all pathogens and is an important aspect of their overall 'epidemiological competence', using this term in the sense of Crosse (1967) for their ability to sustain the continuous sequence of infection necessary for survival. The precise requirements depend on the pathogen, on the type and range of hosts infected and on the habitats frequented. Nevertheless, in ecological terms there are obvious advantages in a dual strategy of dispersal that permits the colonization of new habitats and the exploitation of those already invaded (Thresh 1980). This is achieved by a single versatile means of spread or by two or more distinct but complementary methods that together achieve an effective distribution of inoculum.

In evaluating the different means of spread there are obviously great differences between viruses, bacteria and fungi and between facultative and obligate parasites in their ability to invade undamaged host tissue and to survive away from their hosts. There are also profound

differences between higher plants and vertebrate animals in the habitats they provide for viruses, notably the relative immobility of rooted plants, their inability to recover from infection by producing antibodies and the lack of suitable sites for the entry of virus particles or their release to the outside environment. These features account for the differences between the means of spread of viruses and other pathogens and between viruses of rooted plants and vertebrate animals.

TABLE 1. METHODS OF PLANT VIRUS SPREAD LOCALLY AND OVER GREATER DISTANCES

transmission	spread	
	local	distant
contact	+	-
pollen	+	±
seed†	+	+
vegetative propagules†	+	+
nematodes	+	-
soil fungi	+	-
arthropods: active forms	+	+
arthropods: less active	+	-

Distant spread is mainly through the traffic in commercial and other plant material.

Plant viruses exploit diverse means of spread (table 1), and it suffices here to discuss their overall effectiveness in distributing inoculum locally within plantings and over greater distances into or between them. Local spread leads to a progressive enlargement of existing outbreaks with little loss of inoculum except to plants already infected. However, spread is circumscribed, mainly to plants growing under the same conditions and in similar phase of development. Spread over greater distances is much more hazardous because much of the inoculum is carried into unfavourable habitats or beyond the range of susceptible hosts. Nevertheless it is of crucial importance in starting new outbreaks in additional areas or younger plantings as existing habitats become unfavourable.

In considering the nature and degree of epidemiological competence required of plant viruses it is important to appreciate the very diverse habitats provided by crops (table 2). Many of these are short-lived annuals grown for brief periods of the year in regions of markedly seasonal climate. They are often isolated in time from previous and later plantings and provide a transient habitat for viruses and vectors that encounter formidable problems of survival during the sometimes prolonged periods of drought or extreme cold. The risk of extinction is much less where susceptible crops are grown in continuous sequence throughout the year or as long-lived perennials. Many of these are propagated vegetatively and retained for many years at the same site or at a sequence of different sites.

These considerations explain why viruses with the necessary capacity to survive in sparse or ephemeral natural communities become prevalent and cause serious epidemics in crop stands, especially when irrigation, protection and other practices are adopted to extend the growing season and decrease the interval between successive crops. It is also apparent that there is no single optimum survival strategy and very diverse strategies are exploited with great differences between viruses in mode, pattern and rate of spread. Time is an unimportant factor in the epidemiology of viruses of perennial crops, whereas it is of crucial importance for those of short-lived annuals. Thus it is hardly surprising that many viruses of annual crops have

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arthropod vectors that are particularly well adapted to colonize and exploit transient habitats as they become available. Vectors of this type provide an effective and versatile means of virus spread locally within plantings and also over greater distances. Transmission by pollen is the only other natural means of spread that can be expected to achieve this. However, few viruses are transmitted between plants by pollen and there is no evidence of long-range spread in this way except the recent report that *Prunus* necrotic ringspot virus may be carried in or on pollen by bees, including those transported in hives between different states of U.S.A. (Mink 1983).

TABLE 2. SOME FEATURES OF CROP HABITATS INFLUENCING THE SPREAD OF VIRUS DISEASES

feature	spread	
	facilitated	impeded
host susceptibility	high	low
host longevity	long	short
plantings	many	few
stands	continuous sequential pure	scattered discrete mixed
spacing	close†	wide
sources of infection	many potent nearby	few less potent distant
growing seasons	long overlapping	short distinct
winter/dry season	mild short	extreme prolonged

† The spread of some aphid-borne viruses is decreased at particularly dense spacings that soon lead to a closed crop canopy that is unattractive to incoming migrants (see, for example, Hull 1964).

TABLE 3. REQUIREMENTS FOR LONG-RANGE SPREAD

- (1) source of virus and vector
- (2) suitably mobile vector
- (3) vector viruliferous at or soon after take-off
- (4) virus retained throughout flight
- (5) appropriate wind system (direction, duration, speed, temperature, humidity)
- (6) suitable 'target' (plants susceptible and vulnerable)

The ensuing discussion of long-range spread is concerned exclusively with arthropod-borne viruses and mainly those of annual crops transmitted by leafhoppers, planthoppers or aphids. There are several important requirements for long-range spread in this way (table 3). However, as stressed at many points in this review the available information on at least some of these features is seldom adequate for a definitive assessment of the evidence that distant spread occurs.

## SPREAD BY LEAFHOPPERS OR PLANTHOPPERS

Many pathogens that cause virus-like diseases of plants are transmitted by leafhoppers (Cicadoidea) or planthoppers (Fulgoroidea). Some of these diseases are now attributed to mycoplasmas, spiroplasmas or rickettsiae and are not considered in this review. However,

sugar-beet curly top and several other important diseases are known to be due to hopper-borne viruses that can be spread far. These viruses persist in their vectors for long periods and they are retained through the moult and in some instances for life. Several multiply in their vectors and pass to the progeny. Thus they are likely to be transmitted by winged migrants that have developed on infected host plants, and each infective vector can reach and inoculate many different plants during the course of its life. This compensates for the longer generation times, decreased rates of reproduction and generally smaller populations of hopper vectors compared with aphids and whiteflies.

The initiation, take-off, flight and subsequent settling of the active winged migrant forms of leafhopper and planthopper vectors have received less attention than has been given to equivalent studies of aphids. Nevertheless, the adults of several vector species are known to be unable or reluctant to fly at certain times, whereas at others they fly strongly and for prolonged periods and can disperse far.

*Beet curly top virus*

Sugar-beet curly top disease has caused serious problems in the southeast region of the U.S.A. since the end of the nineteenth century (Bennett 1971). Growers have long been aware that devastating outbreaks can develop suddenly and affect entire plantings over very extensive areas soon after a major influx of the beet leafhopper (*Circulifer (Neotalitrus) tenellus*). This was soon shown to be an efficient vector of the causal virus that also infects tomato, beans and many other crop or weed species.

The beet leafhopper overwinters mainly on the vast stands of herbaceous weeds that develop in the semi-desert areas and mountain foothills during the winter rains. Very large populations develop on the weeds during the spring breeding period, and enormous numbers of winged adults migrate to irrigated crops or summer weeds as the original hosts mature, deteriorate and die with the onset of the summer drought. The migration mainly involves sexually immature females, and Johnson (1969) has stressed that this is a general feature of many other migrant vectors with the important ecological effect of maximizing reproduction in the new environment.

There are seasonal and regional differences in the magnitude and timing of the annual migrations to and from the cultivated areas and in the proportion of spring migrants that are infective after having acquired curly top virus from weed hosts. Some crops, as in Idaho and in the San Joaquin valley of California (figure 1) are invaded regularly by leafhoppers from nearby breeding grounds. Other areas are invaded in at least some years, even though there are no sources in the entire region. Evidence of spread over great distances has been obtained by aerial trapping, field surveys (Annand *et al.* 1932), by using irrigation to establish 'trap' plots in arid areas (Dorst & Davis 1937) and by assessing changes in sex ratio (Lawson *et al.* 1951) or gut content (Fulton & Romney 1940) as a measure of distance travelled. Dispersal occurs regularly over great distances from the extensive overwintering areas in Arizona and New Mexico to give shallow gradients in the incidence of curly top virus in beet or other crops extending tens or hundreds of kilometres from the nearest breeding grounds (figure 2). There are also occasional reports of the beet leafhopper or curly top virus, or both being swept even further eastward to sites in Illinois, Indiana, Iowa, Kansas, Maryland, Minnesota and North Carolina (Bennett 1971).

There is evidence for the long range dispersal elsewhere in North America of other leafhoppers (Johnson 1969), aphid vectors (see later) and of mosquito vectors of viruses



affecting man or livestock (Sellers 1980). The evidence for leafhoppers mainly relates to *Empoasca fabae*, which is not a vector, and to *Macrostelus fascifrons*, which is only important as the vector of the aster yellows mycoplasma and is therefore beyond the immediate scope of this review.

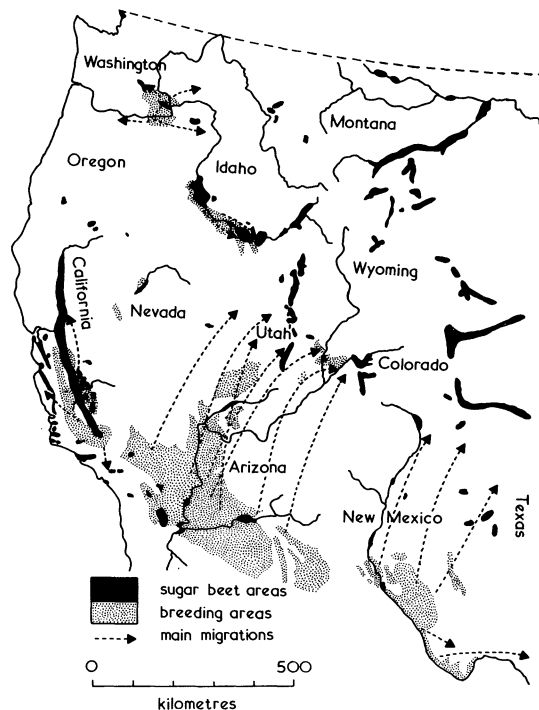


FIGURE 1. The long-distance spread of beet curly top virus by leafhoppers flying from breeding grounds in western U.S.A. (adapted from Douglass & Cook 1954).

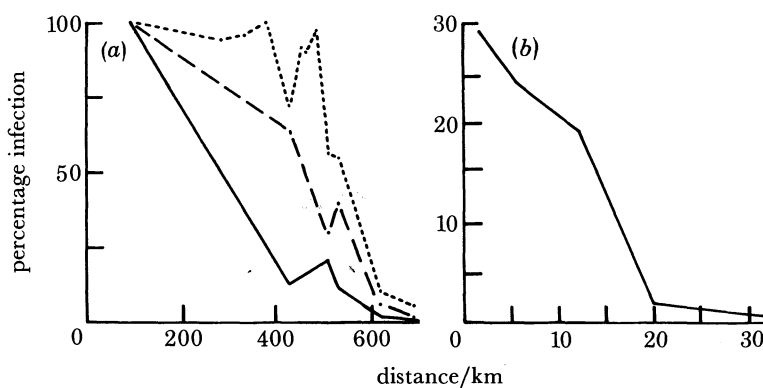


FIGURE 2. Gradients in the incidence of insect-borne viruses of sugar-beet in southwest U.S.A. (a) Beet curly top virus at different distances from breeding grounds of the leafhopper (Romney 1939); (b) beet mosaic virus at different distances from overwintered beet fields (Shepherd & Hills 1970).

#### *Sugar-cane Fiji disease virus*

Sugar-cane Fiji disease has been known in Australia for many years and a particularly damaging epidemic developed in Queensland during the 1970s (Egan & Hall 1983). This followed the introduction and widespread cultivation of the high-yielding South African variety NCo 310. The variety proved to be moderately susceptible to Fiji virus and highly susceptible

to its leafhopper vector (*Perkinsiella saccharicida*). Vector populations increased to unprecedented levels and this led to a rapid increase in the incidence of Fiji disease that had not previously been recorded in the area for several years.

Fiji disease was first recorded during the latest epidemic in 1969, when three farms were affected. The area with an overall incidence of disease exceeding 1% then increased rapidly from an estimated 10 km<sup>2</sup> in 1974 to 1400 km<sup>2</sup> in 1980 (figure 3). In annual surveys it was found that disease incidence decreased with distance from the original locality, and gradients of infection along sample transects of farms ultimately extended beyond 30 km (Egan & Hall 1983).

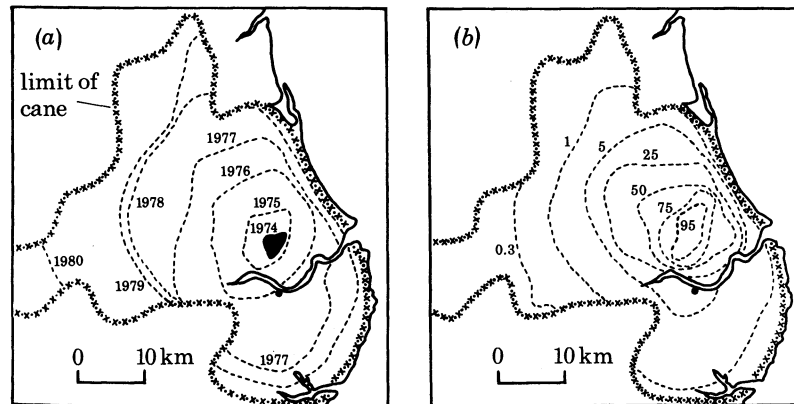


FIGURE 3. Sugar-cane Fiji disease in the Bundaberg district of Queensland (adapted from Egan & Hall 1983). (a) Annual changes in the area with an overall incidence of disease of 1% or more; (b) contours (percentages) in the incidence of disease established during the 1978 survey.

Such a rapid deterioration was partly due to the dissemination of infected planting material, but this was restricted or prohibited at an early stage of the epidemic; spread was attributed mainly to vectors. The nymphs are wingless and move only short distances between adjacent plants, while for much of the year the dispersal of winged adults is mainly within plantings or between adjoining fields. Thus Fiji disease tends to spread locally and appear in discrete patches. However, for about two months towards the end of summer, when vectors are most numerous, spread over much greater distances occurs as adults move to the tops of plants and fly off in great numbers (Bull 1981).

Mass swarms 300–500 m in diameter with a density of up to 50 individuals per cubic metre have been recorded during the main dispersal period and over such large areas as to be a nuisance to motorists and urban householders. Swarms occur occasionally 30 km out to sea and appear frequently more than 10 km from sugar-cane areas. New disease outbreaks have developed at sites far from known sources, including some used to raise planting material at least 4 km outside the main cane-growing areas. At one such site leafhoppers appeared at an estimated density of 2.2 per stalk (242500 ha<sup>-1</sup>) throughout a 56 ha field 8 km away from commercial plantings.

In view of these findings Fiji disease might have been expected to spread even faster from the original foci than actually occurred. However, the casual virus is only acquired by vectors as nymphs and in the early stage of the epidemic only a small proportion of the migrants dispersing great distances would have originated from infected plants. Many hoppers would have been swept outside the cane belt into urban, grassland or wooded areas, or out to sea. There

is also evidence that sugar-cane is somewhat resistant to infection and that only a proportion of the vectors that develop on infected plants become infective. Fiji virus persists throughout the life of any vectors that do become infective, but it is not known whether it affects their fecundity, longevity or flight capacity. Differences within populations of the type observed with *Cicadulina* spp. (see next section) have not been reported but may not have been sought.

#### *Maize streak virus*

Maize streak virus causes serious diseases of maize, sugar-cane, millet and wheat and also infects many grasses. The virus occurs in southeast Asia and Africa south of the Sahara. It is transmitted persistently by several leafhopper species of the genus *Cicadulina* that feed on cereals and grasses.

The most detailed studies on the epidemiology of maize streak disease have been in Zimbabwe, where two contrasting types of spread have been observed (Rose 1974). Throughout much of the year leafhopper vectors were seldom caught in suction traps at 8–10 m and few invaded crops from surrounding areas of grassland. The only crops then at serious risk were immediately alongside infested cereals or grassland and gradients of infection into such crops were steep. The overall disease incidence was generally low and foci tended to be scattered and increased slowly. By comparison, large numbers of leafhoppers were caught at the end of the

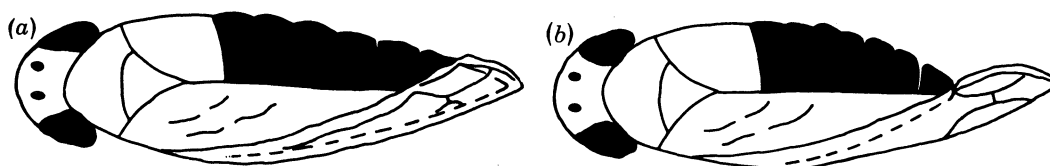


FIGURE 4. Long-bodied (a) and short-bodied (b) forms of *Cicadulina* spp., vectors of maize streak virus in Zimbabwe (Rose 1972).

summer rainy season as the grasses began to mature and dry out. Young irrigated crops were then invaded by large numbers of leafhoppers, even at sites far from the nearest known sources. The incoming vectors seldom settled for long and populations were continually changing. This led to rapid 'exponential' increases in the incidence of infection, mainly due to secondary spread around initial foci started by incoming migrants.

Marked differences were found within populations of adult leafhoppers in their ability to fly. 'Long fliers' flew for long periods when tethered on pins and tended to be short-bodied (figure 4). These forms predominated during the main flight period, whereas short fliers with relatively long bodies predominated at other times (Rose 1972). Laboratory experiments indicated a mean flight duration of about 15 s for short fliers, giving an estimated range of only 4–12 m without wind assistance. The equivalent mean flight time for long fliers was 500 s, but there was great variation between individuals. Half could have travelled 1.8 km downwind in a single flight at the usual wind speeds encountered, and some could have travelled 118 km (Rose 1973).

Short-bodied forms seem less fecund than those with long bodies. Thus field populations of leafhoppers contain a balance of long-bodied, poor fliers that are well adapted for reproduction in the favourable grass habitats that are widespread during the wet summer months, and short-bodied, strong fliers suited for dispersal to more favourable habitats as the original ones



deteriorate. This type of structural and behavioural polymorphism has obvious survival value for leafhoppers inhabiting grassland areas subject to periodic drought. It facilitates the colonization and subsequent exploitation of suitable habitats as they become available and also provides an effective means of virus spread.

The studies in Zimbabwe are important in explaining seasonal differences in the pattern and sequence of spread of maize streak and in the effectiveness of isolation and roguing as control measures. The findings are likely to be relevant in other areas and with other diseases and not only to those caused by leafhopper-borne viruses.

#### *Rice hoja blanca virus*

Rice hoja blanca is the most important disease of rice in the Western Hemisphere. The causal agent is believed to be a virus and it is transmitted persistently by the planthoppers *Sogatodes oryzicola* and *S. cubanus*. These occur as long-winged (macropterous) and short-winged (brachypterous) forms of very different mobility.

Infection is prevalent in many parts of Central and South America and has also been reported occasionally in the rice-growing areas of the southern U.S.A. The infestations of vectors that occurred in 1959, 1962 and 1964 were apparently eliminated by subsequent winter frosts or by using insecticides. Later infestations have been attributed to spread from Cuba by cyclonic or hurricane winds (Everett & Lamey 1969). This is possible because macropterae can be transported far, and Cuba provides an extensive endemic source within the tropics that is only *ca.* 220 km from the southern tip of Florida and *ca.* 1000 km from Louisiana and Mississippi. The situation seems to resemble that encountered with other planthopper-borne viruses of rice in the Far East, which are discussed in the next section. However, the circumstances in which dispersal occurs into the U.S.A. and evidence of spread in this way have not been determined.

#### *Rice grassy stunt and ragged stunt viruses*

Serious losses have occurred recently in many of the rice-growing areas of the Far East, due to the brown planthopper *Nilaparvata lugens*. This causes direct damage referred to as 'hopper burn' and also transmits rice ragged stunt and grassy stunt viruses (Rivera *et al.* 1966; Hibino 1979). Adult hoppers occur as non-flying brachypterae with rudimentary wings that soon settle to feed and reproduce and active macropterae with well developed wings that do not usually settle or feed before dispersing (Kisimoto 1968). The great differences in mobility between these 'colonizers' and 'exploiters' explains why outbreaks due largely to populations of brachypterae can be localized in discrete patches, even though initiated by incoming macropterae from afar.

*N. lugens* occurs throughout the rice-growing areas of the Far East from Korea and Japan to the East Indies and northern Australia (Dyck & Thomas 1979). In tropical areas breeding is continuous wherever crops are available, and there are numerous generations a year. At higher latitudes rice is grown only during the summer period and there is little or no survival during the cold winter months. Plantings are reinvaded annually by migrants from warmer areas towards the Equator, and few generations are produced before crops are harvested.

The annual invasion of crops by macropterae was first studied in detail in Japan, where hoppers rarely survive the winter and yet reappear regularly each summer and sometimes cause very damaging outbreaks. Incoming migrants are usually seen first and in greatest numbers in the southwest parts of the south island of Kyushu; more northerly areas are affected later

and to a lesser extent (figure 5). Migrants have also been caught in large numbers at sea from a weather station *ca.* 500 km south of mainland Japan and from a fisheries research vessel in the East China Sea. Back-tracking procedures suggest that the main migrations originate in mainland China between 25° and 35° N, but the precise source is not known (Kisimoto 1971, 1976).

Studies in China have shown migrations northward in late spring and summer, and southward in autumn. The main overwintering zones are usually south of latitude 22° N (Tu 1980) and more northerly areas are invaded by successive migrations that ultimately extend into Korea (figure 5). Evidence of comparable migrations within the tropics has not been sought until recently, although *N. lugens* has been caught at sea off the Philippine islands (Saxena & Justo 1980). This suggests that populations intermingle and are redistributed within and beyond areas where rice is grown throughout the year and do not remain localized as formerly assumed.

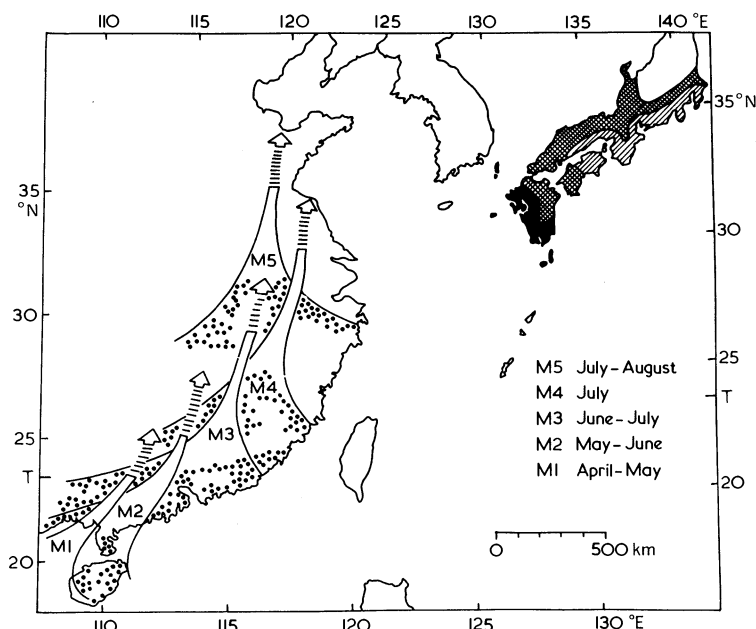


FIGURE 5. Map of eastern Asia showing successive northerly migrations of the rice brown planthopper (*Nilaparvata lugens*) across China during the summer of 1977 (adapted from Cheng *et al.* 1979). The overwintering areas in China are south of 25° N. The degree of shading in Japan indicates the intensity of the annual influx of immigrant planthoppers (Hirao 1979).

These findings are of obvious importance in studying the epidemiology and control of rice grassy stunt and ragged stunt viruses. However, these have received little attention in relation to that given to hopper burn and were not seen until 1963 and 1977, respectively. They are now known to occur in many rice-growing countries including Indonesia, where grassy stunt caused particularly serious losses in 1974 (Mochida & Tatang 1976). The viruses have also been reported in southern Japan, where they do not infect overwintering hosts and are assumed to be reintroduced each year by incoming migrants (K. Kiritani, personal communication). The situation is likely to be similar in central and northern China, Korea and elsewhere, but definitive information may be difficult to obtain because virologists in many countries of the Far East are few in relation to the number of entomologists. There is obvious scope for collaborative work in monitoring the infectivity of migrating vectors caught in traps. This has

been done already for *Laodelphax striatellus*, the planthopper vector of rice stripe virus in Japan, and infective macropterae have been taken at sea, suggesting that the virus can be transported far (R. Kisimoto, unpublished). It may eventually be shown that ragged stunt, grassy stunt, hoja blanca and some other hopper-borne viruses of rice resemble several insect-borne viruses of livestock in spreading regularly from endemic areas in the tropics to cause seasonal epidemics at higher latitudes during the warm summer months (Sellers 1980).

#### SPREAD BY APHIDS

Aphids form the most important single group of virus vectors, and the efficiency with which they disseminate a wide range of viruses of diverse size, structure and transmission characteristics has long been recognized. Some of the most important features of aphids that contribute to their overall effectiveness as vectors are the ability to reproduce rapidly and produce winged adults (alatae) at certain stages of the life cycle. The alates do not readily settle to feed or reproduce before they take off on a migratory flight, during which they can be swept high into the air and carried downwind for considerable distances. This provides an efficient means of transferring a portion of the population of sexually immature adults to new hosts or habitats as the existing ones become crowded or begin to deteriorate and become unsuitable for further breeding. There is also an opportunity for viruses to be spread far by alates that are infective on initial take-off or acquire viruses while dispersing.

The migratory behaviour of aphids differs between species and sometimes between regions (Kring 1972). Some migrations are between primary, woody and secondary herbaceous hosts, whereas others are between a succession of herbaceous plants at different stages of growth. Dispersal takes precedence over host-finding and reproduction during the migratory phase, and alates of some species alight, probe and take off repeatedly from host and non-host species until the wing muscles begin to deteriorate and reproduction commences. This behaviour greatly facilitates the spread of those viruses that are acquired and transmitted in brief feeding probes. Indeed, some of these viruses are transmitted very effectively by aphid vectors that do not settle, feed or breed within the crops affected.

There is abundant evidence that migrating aphids can disperse far and this has been obtained by trapping from kites, aircraft or balloons and from observations on the occurrence of aphids at sea, on glaciers or snowfields and in deserts remote from any possible source (Johnson 1969). The long-range dispersal of viruses by aphids is less readily established and it is appropriate to assess the available evidence in relation to the transmission characteristics of the viruses considered, because this influences the likelihood of spread over considerable distances.

#### *Persistent or semi-persistent viruses*

The evidence for long-range dispersal by aphids mainly relates to persistent viruses that are retained for periods of several days by their vectors, whether these are starved or allowed access to non-host plants. Many important viruses are of this type and they are more likely to be spread far than viruses retained for shorter periods.

#### *Barley yellow dwarf virus*

It has been known for many years that several aphid species can be found regularly on cereal crops in the north-central states of the U.S.A. and adjoining parts of Canada, where anholocyclic populations cannot survive the severe winters on cereals and before populations have had time

to develop from eggs overwintering on woody, primary hosts. Alate aphids sometimes appear suddenly in great numbers and over very large areas, suggesting an influx from southerly states where conditions are favourable for overwintering and where cereals are sown and mature earlier than in the north.

Particular attention has been given to the greenbug *Schizaphis (Toxoptera) graminum* that directly damages cereals and also transmits some strains of barley yellow dwarf virus. Damaging greenbug infestations occurred in Minnesota in 1926 and 1927, when the nearest source was considered to be about 330 km southward (Wadley 1931). More recent influxes include those into Minnesota and Wisconsin in 1959, when the sources were thought to be even further away in Oklahoma, Texas, Kansas or Missouri (Hodson & Cook 1960; Medler & Smith 1960).

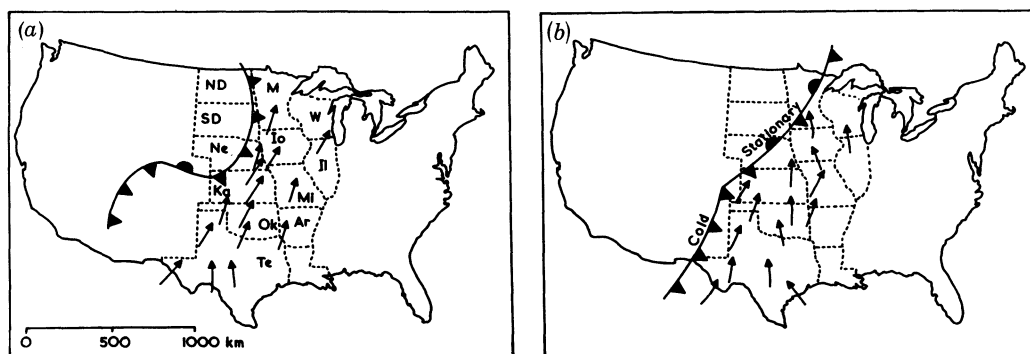


FIGURE 6. Weather conditions at 12h00 on 3 and 4 May 1959 ((a) and (b) respectively) associated with the dispersal of the greenbug (*Toxoptera graminum*) into Minnesota (adapted from Hodson & Cook 1960). Abbreviations: Te, Texas; Ok, Oklahoma; Ar, Arkansas; Mi, Missouri; Ka, Kansas; Ne, Nebraska; Io, Iowa; Il, Illinois; ND, North Dakota; SD, South Dakota; M, Minnesota; W, Wisconsin.

Migrations over these great distances are associated with sustained south or southwest winds blowing over crops maturing in the south and on into northerly states and Canada (figure 6). Suitable winds occur during spring and early summer as a warm southerly air stream becomes established over much of central U.S.A. (Medler 1962). Moreover, aphids can be swept northwards very rapidly by fast, low level jet-stream winds of up to 90–110 km h<sup>-1</sup> blowing at 300–1000 m and sometimes for several days. The jet-stream winds seem to be particularly important and their incidence has been related to the first appearance of *S. graminum* in Iowa and to the occurrence of barley yellow dwarf virus 2–3 weeks later (Wallin *et al.* 1967; Wallin & Loonan 1971 *a*). Similar observations have been made on the appearance of *S. graminum* and other cereal aphids in South Dakota, where infestations were usually seen during or soon after southerly jet-stream winds (Kieckhefer *et al.* 1974). It was concluded that many of the cereal aphids arriving in the state were brought in by such winds, although only some jets led to a detectable influx. This is hardly surprising because an influx is likely to occur and be recorded only when conditions are suitable for numerous aphids to develop and take off, and then to land and become established in parts of the catchment zone that are being monitored.

Aphid establishment and virus spread in Iowa tend to be greatest when crops are invaded at the vulnerable early stage of growth and when conditions are warm and relatively dry during the week after aphid fall-out has occurred (Wallin & Loonan 1971 *a*). Some attention has also been given to factors influencing aphid populations in the source areas. Rainfall during the autumn and winter months appears to be important in Texas and Oklahoma (Wallin & Loonan



1971*b*) and the appearance in 1968 of a new biotype of *S. graminum* that infests sorghum has led to a great increase in total aphid populations on southern cereals (Daniels 1981). However, there is a continuing need for extensive monitoring and more detailed studies, adopting a closely integrated team approach involving entomologists and virologists in the source and catchment areas. Only in this way and with the full cooperation of meteorologists will it be possible to determine the origins of the aphids periodically carried northwards and whether they come from the same areas at all times during the migration period and in different years. It may eventually be possible to determine the precise conditions in which deposition occurs and the probability of damaging infestations occurring in the various parts of the very extensive northern catchment zone. This information will facilitate the development of reliable forecasting methods so that insecticides, resistant varieties and other control measures can be used more efficiently than at present.

Barley yellow dwarf virus is so widespread and has such a wide host range in the Gramineae, including pasture grasses, oats, wheat, barley, maize and possibly rice, that long-range dispersal is unlikely to occur only in parts of North America. This suggests that the results obtained there may be generally applicable elsewhere, including parts of South America, Africa and Australasia, where cereals are grown seasonally in areas where hosts of barley yellow dwarf virus and its vectors are unable to persist throughout the year because of long periods of extreme drought or cold. Indeed, the opportunities for long-range migration seem greater for cereal aphids than for any other group of vectors because of the vast numbers produced over huge areas and because cereals and grasses provide such transient habitats for aphids. This leads to great fluctuations in populations and periodic migrations between woody and herbaceous plants or between herbaceous plants in different phases of growth.

These migrations can be spectacular and involve enormous numbers of aphids, as recorded recently into Ontario, Canada (Rose *et al.* 1975) and over Northern Europe (Dewar *et al.* 1980). The full significance of such migrations in relation to the epidemiology of barley yellow dwarf virus has yet to be established (Bruehl 1961; Plumb 1983). The situation is complicated by the very diverse cropping patterns adopted in different areas of the world, involving spring-sown or autumn-sown cereals, summer crops of rice or maize and longer-term plantings of grass leys or permanent pastures. Moreover, it is known that at least in some circumstances cereal aphids reproduce more rapidly, live longer and produce a greater number of alates on virus-infected plants compared with healthy ones (Markkula & Laurema 1964; Miller & Coons 1964; Gildow 1980).

#### *Potato leafroll virus*

Potato leafroll virus is transmitted in the persistent manner by *Myzus persicae* and several other aphid species. The virus is also widely disseminated around the world in tubers and probably occurs wherever the crop is grown.

Spread by aphids mainly occurs early in the growing season as potato crops are infested by incoming alates. These usually originate from other hosts, acquire virus within potato plantings and lead to local spread over short distances within crops around initial foci of infection (Hille Ris Lambers 1955).

There is an opportunity for leafroll to be spread over greater distances during the later summer migrations, when alates move between potato crops. Spread over several hundred metres has been reported in England (Doncaster & Gregory 1948). Elsewhere there is a report



from the Netherlands of spread over about 100 km (Hille Ris Lambers 1955). This occurred in 1951 when leafroll became prevalent in northern areas after a sudden influx of alate *M. persicae* from the southwest. Sudden increases in trap catches of *M. persicae* in areas where few aphids were present locally were also detected in central England on two occasions in July 1947 (Hurst 1969; Johnson 1969). The resulting infestations were associated with extensive spread of potato viruses, and the calculated trajectories suggested that the aphids originated 200–300 km away in mainland Europe or in eastern England (figure 7).

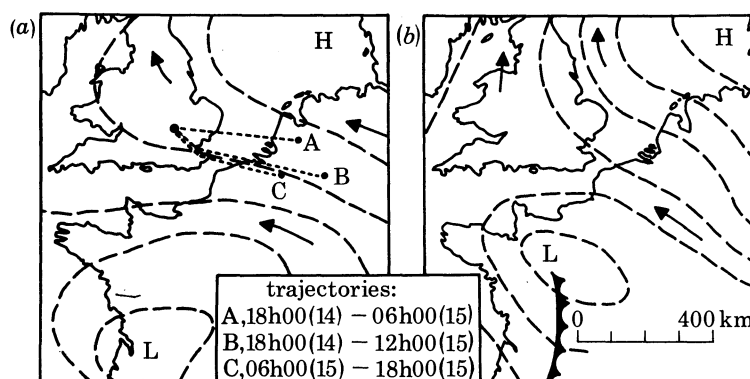


FIGURE 7. Synoptic charts for (a) 00h01 and (b) 12h00 G.M.T. on 15 July 1947 and wind flow associated with large aerial densities of *Myzus persicae* over central England. The trajectories were calculated assuming 12 or 18 h flights from 18h00 on 14 July or 06h00 on 15 July. (Adapted from Hurst (1969).)

Potatoes are grown so widely and in so many countries that long-range dispersal could occur frequently, even though it is seldom detected. However, Doncaster & Gregory (1948) point out that spread in this way is usually unimportant compared with local spread within crops from foci introduced at planting by the use of contaminated stocks of tubers.

#### *Sugar-beet yellowing viruses*

Virus yellows is an important disease of sugar-beet caused by three aphid-borne viruses acting singly or in combination. The most important vector is *Myzus persicae* that is attracted to and thrives particularly well on virus-infected plants (Hijner & Cordon 1953).

Sugar-beet is a widely grown crop and can support large aphid populations so that there is an opportunity for spread into or between crops over considerable distances. Gradients of infection extending over several kilometres have been recorded around overwintering sites in England (Hull 1965) and over *ca.* 20 km in California (Shepherd & Hills 1970). Evidence for spread over greater distances has come from Sweden, where yellows is seldom important because of the limited survival of vectors and host plants during the cold winters. Infection usually occurs late in the growing season and spreads slowly, but sometimes a sudden influx of aphids occurs in mid-summer and leads to severe losses. A particularly serious epidemic developed in 1959, when swarms of aphids appeared in July and crops were almost totally infected by October. Two continental strains of yellows virus became prevalent where previously they had been rare and crops in Gotland and Finland were infected for the first time (Björling & Mollerström 1974). Such rapid and extensive spread was attributed to an influx of infective aphids from across the Baltic Sea, although the migration was not monitored and the source was not located.

Additional circumstantial evidence of long-range dispersal northwards into southern Sweden has been obtained by analysing data on the final incidence of yellows during the years 1961–75 in relation to weather conditions (Wikteliuſ 1977). The highest incidence of yellows during the period was in 1964, when there was the greatest southerly air flow into Sweden during June and July, as based on windspeed and duration. Moreover, the most important single weather variables considered over the entire 15 year period were the southerly air flows in June and July or in July alone (figure 8). Winter and spring temperatures appeared relatively

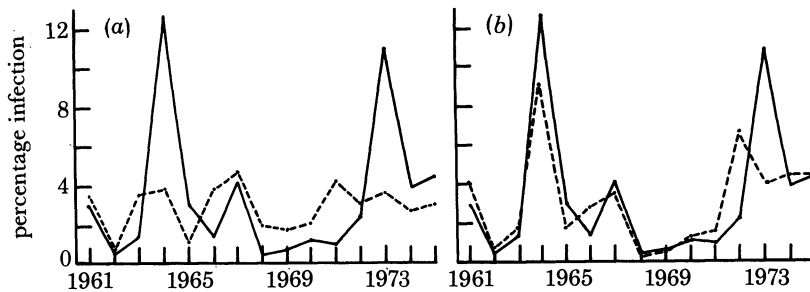


FIGURE 8. The annual incidence of beet virus yellows in Sweden at the end of September, 1961–75. Actual values (—) and estimated values (----) from multiple regressions based on (a) number of frost days in March and mean May temperatures or (b) number of frost days in March, mean May temperatures and southerly airflow in June and July. (Adapted from Wikteliuſ (1977).)

unimportant and it was concluded that infective aphids from mainland Europe were more important than those overwintering in Sweden. Additional information on aphid migrations in countries around the Baltic Sea should soon be available now that suction traps are being operated in Denmark, Sweden and possibly Poland (Taylor 1983). There is a precedent for spread across the Baltic in that the 1966 outbreak of foot-and-mouth disease of livestock was attributed to windborne inoculum from Denmark (Gloster *et al.* 1982).

#### *Subterranean clover stunt virus*

Subterranean clover stunt virus causes important diseases of subterranean clover and other pasture legumes in southern Australia (Grylls & Butler 1959). The virus is transmitted in the persistent manner by the cowpea aphid (*Aphis craccivora*), which is an introduced species in Australia, where eggs and males are unknown. Anholocyclic populations occur throughout the year and fluctuate according to temperature and rainfall conditions influencing the survival and reproduction of the aphid and its host plants.

*A. craccivora* is very sensitive to weather conditions and these become unfavourable for plant growth and aphid survival over large tracts of southern Australia during the hot, arid summer months (figure 10) (Gutierrez *et al.* 1974 *b*). Many of the drought-affected areas soon become favourable after the autumn rains have stimulated the germination and growth of pasture legumes, some of which are colonized by alate aphids migrating from populations that persist throughout the summer in the cooler upland areas or along the coast. Conditions again become generally unfavourable over much of the region with the onset of winter frosts, and aphid populations decline and die out over large areas, although some are colonized or recolonized in spring by aphids from relatively mild parts of northern New South Wales and Queensland.

Johnson (1957) described a particularly spectacular spring migration over distances of several hundred kilometres into the coastal districts around Sydney. More recent migrations

## DISPERSAL OF PLANT VIRUSES

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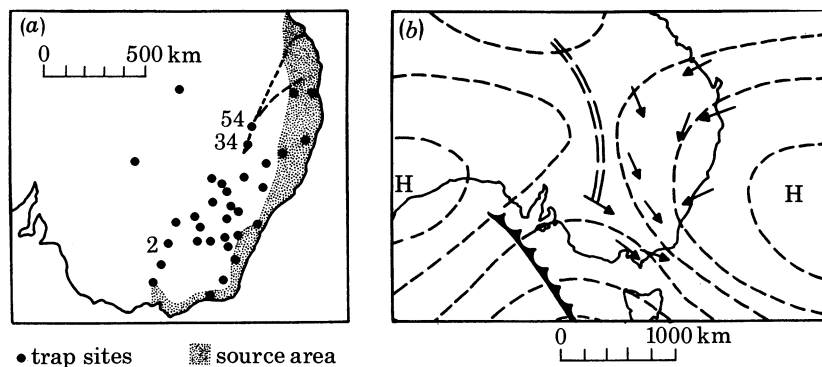


FIGURE 9. A long-range migration of *Aphis craccivora* in southeast Australia (adapted from Gutierrez *et al.* 1974*b*). (a) Trap sites and aphid catches on 22 February 1970 and possible trajectories from source areas along the coast; (b) the synoptic weather pattern in the area at 09h00 on 22 February 1970.

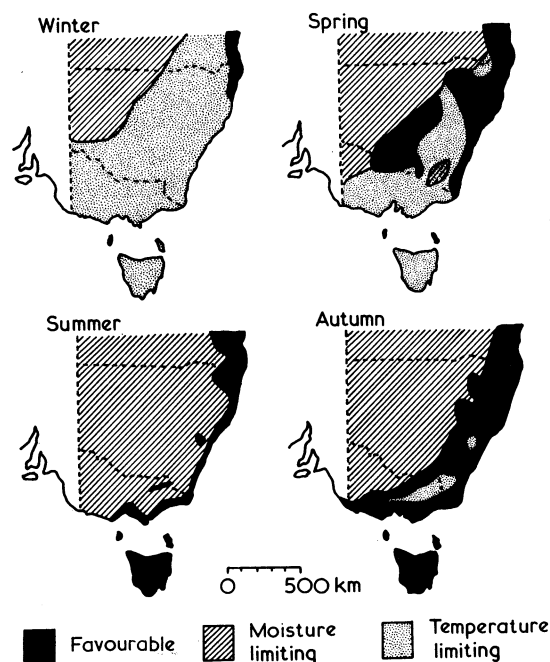


FIGURE 10. Quarterly maps of southeast Australia showing areas where rainfall and temperatures are generally favourable for the development of *A. craccivora* based on 30 year means. Outside the black areas conditions are generally unfavourable because of low temperatures or moisture stress. (After Gutierrez *et al.* (1974*b*).)

were recorded and analysed by Gutierrez *et al.* (1971, 1974*a, b*) (figure 9), who discuss the annual cycle of colonization and recolonization in relation to the epidemiology of subterranean clover stunt virus. They observed virus spread into pastures by incoming autumn migrants that could not have developed locally and that must have originated outside the area. Virus symptoms first appeared 3–4 weeks after the influx of aphids, and the initial incidence of infection was usually low. It tended to be greatest around the margins of fields, along drainage channels and among weak or sparsely distributed plants growing against a background of bare soil. It is well known that such plants are particularly prone to aphid infestation and they were considered to be important foci for secondary spread of virus because they were unlikely to have been killed off by competition from healthy neighbours.

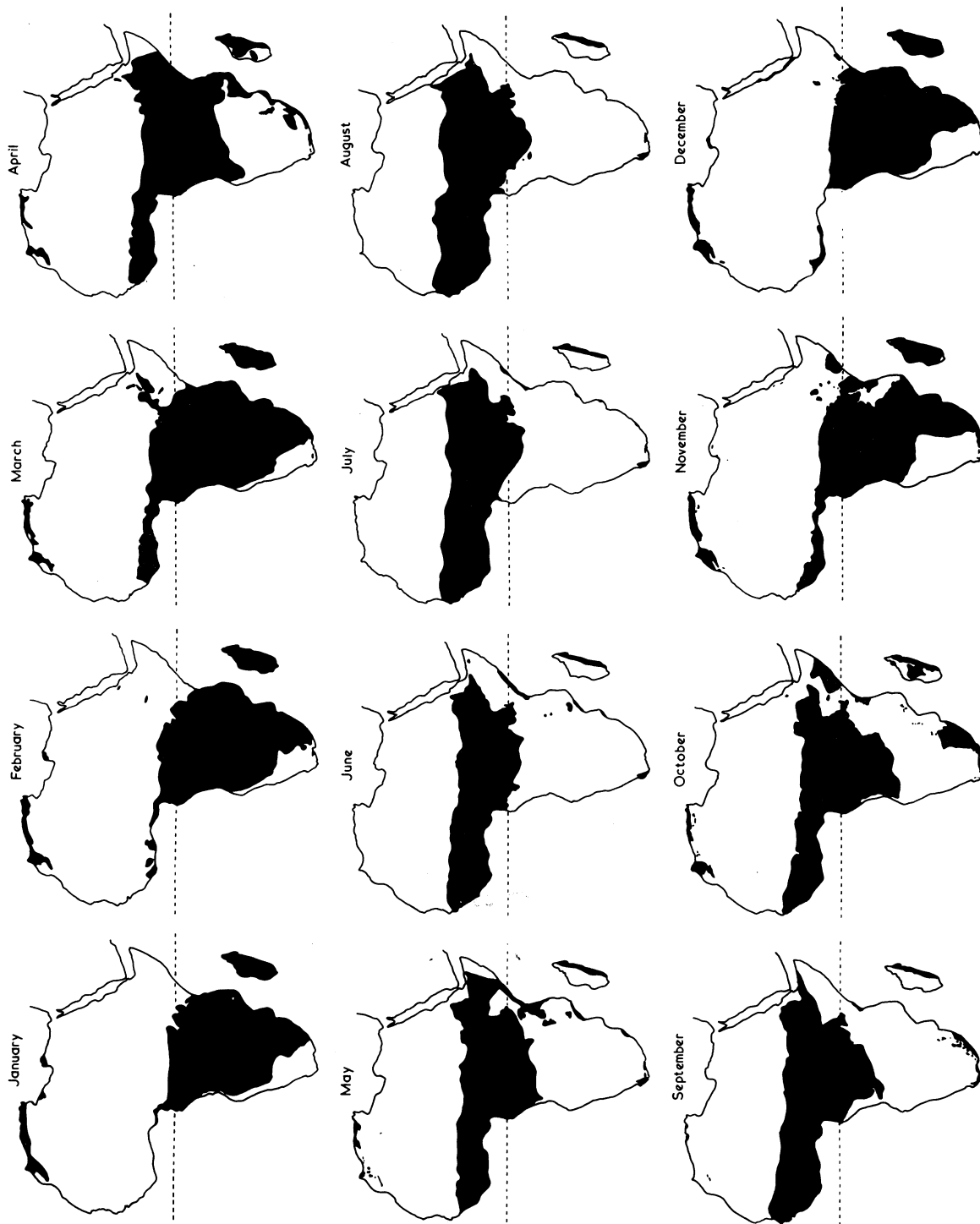


FIGURE 11. Monthly maps showing regions in Africa receiving more than 50 mm of rain. Note the seasonal movement of the equatorial rain belt northwards and then southwards, associated with movements of the Inter-Tropical Front. (Adapted from Thompson (1965).)

Regional maps were produced showing for each season the areas of southeast Australia considered suitable for *A. craccivora*, based on yearly or 30 year means of rainfall and temperature and computer models of aphid population dynamics and host plant growth (figure 10). *A. craccivora* has been described as a 'super-migrant' (Gutierrez *et al.* 1971) because of several important features that enable it to survive very effectively on the seasonal, continually shifting habitats available over much of its range. For example, the aphid has a rapid rate of development and high reproductive potential compared with other species. It also has a low population density threshold for alate production and produces a large proportion of migrant forms early in its population growth. These attributes enable the aphid to reach and exploit a sequence of transient habitats as they become available. They also explain the survival of clover stunt despite the periodic obliteration of its host plants over very large areas.

The approach adopted by Gutierrez and coworkers in using plant and insect physiological data to develop a regional phenology of *A. craccivora* has several novel features and merits more attention than it has so far received. The methods are likely to be applicable to other species, and provide a basis for detailed studies on any further outbreaks of clover stunt or of other viruses transmitted by *A. craccivora*.

#### *Groundnut rosette virus*

*A. craccivora* is the main vector of the virus or viruses causing groundnut rosette disease, which is prevalent in India and many parts of Africa. The precise aetiology of the disease is uncertain, but there is general agreement that wild hosts are unimportant and that initial spread is mainly from other groundnut crops or from self-sown groundnut 'volunteers' regenerating from seed left in the ground from previous harvests.

Rosette causes serious problems in areas such as Uganda, where rainfall or irrigation allow crops or 'volunteers' to grow throughout the year and so maintain a continuous cycle of infection (Davies 1972). Elsewhere rosette tends to occur late or sporadically as in northern Nigeria and central Malawi, where there is such a prolonged dry season that crops and 'volunteers' cannot survive and few aphids persist on local weeds or natural vegetation. In these circumstances it has been suggested that rosette is reintroduced at the beginning of each growing season by infective aphids from regions where conditions are more favourable for groundnuts to survive. Southern Malawi is a possible source for spread to the Central Province (Nutman *et al.* 1964; Adams 1967) and the extensive plantings in northern Nigeria may be colonized by aphids from populations established on crops sown earlier in the riverine areas to the south (J. A'Brook, personal communication). Any such movements are likely to be facilitated by the initiation of alate *A. craccivora* at low population densities and by the increased production of alates on rosette-diseased plants compared with uninfected ones (Réal 1955).

The prevailing winds in Nigeria at the time that spread occurs are from the southwest, and winged aphids could be swept northeastwards until deposited along the zone of wind convergence associated with movements of the Inter-Tropical Front (figure 11). Rapid accumulations of aphids, whiteflies, leafhoppers and other insects including vectors of medical or veterinary importance have been reported in such circumstances in Sudan or elsewhere in Africa (Joyce 1976; Rainey 1976). However, the phenomenon has not been investigated in relation to plant virus spread and it is not clear whether rosette spreads from afar and on few occasions or whether there is a progressive invasion by successive generations of vectors, each moving relatively short distances. Spread in either way would be from old to young crops



because these are planted sequentially as the rains progress from south to north in Nigeria and adjacent countries. There is an obvious need for further research on the dispersal of rosette and other diseases, including African horse sickness and bluetongue of livestock, that could be associated with seasonal movements of the rainbelt to and fro across Africa (Sellers 1980). Meanwhile, the view that groundnut rosette is regularly carried far should be regarded as a plausible hypothesis rather than an established fact.

#### *Non-persistent viruses*

Non-persistent viruses are acquired and transmitted most efficiently in brief probes and are not retained for long by their aphid vectors. These viruses are mainly spread locally into or within plantings to give characteristically steep gradients of infection. It is sometimes implied that these are steep because the viruses fail to persist in dispersing vectors. However, this is a fallacy because non-persistent viruses can usually be retained for up to several hours, which is quite sufficient for them to be transported considerable distances by windborne alates (Kennedy 1960; Cockbain *et al.* 1963). There must be other limitations on long-range spread, and an important feature of non-persistent viruses is that they are not retained when aphids moult. Thus recently emerged alates that have developed on an infected plant may be non-infective when they take off on their initial migratory flight because they leave before feeding or probing as adults or because they feed for periods exceeding the optimum acquisition time. There is little evidence on this point, although turnip mosaic and sugar-beet mosaic are two non-persistent viruses that are less likely to be transmitted by alates flying voluntarily from infected plants than persistent or semi-persistent viruses of brassicas and sugar-beet (Broadbent 1960; Cockbain & Heathcote 1964).

Another feature of non-persistent viruses that limits the opportunity for long-range spread is that they are soon lost when infective aphids probe non-hosts (Cockbain & Heathcote 1964). Thus alates that are infective on take-off are unlikely to transmit at the end of a long migratory flight unless they alight first on a virus-susceptible host plant. This is unlikely to occur unless the virus has a very wide host range or susceptible hosts are grown widely in weed-free monoculture over very large areas.

Sugar-beet, maize and cucurbits are three of the crops that are sometimes grown in this way and in which non-persistent viruses may occasionally spread far, as in some of the intensive agricultural areas of the U.S.A. The possibility became apparent in the Sacramento valley of California during the 1960s, when shallow gradients in the incidence of sugar-beet mosaic were recorded in young plantings extending up to 24 km around older overwintered crops retained for late harvest (figure 2*b*). However, a precise interpretation of these findings is difficult because at least some of the infection around the overwintered fields could have been due to greater vector populations in these areas than elsewhere, leading to local spread from sources within or alongside the young plantings.

Apparent spread over 9.6 km has been noted in a winter vegetable-growing area of Florida (Adlerz 1981). Elsewhere it has been suggested that water-melon mosaic and other non-persistent viruses have been spread into southern Europe by aphids from North Africa or the Middle East (Lovisolo *et al.* 1980). No supporting evidence has been presented, although several of the viruses persist for long enough in their vectors for such a long transit to be possible. There seem to be precedents in that strong circumstantial evidence is available for spread of two viruses of livestock into southern Europe by insect vectors blown across the Mediterranean from North Africa (Sellers *et al.* 1977, 1978).

*Maize dwarf mosaic virus*

Observations on the damaging 1977 epidemic of maize in sweet corn in parts of Minnesota and adjoining states have provided new evidence on the possibility that non-persistent viruses can be spread far, and merit further consideration (Zeyen *et al.* 1978). The epidemics occurred suddenly over extensive areas with no previous history of large-scale outbreaks. The affected plantings had been made on different dates with seed stocks of different variety and provenance, including some that performed satisfactorily elsewhere. There was no evidence of build-up from initial foci of infection within or alongside plantings, and the outbreaks were due to both the A strain of virus that infects Johnson grass (*Sorghum halapense*) and the B strain that does not.

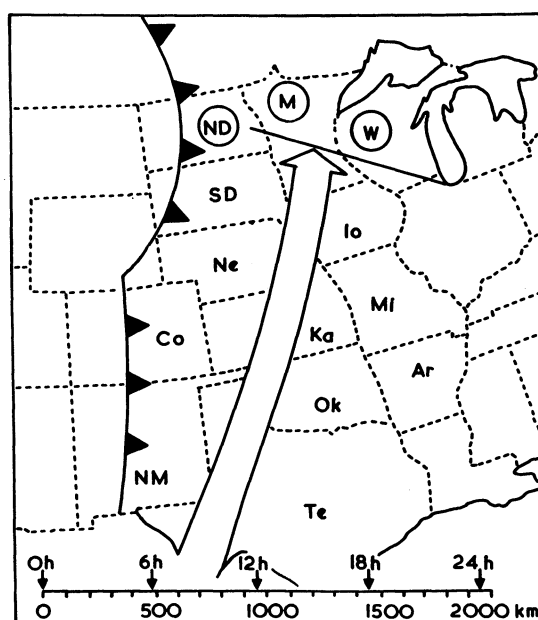


FIGURE 12. Weather conditions at 19h00 on 2 July showing the path of the low-level jet-stream wind associated with the 1977 epidemic of maize dwarf mosaic virus in Minnesota. The greatest incidence of infection was south of the line of thunderstorm activity extending from the eastern border of North Dakota to southern Wisconsin (Zeyen & Stromberg 1977). State abbreviations as in figure 6. The arrows indicate the time taken for aphids to be carried by a jet wind of  $80 \text{ km h}^{-1}$ .

These findings suggested that the epidemics had not originated from seedborne inoculum or other local sources and led to the conclusion that they could have been due to infective aphids swept into the area in large numbers from either plantings of maize or sorghum to the south. An examination of the weather data showed that this could have occurred on 2–3 July when low-level (300–600 m) south westerly jet-stream winds blew into Minnesota until interrupted by a line of thunderstorm activity extending from North Dakota to southern Wisconsin (figure 12). Areas south of the line were those most seriously affected by dwarf mosaic and they received little rain (less than 0.5 cm) during the period of thunderstorm activity compared with less severely affected areas of higher rainfall (2–5 cm) to the north. Almost all the serious outbreaks could be attributed to aphid fall-out from jet-stream winds along the thunderstorm front in areas where aphid colonization was not impeded by heavy driving rain.

The half-life of maize dwarf mosaic virus in starved aphids is 1–3 h depending on the test procedure, but some aphids remain infective for 18–72 h. This enables aphids to remain

infective while being carried far by jet-stream winds of *ca.* 80 km h<sup>-1</sup>. Moreover, maize and sorghum are grown so widely that many aphid migrants from maturing crops in the south are likely to alight first on young plantings in the north. Thus long-range dispersal is possible, especially in years such as 1977 when favourable weather early in the season led to large populations of aphids on crops in the south and was then followed by a period of severe drought that stimulated the production and dispersal of alates.

The precise origin of the aphids reaching Minnesota in 1977 was not determined and there is continuing uncertainty as to the initial sources of the A and B strains of dwarf mosaic virus throughout the northern maize-growing areas of the U.S.A., where *S. halapense* does not occur and other overwintering hosts have not been found. There is obvious scope for further studies and for developing monitoring and forecasting procedures along the lines of those proposed for cereal aphids and barley yellow dwarf that regularly traverse the same areas (figure 6).

#### SPREAD BY OTHER ARTHROPODS

There is scant information on the possible long-range spread of plant viruses by other types of vector. However, as shown in the following sections many of these are known or are likely to be dispersed far, and further study can be expected to show that at least some of the viruses they transmit are transported over long distances.

##### *Beetle-transmitted viruses*

Several important viruses are transmitted by beetles and are spread rapidly as winged adults fly or jump actively into or within crops. Few detailed epidemiological studies have been undertaken on the pattern and sequence of infection, and there are no reports of distant spread. However, one vector species (the southern corn rootworm or spotted cucumber beetle, *Diabrotica undecimpunctata*) migrates over long distances in the U.S.A. and has been caught on mountains, 24 km out to sea and from aircraft (Johnson 1969). Sexually immature adults that had recently emerged from pupae and overwintered adults have been seen leaving sites in Louisiana in large numbers during the spring. They fly northwards along the Mississippi valley and colonize colder areas far to the north, where populations do not survive the winter (Smith & Allen 1932). Distances of up to 850 km seem to be traversed in 3–4 days and there is a southward migration in the autumn. However, the significance of these findings in relation to the epidemiology of cowpea chlorotic mottle and other viruses transmitted by *D. undecimpunctata* is uncertain.

There is no reason to suppose that the migratory behaviour of this species of beetle is in any way unique, and the need for further information is emphasized by the recent finding that corn rootworms transmit one of the viruses responsible for corn lethal necrosis, now causing serious epidemics in Kansas and Nebraska (Uyemoto 1983), where there are limited opportunities for *D. undecimpunctata* to overwinter.

##### *Mealybug-transmitted viruses*

Cocoa swollen shoot is the most important of the diseases caused by viruses with mealybug (pseudococcid) vectors. The disease occurs in all cocoa-growing areas of West Africa and causes particularly serious losses in Ghana. All natural spread is due to wingless nymphs of either sex, or to female adults, because only the adult males develop wings and they are unable to feed or transmit viruses as they do not possess functional mouthparts.

There is general agreement that the main spread of swollen shoot is over short distances by nymphs or adults moving between the interlocking branches of adjacent trees. This explains why diseased trees tend to occur in discrete patches and why little spread occurs until new plantings have established a continuous canopy of foliage (Thresh 1958). New outbreaks are attributed to windborne mealybugs, mainly the first instars that are small and more active than later stages. They are easily dislodged by sudden gusts of wind and can be swept far, especially when falling from the tops of trees in open plantations of cocoa or from the tall indigenous trees that occur in or around plantations and are initial sources of virus and vectors.

Windborne mealybugs have been caught in Ghana on sticky traps, with greatest numbers taken during the dry season (Strickland 1950). They have also been caught on seedlings exposed in clearings alongside cocoa plantings and on rafts placed on a reservoir up to 47 m from the nearest source (Cornwell 1960). Gradients of deposition were steep but occasional individuals could have been swept much longer distances and infective mealybugs retain swollen shoot virus for several hours. Thus the virus might sometimes be carried far, although there is no direct evidence that this occurs and field observations suggest a very low probability of spread over great distances. Nevertheless, even very occasional spread in this way is of disproportionately great importance in introducing inoculum to new areas and to established mealybug populations not previously infective.

#### *Thrips-transmitted viruses*

Tomato spotted wilt virus is the most important of the viruses with thrips vectors. The virus is widely distributed and infects tomato, tobacco, pineapple and many other weeds, ornamentals and crop species. It is acquired by vectors as nymphs and is transmitted only by adults, which are winged and remain infective for long periods. Thus spread is due exclusively to adults originating from infected plants.

Adults of some thrips species fly in large numbers at certain seasons and can be blown far when migrating to or from overwintering sites or from crowded populations or deteriorating host plants (Johnson 1969). However, there is little information on the flight characteristics and distances travelled by *Thrips tabaci* or other important vector species. In some instances spread into crops is due to a sudden influx of vectors from outside sources and there is little or no secondary spread within plantings (Bald 1937; Vanderplank & Anderssen 1944). It is also known that *T. tabaci* thrives particularly well on certain virus-infected weeds (Carter 1939). These findings emphasize the scope for further studies on factors influencing the development and behaviour of the migrants that periodically invade crops and on the possibility that migrants differ morphologically or physiologically, or both, from other forms, as with other types of vector.

#### *Whitefly-transmitted viruses*

It has long been known that whiteflies are the vectors of several important viruses, including tobacco leaf curl and cotton leaf curl. More recently whiteflies have attracted increasing attention in many tropical and subtropical countries because of their direct damage to crops, or as the vectors of other viruses currently causing serious diseases of tomato, cucurbits, cowpea, soybean or other legumes.

Whitefly larvae are largely immobile although the first instars sometimes move short distances. All adults are winged but their mobility and flight characteristics have received little attention and the only detailed studies have been in England on the non-vector species *Aleyrodes*



*brassicae*. For much of the year gravid females of this species fly locally between adjacent plants, whereas in the autumn non-gravid females make longer migratory flights into entirely new habitats (El Khidir Nour 1963).

It is not known whether any other whitefly species behave similarly, although several observations suggest that the most important vector (*Bemisia tabaci*) can fly or be blown far, at least in some circumstances. For example, dense swarms of whiteflies have been seen flying above soybean plantings in Brazil and in adjacent townships several kilometres away (Costa 1975). Other observations have been made in India, where plants soon became infested when exposed on the roof of a building 13 m above ground level and 100 m from the nearest source (Nene 1972). Elsewhere numerous whiteflies were caught at similarly isolated sites in Israel, where catches sometimes exceeded 1000 adults per trap per week (Melamed-Madjar *et al.* 1979).

Whiteflies have also been caught on several occasions from aircraft, and vertical density profiles have been determined above cotton-growing areas of the Sudan Gezira irrigation scheme (R. C. Rainey & M. J. Haggis, personal communication). Densities late on the afternoon of 9 November 1971 decreased from 1 whitefly in 200 m<sup>3</sup> at 8 m to 1 in 500 m<sup>3</sup> at 30 m and 1 in 3000 m<sup>3</sup> at 60 m. By contrast, during an evening flight on 12 October 1974, probably through the Inter-Tropical Front, the density was almost uniform at about 1 in 1200 m<sup>3</sup> from 60 to 1200 m, with 1 in 400 m<sup>3</sup> at 30 m and less than 1 in 5000 m<sup>3</sup> at 1300–1800 m. In other low-level flights the numbers of whitefly caught at 3 or 6 m were as great or greater above fallow as above adjacent cotton. On one of these occasions the density of whitefly 3 m above fallow was 1 in 50 m<sup>3</sup> which is a value rarely attained in suction traps at 1–2 m within cotton plantings. Other evidence for wind dispersal over considerable distances has come from observations on the sudden appearance of damaging populations of *B. tabaci* on young cotton in the Sudan. These have been associated with movements of the Inter-Tropical Front, and abrupt increases in suction trap catches of whiteflies coincided with passages of such zones of wind convergence (Joyce 1976).

These findings suggest that whiteflies are more mobile and disperse further than is generally recognized. This raises the possibility that at least some of the viruses they transmit are also dispersed far, especially as several of these viruses can persist for days in the vector and are transmitted by adult whiteflies on emerging from pupae collected from infected plants (Varma 1963; Costa 1969). There is currently no evidence of long-range virus spread, but this has not been sought and few detailed epidemiological studies have been made on whitefly-borne viruses. In observations on cotton leaf-curl in the Sudan, local gradients of infection were recorded around initial foci and related to the direction of the prevailing wind (Giha & Nour 1969). Elsewhere, cotton common mosaic virus has been observed to spread several hundred metres into plantings in Brazil from weed hosts around the margin (Costa 1969).

Much further evidence is required and on a wider range of viruses before it is possible to make generalizations on spread by whiteflies and on the likelihood of dispersal over very great distances. Particular difficulties are likely to be encountered in distinguishing between local and distant spread because many whitefly-borne viruses infect tropical crops grown in small plots and in sequence throughout the year, in areas where weed hosts are common and widely distributed. Nevertheless, the possibility of long-range dispersal into areas of seasonal rainfall should be recognized and also the opportunity for infectious windborne whiteflies to accumulate on crops in zones of wind convergence along tropical frontal systems.



*Mite-transmitted viruses*

Several important viruses are transmitted by eriophyid mites. These are small and do not develop wings at any stage of their life cycle, but they move between adjacent plants by crawling and over greater distances when swept away by wind currents.

The vector of wheat streak mosaic (*Aceria tulipae*) is dispersed voluntarily by wind, and adults crawl upwards onto exposed surfaces, rear up on their anal pad and then leap off in response to air currents (Nault & Styer 1969). The vector of blackcurrant reversion virus (*Cecidophyopsis ribis*) behaves similarly (Taylor 1914) and in some species, including *A. tulipae*, seasonal wind dispersal over considerable distances is greatly facilitated by the periodic appearance of robust, thick-bodied forms that seem less vulnerable to desiccation than the thin-bodied forms usually encountered (Somsen 1966).

*A. tulipae* has been trapped in large numbers on sticky glass slides in Ohio, where peak numbers coincided with dispersal from maturing wheat to new plantings of maize in mid-summer and from maturing maize to young plantings of wheat in autumn (Nault & Styer 1969). All plants became infested during July in a field of maize 1.6 km away from the nearest wheat and in other studies *A. tulipae* was trapped at a height of 45 m and 2.4–3.2 km from the nearest source (Pady 1955).

These findings suggest that mite-borne viruses can be dispersed far, especially as *A. tulipae* can survive without food for 15–20 h (Staples & Allington 1956). There is little evidence to confirm or deny this supposition other than the shallow gradient observed in the incidence of blackcurrant reversion disease extending 200 m downwind from a large, seriously affected plantation (J. M. Thresh, unpublished).

## DISCUSSION

Evidence for the long-range dispersal of plant viruses was last discussed by Johnson (1967, 1969), who stressed the various difficulties encountered in such studies. Considerably more information is now available but overall progress has been limited and much of the relevant evidence is anecdotal, circumstantial or inadequate for definitive interpretation. Thus it remains unclear whether long-range dispersal is likely to be a very occasional phenomenon that occurs only in exceptional circumstances or whether it is a regular feature in the epidemiology of many viruses with arthropod vectors.

There are various technical and logistic problems in obtaining less equivocal evidence, and these are unlikely to be resolved at all readily. For example, sporadic, seasonal phenomena require long-term study over a sequence of years to encompass a suitably wide range of conditions and it is both difficult and expensive to set up the multidisciplinary teams required. These should include entomologists, virologists and meteorologists able to coordinate the activities of local collaborators operating traps, equipment or surveys over very large areas of sometimes inhospitable terrain. Past experience even in a country such as the U.S.A. suggests that there is likely to be inadequate funding or continuity in organizing inter-regional projects. The difficulties are likely to be even greater in studies of the type now in progress on the rice brown planthopper that require close international cooperation between countries of different languages and political ideologies.

Even if these practical problems are overcome it may be impossible to establish that spread

has occurred from afar if there are local sources nearby. This suggests that definitive evidence for distant spread will continue to come mainly from a thorough investigation of exceptional incidents in areas where local sources are not involved. Considerable progress is possible by using the latest techniques and facilities, and these could be used to resolve such long-standing problems as the source of the maize and cereal aphids that are periodically swept northwards into Minnesota and adjoining parts of the U.S.A. and Canada. Indeed, a new approach to this topic is being planned at the University of Illinois with collaboration from the southern states (M. E. Irwin, personal communication). This work will involve the deployment of high resolution radar of the type that has already been used to track the movement of individual insects (Schaefer 1976). Elsewhere back-tracking procedures and trajectory analyses are being used to estimate the migratory flights of the rice brown planthopper in the Far East, from routine weather data and the known flight characteristics of this species and assuming take-off from sites in rice-growing areas at times when large populations are likely to have occurred (Rosenberg & Magor 1983). Much new information will also be forthcoming from the network of 39 aphid suction traps now erected in seven countries of western Europe (Taylor 1983). Such traps are also operating in eastern Europe, North America and Australasia and there have been considerable advances in recent years in methods of detecting viruses in trapped insects by using various sensitive procedures including serology, electron microscopy and fluorescent stains (Racah 1983). Progress has also been made in developing precise biochemical techniques for 'typing' vectors and virus strains, and these are being used already to indicate the possible origin of new pest or disease outbreaks (Baker 1978; King *et al.* 1981).

It seems likely that further studies will show that the long-range dispersal of plant viruses is more important and occurs more widely than is suggested by the present limited evidence. This is to be expected from the close interrelations of many viruses with arthropod vectors that are well adapted to colonize and exploit ephemeral habitats. Many arthropods do this by some type of polymorphism that involves the production of different adult forms of contrasting mobility (table 4). The 'colonizers' are particularly active and seldom settle to feed or reproduce until dispersal has occurred, whereas the 'exploiters' are relatively immobile and usually reproduce soon after becoming adult. With some species there are obvious morphological distinctions between the different forms, as between alate and apterous aphids, or between macropterous and brachypterous planthoppers. Differences within populations of eriophyid mites are less obvious, and other types of polymorphism are mainly physiological or behavioural as between the long-flying and short-flying forms of whiteflies and leafhoppers. In all groups the initiation and development of the different forms is determined by seasonal and other factors including crowding. Consequently the proportion of active colonizers tends to be high as plants mature and populations become crowded, or when conditions otherwise become unfavourable. It is likely to be of great significance that barley yellow dwarf and several of the other viruses considered in this review have effects on their host plants equivalent to premature senescence. Thus infected plants are particularly attractive or palatable to vectors and this stimulates increased multiplication, crowding and the production of active migrants that lead to further virus spread.

The occurrence and significance of polymorphism within vector populations is not always recognized by entomologists and is seldom fully appreciated by virologists. Thus differences between forms are sometimes ignored in assessing field populations or in analysing and presenting the results obtained. Moreover, virus transmission tests are usually done with

laboratory cultures of the least active forms because these are easy and convenient to handle. This is a serious limitation of current attitudes because many viruses are spread largely or entirely by active migrants. These are infective on take-off or acquire virus while dispersing to initiate new outbreaks and make at least some contribution to the enlargement of outbreaks already established.

TABLE 4. STRUCTURAL-BEHAVIOURAL POLYMORPHISM IN ARTHROPOD VECTORS

	'colonizers'	'exploiters'
aphids	alatae	apterae
planthoppers	macropterae	brachypterae
leafhoppers	long fliers	short fliers
beetles	long fliers	short fliers
whiteflies	long fliers†	short fliers†
mealybugs	first instars	later stages
mites	thick body walled	thin body walled

† Not established for a vector species.

It follows that virus spread into, between and sometimes within plantings is largely determined by factors influencing the initiation and behaviour of active migrants, which explains the many striking examples of rapid virus spread due to migrants moving from the crowded populations that develop on ripening crops, weeds or wild plants as these begin to senesce and die with the onset of unfavourable conditions. All known or suspected examples of long-range virus dispersal occur in such circumstances and there is obviously a close association between virus spread and migration. This was at one time considered to be a wasteful and haphazard process, whereas it is now seen as an important feature of the many arthropods that exploit short-lived hosts or transient environments (Southwood 1962). It is of crucial importance in survival, enabling the transfer of a part of the breeding population to fresh sites before the original sites disappear or become untenable and before the main reproduction period has begun. Migration also performs a similar role in the survival and perpetuation of viruses, enabling them to reach and colonize new habitats including some that are far from the original source. However, all the evidence suggests that occasional spread over great distances should be regarded as an extreme expression of dispersive processes occurring repeatedly and in many areas but over a generally shorter range.

An acceptance of this view is fully compatible with the previous conclusion that many plant viruses cause 'crowd' diseases (Thresh 1976), using this term in the sense of Vanderplank (1948) for diseases that seldom spread far in any considerable amount. Local spread from nearby sources within or alongside crops is always likely to occur earlier and more frequently than spread from afar. This explains the overall effectiveness of isolation, eradication and hygienic measures in decreasing or at least delaying the onset of disease and also the success of official schemes for raising certified stocks of healthy planting material for release to growers (Thresh 1976, 1983). Avoiding or removing sources of infection within and immediately alongside plantings can be surprisingly effective, even when practised on individual farms or holdings, or when only limited isolation is possible. However, as discussed in previous sections, such measures are not always effective, especially for crops that are grown extensively over very large areas subject to a massive influx of infective vectors from distant sources.

Spread in this way, and the circumstances in which it occurs, merits further study because of its intrinsic biological interest and its practical importance in devising adequate control measures and schemes for providing healthy stocks of planting material. Furthermore, it will become increasingly important to monitor the distribution and spread of vector biotypes and virus strains as increasing numbers of vector species develop tolerance to pesticides, or overcome host plant resistance mechanisms, and as virus-resistant varieties become generally available. These aspects of dispersal have received only limited attention; the main emphasis has until recently been on determining sources of infection. This is unsatisfactory because the type as well as the source and amount of inoculum being distributed is important and virus strains differ greatly in virulence, transmissibility and other features affecting their overall epidemiological competence. Moreover, the success of resistant varieties will partly depend on the rapidity with which resistance-breaking strains of virus or biotypes of vector emerge and become widely distributed.

In studying long-range dispersal there is obvious scope for further work in additional areas and on a wider range of viruses and vectors than has yet been considered. Such studies should investigate the possibility that viruses can directly or indirectly influence the host range, reproduction, longevity, behaviour, flight and overall mobility of their vectors even more profoundly than the current limited evidence suggests. Various direct or indirect effects have been reported and they can be so beneficial to the vector that the ability to transmit is of considerable survival value, as reported with blackcurrant reversion virus (Thresh 1967). Conversely, some of the viruses that replicate in their vectors have such deleterious effects on fecundity or longevity, or both, that they are likely to impair mobility and flight performance. This possibility has not been investigated, although the harmful effects of rice hoja blanca and rice dwarf viruses on their hopper vectors are known to be of great epidemiological importance (Jennings & Pineda 1971; Nakasuji & Kiritani 1970).

The long-range dispersal of plant viruses by arthropods has many features in common with the dispersal of other arthropods that directly damage crops or transmit pathogens of medical or veterinary importance. It may eventually be possible to relate studies on these phenomena with equivalent work on airborne fungal spores, or with aerosols disseminating viruses of vertebrates. It is already clear that the movement of such diverse types of windborne particles is influenced by similar features of the atmospheric environment. This permits a unified approach to aerobiology and has obvious advantages in making the best use of the facilities and expertise available.

Other unifying concepts of wide applicability in comparative epidemiology can be derived from an overall ecological approach that seeks to relate the dispersive abilities of pathogens to the type and stability of the habitats exploited (Thresh 1980). On this view the ability to disperse frequently and far is seen as an important attribute of 'colonizing' species that attack widely distributed or short-lived hosts in ephemeral environments. A similar approach is possible in considering the behaviour of viruses of mammalian hosts, even those that are very long-lived and occur in dense communities. This is because mammals either die, or recover and become immune, after virus infection, and some populations provide transient habitats in which viruses are unable to persist indefinitely because the number of susceptible individuals falls below a minimum critical level. Moreover, weather or other conditions can lead to extreme fluctuations in vector populations or to their periodic extinction. In such circumstances there are obvious advantages for viruses, vectors and immunologically distinct strains in having the



ability to disperse far and colonize fresh habitats. Thus vectors of at least some animal viruses can be expected to have some of the morphological or behavioural polymorphisms that are such a feature of plant virus vectors. Indeed, the epidemiological characteristics of arthropod-borne viruses of animals and plants are likely to share more common features than are currently appreciated.

It is a great pleasure to acknowledge the influence of C. G. Johnson, who contributed so much to the study of long-range dispersal in an overall ecological context and many of whose ideas and suggestions have still to receive detailed consideration. Acknowledgements are also due to Dr R. C. Rainey, F.R.S., and Dr M. J. Haggis for permission to quote unpublished data.

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#### Supplementary comment

R. C. RAINEY, F.R.S. (formerly Centre for Overseas Pest Research, London, U.K.). At the suggestion of Dr Thresh, I am taking this opportunity of putting on record details of some of our aircraft trapping catches of *Aphis craccivora*, a species taken incidentally in the course of field research in the Sudan primarily concerned with cotton pests. One particularly noteworthy catch was of 491 aphids, identified by Victor Eastop at the British Museum as largely if not entirely *A. craccivora* Koch, and taken at a height of 15 m (by radar altimeter) during a 9½ min trapping run of some 22 km across a crop-rotation mosaic of 42 ha fields of groundnuts, cotton, sorghum and fallow, in Radma, Kumor and Darwish blocks of the Gezira irrigation scheme. With an airflow of 215 m<sup>3</sup> min<sup>-1</sup> through the Cranfield/Spillman trap on the Pilatus Porter aircraft, the volume density of the *craccivora* would have been 0.24 m<sup>-3</sup>, i.e. with each aphid on average

0.9 m from its nearest neighbour on the assumption of random (not uniform) spacing; this is the highest insect density that Margaret Haggis and I have encountered in the course of more than 100 h of aircraft trapping in tropical Africa.

The catch, sorted by Robert Cheke, also included 47 other insects, 9 of them Ceratopogonidae (biting midges, as discussed by Dr Sellers), 8 Thysanoptera, 5 parasitic Hymenoptera and 18 Coleoptera. The catching run was begun at sunset (on 22 October 1974) and ended at 17h39, and so was within the period of the marked diurnal peak of suction-trap densities between 16h00 and 18h00 found for this species by John Peregrine in the same area and season of the following year. A major factor in this particularly high aircraft catch is, however, believed also to have been wind-convergence. Thus the routine synoptic analyses every 3 h of the Sudan Meteorological Department had indicated the proximity of the intertropical front, and a further, wind-finding flight over the same area, begun within 25 min of the trapping run and using the Porter's/Doppler navigation system, showed that the trapping run had actually intersected the position of the Inter-Tropical Front, sharply defined between undercutting west-northwesterlies and overriding northeasterlies. Wind-convergence into a triangular area of 24 km<sup>2</sup> astride the front was found to be at a rate of  $1.7 \times 10^{-3} \text{ s}^{-1}$ , implying on the simplest of assumptions a concentration of airborne insects at a rate giving a sevenfold increase in area density per hour.

On other occasions, also on dates of passage of the Inter-Tropical Front, and well after sunset, we trapped *A. craccivora* at heights up to 1200 m above the ground, in much lower numbers but showing relatively uniform densities over a considerable range of height. Thus, in 1971, on 13 October at 450 m three *craccivora* were taken in 32 min trapping, starting at 20h02, and two of the same species in 18 min from 21h37 between 300 and 1200 m while on 17 October one *craccivora* (also identified, like the others, by Victor Eastop) was taken at 1200 m during a 10 min trapping run from 18h58 at an air temperature of 22 °C, at a height that would have been within the range of convection currents from the ground during the preceding afternoon; for all three of these catches the density of these aphids was between 4.4 and 5.2 per 10<sup>4</sup>m<sup>3</sup>.

Observations by John Bowden in 1970 had shown that suction-trap catches of aphids in the Gezira had been mainly *A. craccivora* during October, while the intertropical front was oscillating to and fro across the area, in contrast with his catches mainly of *Rhopalosiphum maidis* in November, after the front had finally moved off to the south and the seasonal northerlies had become established.

These Sudan observations on *craccivora*, all made in the course of coordinated research programmes under the direction of Vernon Joyce, thus provide further circumstantial evidence of redistribution of aphid populations by seasonal wind systems, as envisaged for example by Davies (1972) for viruliferous alatae of this species in Uganda.

#### Discussion

R. S. SCORER (*Imperial College, London, U.K.*). Dr Thresh's examples of long-distance transport of aphids in the U.S.A. and possibly across the Baltic, particularly the former, where the presence of a front would indicate that the high-altitude (*ca.* 4.6–10.7 km) wind could achieve a high velocity (up to 185 km h<sup>-1</sup>) in the relevant direction, prompt the question 'How high may aphids go and still survive?'

Carriage by convection currents up to 3 km or more could well take place even if the aphids



were attempting to fall freely and so they do not need to fly up to those altitudes. I have seen desert dust at 11 km over central U.S.A. While up there involuntarily would they survive the cold?

Although under different circumstances, C. G. Johnson (in the late 1950s) did detect, with balloon and aircraft-borne traps, aphids that had been airborne all night in a layer above an inversion at dawn, presumably flying up there to keep out of the cold air immediately below, and I remember discussing with him then the possibility of their rising to cumulus top levels above 6 km.

R. HARRINGTON (*Rothamsted Experimental Station, Harpenden, U.K.*). Aphids normally settle out of the atmosphere at about sunset, responding to declining light intensity. They will continue in flight during the night when they are in warm low-level jet-streams above cold deep inversions and have been sampled at 610 m by aeroplane over Kansas (Berry & Taylor, *J. Anim. Ecol.* **37**, 713–722 (1968)). Taylor (*Nature, Lond.* **186**, 410 (1960)) collected aphids up to a height of 1500 m and found them to be alive and able to reproduce.

*Myzus persicae* can supercool to  $-25^{\circ}\text{C}$  for short periods and for increasingly longer at higher temperatures. It is perfectly possible to be carried in the jet-streams and fall to the ground without encountering such low temperatures.

It is wrong to consider that aphids are carried in the same way as inert particles. If they ceased flying actively they would fall quickly through the cold layers of air to the ground, and not continue to be carried by high-level winds. It is of course true that if they were caught in exceptional conditions such as those causing ‘dust devils’ they could be carried upwards without actively flying, but it is very likely that they would die during the experience. Under perfectly ordinary circumstances high-altitude survival is possible.

D. E. PEDGLEY (*Centre for Overseas Pest Research, London, U.K.*). Insects taken to great heights in the way suggested by Professor Scorer are unlikely to have reached the places discussed in the case studies quoted by Dr Thresh because, with the usual veering of wind direction with height, back-tracks would not have come from likely sources. This can be taken as evidence to support the argument that the great majority of insects involved in such long-distance movements fly in the lowest 1–2 km of the atmosphere.

PATRICIA A. NUTTALL (*N.E.R.C. Institute of Virology, Oxford, U.K.*). With reference to the question ‘Are insect vectors affected by the viruses they carry?’, I believe there are some results indicating that mosquitoes infected with yellow fever virus show a change in flight behaviour. However, there is very little evidence that vectors are affected by the viruses they carry, probably because relatively few studies have been made.

R. F. SELLERS (*Animal Virus Research Institute, Pirbright, U.K.*). It is not known whether the presence of virus in infected midges or mosquitoes has an effect on their flight. In the laboratory (J. Boorman, personal communication) there is no effect on longevity.