Vector Relationships and the Development of Epidemics: The Epidemiology of Plant Viruses

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Introduction.—Viruses of bacteria, fungi, higher plants, and animals are of diverse structure and composition but they share important features. They cannot replicate outside their hosts and their survival in nature depends upon an effective means of transmission (1). The frequency, ease and mode of spread differ widely, as may be expected from the great differences in the biology, habits, longevity, and resistance mechanisms of the hosts.

Some plant viruses are seed-borne and a few are transmitted by pollen or by contact. However, the immobility of plants and the resistance to infection conferred by the cell wall and lack of suitable entry points limit the effectiveness of direct spread. Hence the paramount importance of vectors in the epidemiology of plant viruses. Spread by man and by fungi is considered elsewhere (4, 25). This review deals with spread by the main groups of nematode and arthropod vectors, with special reference to factors influencing epidemiology. It is stressed that much virus spread, especially between crops and over long distances, is due to particularly active and mobile forms of the vector species. Such migrants are mainly sexually immature females that are well adapted to reach and exploit new habitats and so ensure their own survival and that of the viruses they transmit.

Transmission by Vectors.—An assessment of the performance of different types of vector is hampered by the paucity and biased nature of the available information. The literature mainly concerns work on viruses which cause serious diseases of economically important crops in countries with highly developed agricultural systems. Much less attention has been given to less widespread viruses and to many of those which infect unimportant crops or cause inconspicuous symptoms. There has been no detailed virology in many countries, and little work on viruses of natural vegetation.

Depite these limitations, it is clear that some viruses are much more readily established within crops than others. Viruses that are spread widely by natural means are mainly those with efficient vectors. Other viruses have a limited distribution or fail to survive unless they are disseminated by vegetative propagation, or other human activities.

The effectiveness of the transmission process required to ensure the perpetuation of a virus, depends upon the nature and distribution of its hosts and on environmental conditions. Occasional spread by a rare, immobile, or otherwise inefficient vector may ensure survival in common perennials, but is likely to be inadequate for a virus with a limited host range, or one restricted to short-lived or widely-scattered hosts. It is hardly surprising, therefore, that various associations have evolved between plant viruses and diverse groups of phytophagous animals. There are different degrees of vector specificity and several apparently distinct mechanisms of transmission (16, 18). The spread of some viruses by vectors is complicated further by a dependence on a specific interaction with an assistor virus (19).

The potential rate of spread of virus between plants depends upon the size and mobility of the vector populations, whose actual performance is influenced by the various factors that determine their infectivity. The optimum feeding conditions for transmission differ between systems; each has features that facilitate spread and others that lead to unreliability. This is because rapid transmission in short probes and long persistence in the vector are mutally exclusive attributes.

An ability to multiply within the vector and to pass to its progeny increases the persistence and versatility of a virus and enhances survival when plant hosts are not readily available. However, the longevity or fecundity of the vector may be impaired and there are instances of virus greatly increasing the mortality of eggs or larvae. This may limit the occurrence of such interrelationships because any disturbance of the delicate equilibrium could lead to the virtual elimination of a virus and its plant or animal hosts.

As discussed in the following sections, the overall efficiency of each method of transmission depends upon the interaction between counteracting processes. Each system is effective for different reasons, despite great differences in the habits and mobility of the vectors. There is therefore a corresponding diversity in epidemiology and in control measures.

Nematodes (Nematoda).—Two quite distinct groups of viruses have nematode vectors (24). The nepoviruses are transmitted by species of *Longidorus* or the closely related genus *Xiphinema*, whereas the tobraviruses are transmitted by *Trichodorus* spp. Claims that other nematodes are vectors of additional viruses have not been substantiated.

Xiphinema index, the vector of grape fan leaf virus reproduces only on the roots of a few woody perennials, and produces many generations per year on grape. Vectors of other viruses have a much wider host range, including woody and herbaceous plants. *Trichodorus* spp. produce several generations a year, whereas *Longidorus* spp. and *Xiphinema diversicaudatum*, the vector of arabis mosaic virus, usually produce only one.

Adults and larvae of most vectors transmit with similar efficiency. There is no evidence of multiplication in any vector or of transmission through the moult or to the progeny. Nevertheless, all the viruses tested are retained by nematodes for weeks or months; much longer than the viruses survive *in vitro*.

Critical feeding times for transmission are difficult to determine and the published data are for access periods. Several viruses have been acquired or inoculated within a few hours, although the proportion of plants infected increases with longer access.

Nematode vectors are unable to travel far through the soil and their slow progress towards roots seems to be less important in spreading virus than the growth of roots towards nematodes. The movement of virus through the root systems of infected plants is also important in increasing the availability of virus to nematodes.

Nematodes transmit virus mainly between the roots of adjacent plants, or by acquiring and retaining virus until they eventually encounter the roots of a later crop. Consequently, nematode-borne viruses often occur in patches that spread slowly and recur at the same sites in successive plantings. Infection tends to be of local rather than of general importance unless there has been extensive movement of virus-infected plant material as with hop, potato, and grapevine.

Numbers of nematodes that can be extracted from soil samples and handled experimentally are few in relation to the enormous numbers in the field. A 200-ml soil sample containing only five individuals is equivalent to 60 million per acre of top soil. Not surprisingly, preplanting treatments with nematicides do not always prevent subsequent infection, even though many nematodes are killed. It is particularly difficult to protect deeply rooted perennials (such as hop) that are often grown in very heavy soils. Better results have been obtained by treating soils used for raspberry, strawberry, or potato and by applying large quantities of fumigant to the light-textured, irrigated soils of Californian vineyards.

Control by crop rotation or fallow periods is limited because of the wide host range and persistence of nematode-borne viruses and their vectors. Nevertheless, a 2-yr bare fallow prevents the recurrence of nettlehead and related diseases of hop, even though populations of the nematode vector decline slowly. Losses can be avoided also by selecting virus-free material and sites where nematode vectors do not occur for all new plantings.

Mites (Acarina).—Several important viruses are transmitted by eriophyid mites that feed superficially and often cause distortion of host tissue (17). All vector species are four-legged, with tubular worm-like bodies and piercing/sucking mouth parts. Free-living species feed and reproduce on leaves; others infest buds, sometimes causing galls.

The most detailed transmission data are for wheat streak mosaic virus and *Aceria tulipae* which produces many generations a year on the leaves of cereals and grasses. The adults produce eggs parthenogenetically and there are two nymphal stages followed by a resting pseudopupa.

Virus is sometimes acquired or inoculated by nymphs within 15 min, although transmission improves with longer access periods. Infection persists through the moult and adult mites transmit only when virus is acquired as nymphs. Mites remain infective for several days when feeding on immune hosts at 23-28 C and for much longer at 3 C. There is no evidence of transovarial transmission or of multiplication in the vector.

Other viruses seem to be transmitted somewhat differently. Ryegrass mosaic is retained for only 6-12 h by mites feeding on an immune host, and wheat spot mosaic can be acquired and transmitted by adult *A. tulipae*.

Eriophyid mites have no special overwintering or winged stages, and some species only move between plants at certain seasons. Mites are then dispersed very effectively by wind after they stand on the anal pad and spring into the air. Large numbers of mites have been caught on sticky traps and they can be blown long distances despite vulnerability to starvation and desiccation.

A. tulipae and other mites of herbaceous plants exploit a succession of hosts throughout the year by dispersing from mature to immature foliage. Hence the importance of crop sequence in epidemiology, and the prevalence of wheat streak mosaic virus in localities where autumn-sown crops occur. These act as overwintering hosts on which mites and virus increase and then spread to spring-grown crops nearby. Mites may also infest maize, from which virus is carried to fresh sowings of wheat in late autumn. Some infection persists between crops on the 'volunteer' growth of wheat seedlings in fallowed land, after storm damage or in the stubble after harvest. Wild hosts are unimportant and control is best achieved by breaking the sequence of cereal plantings.

Species infesting perennial plants usually overwinter in or around dormant buds and disperse onto the new growth in late spring or early summer. Black currant reversion is spread at this time as the gall mite vector moves into fresh buds. Spread from old to young plantations is a particular hazard but the risk of incoming infection is low if sites are isolated and upwind from major sources. Infected bushes should be eradicated before they become good hosts of the vector and potent foci for subsequent spread (26).

Thrips (Thysanoptera).—There are many phytophagous species of thrips and some cause serious damage by feeding on the epidermis and underlying mesophyll of leaves, flowers, or fruits. The only known virus vectors are *Thrips tabaci* and three species of *Frankliniella*. These transmit the ubiquitous tomato spotted wilt virus that has caused serious diseases of diverse crop and ornamental plants (20).

The vector species belong to the Thripidae (sub-order Terebrantia) which lay eggs in slits cut in plant tissue. Nymphs are sluggish and do not move far, whereas the winged adults are very active following emergence from prepupal and pupal stages which are usually spent on the ground. There appears to be little feeding during the early period of adult life, when mating occurs. Many generations develop each year with females predominating and much parthenogenetic reproduction.

Virus can be acquired by larvae in 30 min, although transmission rates improve with longer access. There is a variable latent period, after which virus can be inoculated within 15 min. Virus persists in the vector, sometimes for life, although transmission may become spasmodic. Infectivity is retained through the larval moult and through pupation, but virus does not pass to the egg and there is no evidence of multiplication in the vector.

Adult thrips cannot acquire virus and they do not usually thrive or reproduce readily on some important hosts of spotted wilt. Virus spreads into pineapple, tobacco, and other crops from weeds, of which the composite *Emilia sonchifolia* is particularly important in Hawaii. Lack of further spread within crops explains the unusual pattern and sequence of infection. Newly infected plants tend to be randomly distributed and total field infection increases in a manner analogous to the increase of capital by simple interest (28). The rate depends upon temp and other factors influencing the number of incoming thrips and not on the number or distribution of plants already infected. Consequently the proportion of infected plants is low at high plant density or after thinning an initially dense stand at the latest possible opportunity. These measures have given more effective control than chemicals used to prevent the influx of vectors.

Whiteflies (Hemiptera: Homoptera: Aleyrodoidea).—Whiteflies transmit several viruses, mainly of tropical and sub-tropical crops (8). The flight activity of the winged adults contrasts with the almost complete immobility of larvae. The first instars move only short distances and within 24 h of hatching they settle and remain in a phloem-feeding position until pupation. Consequently only the adults are important as vectors, although larvae can acquire virus which persists through pupation and which can be transmitted immediately when they become adults. The transmission of viruses that are acquired by adults tends to be sporadic and soon ceases.

Adult whiteflies can acquire or inoculate virus in 15-30 min, although transmission rates improve with longer access time. Whiteflies are not always immediately infectious upon leaving an infected source and there is a variable latent period of 4-20 h. Virus usually persists for days and in some instances for life, but transmission may become infrequent, especially after short acquisition periods. There is no evidence of passage to the egg or of multiplication in the vector.

Cassava mosaic, cotton leaf curl, and tobacco leaf curl viruses are spread rapidly by *Bemisia tabaci*. This vector has received particular attention in the irrigated areas of the Sudan where it spreads into cotton from food and garden plants that survive the dry season. The worst outbreaks of cotton leaf curl are associated with rapid spread from the regenerating stumps of previous crops (27).

Adult whiteflies have been caught in traps on roof tops and from high-flying aircraft. They are carried far by wind and so spread persistent viruses over very great distances. However, there have been few detailed studies of flight activity and it is not known whether any of the vector species behave like the cabbage whitefly (*Aleyrodes brassicae*). The summer flights of this species in England are mainly short, to nearby leaves or adjacent plants. The females are mainly gravid at this time and they soon settle and feed after being disturbed. By contrast the long autumn flights involve nongravid females. Their flight behavior is associated with the condition of the ovaries, which develop later in individuals derived from large crowded populations (11).

Mealybugs (Hemiptera: Homoptera: Coccoidea).—Mealybugs are a highly specialized group of sucking insects with characteristic surface waxes. Males are rare and the adult females are wingless and largely immobile. They produce damaging infestations on many tropical and subtropical plants.

Mealybugs are particularly important as vectors of cacao swollen shoot virus in West Africa (7). Nymphs and adults of several species transmit at least some virus strains, although there are nontransmitting forms of some species. The efficiency of transmission increases with the length of the acquisition period up to an optimum of 1 day or longer. Mealybugs are phloem feeders and there is a minimum inoculation time of 15 min. Virus persists through the moult and for 2-3 days in starved or feeding vectors.

Infestations of mealybugs tend to be patchily distributed and many trees, especially young ones, are not infested or carry few colonies. Large infestations are infrequent and usually associated with attendant ants that remove honeydew, maintain the colonies, and build protective carton tents. Ants seldom carry mealybugs to new trees or establish fresh colonies on cacao.

The main spread of virus is by mealybugs walking between the interlocking canopy branches of neighboring trees. An important factor contributing to the slow rate of spread is that newly infected trees are not infective for some weeks or even months and virus may not become fully systemic in large trees for at least 1 yr. New outbreaks are due to wind-borne mealybugs, mainly the small first instar nymphs. These may be blown far especially when dislodged and swept away from tall forest trees that may have been the original indigenous hosts of virus and vector.

Swollen shoot is a typical 'crowd' disease (28) amenable to control by sanitation. Individual outbreaks can be controlled and infection can be eliminated from whole areas by eradicating trees with symptoms and those nearby.

Leafhoppers and Planthoppers (Hemiptera: Homoptera: Auchenorrhyncha).—The status of many of the pathogens transmitted by leafhoppers (Cicadoidea) and planthoppers (Fulgoroidea) remains uncertain. They were long assumed to be viruses and this has been confirmed in some instances. However, certain 'yellows' and other diseases are now associated with mycoplasmas or rickettsias and this necessitates a reassessment of the literature (2, 31).

Clover wound tumour, rice dwarf, potato yellow dwarf, and maize rough dwarf viruses are the most thoroughly characterized of those transmitted by hoppers. Others include sugar beet curly top, rice 'tungro', and the viruses which cause serious diseases of other cereals.

Several of these viruses multiply in their vectors that remain infective throughout life, after a latent period that may be prolonged. These viruses are retained through the larval moults and pass to at least some of the progeny. Indeed, transovarial transmission may be so frequent that a virus can persist through many generations of the vector without further access to infected plants. These are regarded as secondary hosts of what are primarily viruses of insects (9). Beet curly top, maize chlorotic dwarf, and rice 'tungro' viruses are transmitted quite differently and do not seem to multiply in their vectors. Curly top virus passes through the moult and persists for long periods, whereas the others do not.

Beet curly top virus is of continuing importance in the western United States (3). The worst losses occur after an early and heavy influx of winged leafhoppers from the main overwintering sites in the desert foothills of mountain ranges. Such migrations are from the winter annuals that are good hosts of virus and vector until they begin to dry out and die in the spring.

Airborne hoppers are carried far by wind to infect many wild plants and sugar beet, on which breeding occurs. Crops of bean, tomato, flax, and melon are also infected although they are not colonized. Losses are decreased by using resistant varieties and by timing sowing to avoid exposure to infection at a vulnerable stage. Insecticides are only partially effective in protecting crops; greater success has been achieved by spraying the winter breeding sites, or by changed systems of land management.

Much attention is now being given to the hoppers that damage rice and maize and also transmit viruses in many countries (9, 15). Losses are greatest in the tropics where the vectors breed continuously and spread between a succession of rain fed and irrigated crops or from grasses and weeds. Elsewhere the insects hibernate as eggs, nymphs, or adults and infest new crops as conditions improve.

All adult leafhoppers have well developed wings, although some species exhibit behavioral polymorphism including long- and short-flying individuals of a vector of maize streak virus. By contrast, adult planthoppers including the vectors of hoja blanca of rice and maize rough dwarf virus, occur in dissimilar morphological forms. The macropterae have long fore- and hind-wings and disperse far before laying eggs. The adults of later generations are mainly brachypterae with reduced fore-wings and rudimentary hind-wings. These relatively immobile forms are larger and have a shorter pre-oviposition period than the macropterae.

Aphids (Hemiptera: Homoptera: Aphidoidea).—The biology and habits of aphids facilitate the spread of viruses between plants and they are pre-eminent as virus vectors (12). They include more vector species and transmit a far greater number of viruses than any other group.

The diverse viruses with aphid vectors are referred to as stylet-borne or circulative according to the mode of transmission (13). These categories mainly coincide with the earlier persistent and nonpersistent groups based on retention in the vector. However, the two systems are not fully compatible and it is convenient to use the persistence categories in considering epidemiology (30).

Nonpersistent viruses.—Viruses that seldom persist for more than 1 h in the feeding vector are numerous, widespread, and of great economic importance. They include the cosmopolitan cucumber and alfalfa mosaic viruses and the many viruses ascribed to the potyvirus and carlavirus groups. These viruses are transmitted most readily immediately after fasted aphids have probed infected leaves. Virus is inoculated equally rapidly and itinerant aphids can infect plants on which they alight and probe but do not feed or breed (23, 30).

Spread between plants is faciliated by such rapid transmission and by the active restless behavior of winged aphids that are especially reluctant to settle immediately after completing the teneral period. They alight indiscriminately on the leaves of diverse plants and probe briefly before flying on. However, failure to persist in the vector or to pass through the moult or to the progeny prevent repeated transmission without further access to a source of virus.

The early appearance and rapid spread of nonpersistent viruses depends upon the occurrence of local sources of infection within the crop or nearby. The distribution of such primary infection determines the pattern of spread. 'Pools' of infected plants develop around foci within crops, whereas there are steep gradients of infection from outside sources.

Market garden crops are often grown throughout the year in over-lapping sequence and the resulting cycle of infection is difficult to break. There are advantages in fewer, larger, and more widely dispersed plantings if virus originates from outside foci and is seldom carried far into a crop. The likelihood of cross-infection is thus decreased and also the proportion of plants in the vulnerable peripheral areas (28).

Insecticides seldom kill rapidly enough to prevent the transmission of nonpersistent viruses by incoming aphids. Indeed, applications of DDT and some other materials have occasionally enhanced spread by stimulating interplant movement (5). Greater success has been achieved by foliar applications of mineral oils that interfere with virus transmission. Some control has also been obtained by changing conditions within the crop or by using aluminum strips or mulches as repellants to decrease the numbers of aphids that alight and probe (21). A further possibility is to use immune hosts as barrier or cover crops to intercept incoming aphids and so decrease the influx of virus.

Semi-persistent viruses.—A few dissimilar viruses persist for up to several days in their vectors and share other transmission characteristics (30). Brief probes are seldom adequate for acquisition or inoculation and the efficiency of transmission improves with increase in access times. There is no response to preliminary fasting and no latent period in the vectors that are most infective immediately after leaving the infected source. Virus has not been detected in the haemolymph of vectors and does not pass through the moult or to the progeny.

Semi-persistent viruses are not transmitted as rapidly as the nonpersistent ones, but they are retained longer and can be carried further by their vectors. These features facilitate spread and it is perhaps surprising that the semi-persistent mode of transmission is not encountered more frequently. Certainly sugar beet yellows virus remains widepsread and prevalent despite the extensive use of insecticides to check spread within crops and the measures taken to avoid overwintering sources of infection.

Persistent viruses.—Viruses that persist for weeks in their aphid vectors comprise a large and morphologically diverse group including such important pathogens as potato leaf roll, barley yellow dwarf, and beet western yellows. The efficiency with which viruses of this type are acquired is unaffected by preliminary fasting and increases with increase in duration of acquisition feed. There is a delay (which may be prolonged) before aphids that have acquired virus can transmit. However, infective aphids retain virus through the moult and sometimes for life. Some persistent viruses have been detected in the haemolymph and multiply in aphids (30).

The relationships between persistent viruses and their vectors is complex and often highly specific. Prolonged retention of virus within aphids is therefore an important feature that partially compensates for the generally small number of vector species and for the long period required for aphids to acquire virus and become infective. Nevertheless, persistent viruses tend to spread less rapidly and are more readily controlled by insecticides than nonpersistent ones, although they are less dependent on the presence of nearby sources of infection and may be difficult to control by isolation.

Alate aphids that have developed on infected plants are particularly important in epidemiology because they are likely to be infective on take-off and throughout flight. Barley yellow dwarf virus, for example, is regularly carried far in North America and elsewhere by alate aphids from overwintering grasses or cereals (6). Aphids that originate from eggs on woody plants are of less direct importance because they are unlikely to fly frequently or far after they have acquired virus and become infective. Similar factors influence the spread of carrot motley dwarf and sugar beet mild yellowing diseases that tend to appear late and be least prevalent after severe winters when relatively few aphids originate from herbaceous hosts.

Beetles (Coleoptera).—Leaf-eating beetles of the Chrysomelidae are the only known vectors of viruses in the tymovirus and comovirus groups. Beetles have also transmitted a few other viruses that are highly infectious and occur in high concn.

Walters (29) listed adults and some larvae of 21 vector species. Only two species were outside the sub-families Galerucinae and Halticinae. These have active winged adults and larvae of diverse habits, including root and leaf feeders. The immobility of larvae restricts their importance in spreading virus, although some transmit efficiently in experiments. Virus failed to persist through the pupal moult in the single instance it was tested adequately.

Adults often acquire or transmit after access periods as short as 5 min. Efficiency increases with longer feeds and in all instances virus is retained for at least 1 day in starved or feeding vectors. Some viruses fail to persist for 2 days, but the majority are retained for much longer; squash mosaic virus may overwinter in the vector.

Cowpea mosaic virus spreads rapidly under Trinidad conditions with almost total infection of some plantings within a few weeks. Spread is from scattered seed-borne infections and by the movement of infective beetles from older legume crops nearby. Seed-borne infection is also important in the epidemiology of two viruses of field beans (*Vicia faba*) in England.

Other beetle-transmitted viruses spread rapidly, although they do not appear to be seed-borne. At one site, the flea beetle vector of turnip yellows virus jumped frequently over short distances but seldom flew far. There was a steep gradient of infection into a young planting from an older one alongside. The beetle vector of squash mosaic and other viruses behaves differently. Winged adults are carried far to the north of their overwintering range in Louisiana by favorable spring winds. Southern areas are reinfested in the autumn and beetles have been taken at altitudes up to 304.8 m (1,000 ft) and may cover more than 500 miles in 2-4 days (11). Newly emerged adults feed before flight and so acquire virus that may be carried far.

Vector mobility.—There are big differences in the biology and life cycles of the main groups of vectors. Nematodes are unique in that neither adults nor larvae can move far, which limits virus spread. Important compensating features are that infection usually persists once it becomes established at a site and that virus may be disseminated widely in seeds. The soil provides a stable environment and nematode activity and numbers fluctuate less than those of above-ground arthropod vectors. Many of these exploit annual or deciduous hosts and regularly encounter formidable hazards.

Whitefly larvae are virtually immobile and, apart from windborne mealybugs and mites, the immature forms of many other arthropod vectors seldom move very far. Those able to transmit may spread virus to nearby plants by walking, crawling, or hopping. Adults, and especially active winged forms, also spread virus locally, but their separate contribution is difficult to evaluate.

Distant spread by arthropods is due solely to windborne mites or mealybugs or to the wind-assisted flight of adult insects. The spread of eriophyid mites by wind is facilitated by their small size and by the ability of some species to produce resistant migrant forms that leap into the air in conditions favoring dispersal. Some mealybug species produce a thread that increases buoyancy and the diverse wing structures of many insects act similarly.

Among the various groups of winged insects, wide differences in ability and inclination to fly lead to a corresponding diversity in flight activity. Some strongly flying insects can control their flight path, but the winged vectors of plant viruses cannot do so except in the relatively still air of the boundary layer near ground level. Hence the critical importance of wind and mass movements of air in the take-off, lateral displacement, and eventual deposition of winged vectors. Take-off, alighting, and ultimately the incidence of virus, are markedly influenced by topography and by the sheltering effects of buildings, trees, hedges, fences and terrain undulations (14). Factors within the crop planting, such as the size, age, spacing, coloration and the stage of development of plants are also important.

Long flights from initial breeding sites are a regular feature in the biology of many insects. Such flights mainly involve sexually immature females and usually begin early in adult life. Examples include vector species of aphids, thrips, hoppers and beetles (11). The characteristically restless behavior of migrants and an ability to travel far are seldom attributes of an entire adult population. Among the adults of many species there is variation in ability or inclination to fly and some degree of alary polymorphism. Active, winged forms are responsible for the initial colonization of host plants. These are exploited by later generations of relatively immobile individuals that reproduce rapidly. There are obvious morphological differences between alate and apterous aphids and between long- and short-winged planthoppers. In other groups, the differences are primarily physiological or behavioral as with the long- and short-flying forms of leafhoppers.

Aphids have received particular attention due to their special importance as vectors and because of the vast numbers occurring in the air in temperate regions during the summer. Large numbers of many other insects and mites also become air-borne and may be carried far, but only a minute proportion reach suitable habitats. This apparently wasteful and haphazard behavior is a particular feature of arthropods that exploit short-lived hosts or transient environments (22). It is of crucial importance in survival, enabling the transfer of a portion of the breeding population to fresh sites before the original ones disappear or become untenable. Migration also ensures that viruses are carried frequently and far by vectors that are infective on take-off or that acquire virus while dispersing. The rapidity and efficiency with which crops are colonized by vectors accounts for the early appearance and subsequent spread of many viruses.

The factors governing the spread of many viruses into and between crops are clearly those that determine the appearance and behavior of active migrants. These are solely responsible for the spread by arthropods of viruses which cause diseases of the 'simple interest' type, while many 'compound interest' diseases progress from foci of infection started by incoming vectors and enlarged by further local flights either by those vectors or by their progeny.

Migration tends to occur when populations are high or when seasonal or other conditions become unfavorable, especially when the host plants are maturing or beginning to senesce and die. Hence the many striking examples of spread by vectors moving from ripening crops or otherwise deteriorating environments. There are divergent views to account for the appearance of specialized migrants. Johnson (11) has reviewed the evidence on inherent traits, crowding, day-length, and host condition. He stressed the predominance of sexually immature females in many migrations and the apparent antagonism between flight activity and reproduction. Indeed, there is often a temporary and sometimes permanent suppression of flight activity when reproduction begins and this may be accompanied by degeneration of the wing muscles. This occurs with some species of aphids and is one reason why they become less active and tend to settle, feed, and reproduce after an initial period of flight.

Migration in all groups is facilitated by the extended period of sexual immaturity that occurs when there is reduced activity of the corpus allatum and associated endocrines. This occurs as a result of environmental stimuli linked with short day-length, insufficient or deficient food, crowding or high temperature (10). Thus it is possible to integrate flight activity with environmental factors influencing the condition of the host plants, which is modified by their virus status.

The often complex interactions between virus, host, and vector emphasize the need for comprehensive biological studies of virus epidemiology which has been advocated since the early work on sugar beet curly top virus. A similar approach has been made to swollen shoot virus in West Africa and to aphid-borne viruses of sugar beet and potato in Europe and elsewhere. Few other virus diseases have been studied either in such detail or as studies in applied ecology, despite increasing evidence that some viruses multiply in, and act directly upon, their vectors. Many other viruses influence their vectors indirectly through their plant hosts. These may be altered profoundly as a result of infection to the advantage or disadvantage of the vectors. Several diverse vectors reproduce or grow faster on virus-infected than on healthy plants and the gall mite vector of black currant reversion virus thrives only on reverted bushes. The significance of such effects in epidemiology is not always so obvious, but there is no reason to believe that the black currant situation is unique. Viruses are likely to be much more important in the biology of their vectors than the present limited evidence suggests.

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