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Gradients of plant virus diseases

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INTRODUCTION

The spread of plant pathogens tends to decrease with increasing distance from foci of infection and the gradients obtained by plotting the incidence of disease against distance have received much attention (56, 58, 150, 151, 152). The main discussion has, however, concerned fungal pathogens, whereas this review deals almost exclusively with gradients of plant virus diseases. These have unique features and their study is vitally important in epidemiology, in developing control measures and in schemes for producing healthy planting material.

OBTAINING PRIMARY DATA

Some gradients have been noted after spread from obvious sources of infection into nearby experimental plots planted originally for other purposes (9). Other gradients have been recorded in commercial plantings examined in special or routine surveys of disease (147). The resulting data on the infection of crops at different distances from major field sources are somewhat imprecise as it is seldom possible to locate all foci and minor ones may have to be ignored when interpreting the results (42, 109). Nevertheless, such studies have given valuable data of great practical importance in disease control because they provide the only feasible means of obtaining information on spread over distances greater than can be considered in experimental plots.

The most precise and easily interpreted data have been obtained in experiments specially designed to follow spread from small groups of planted infectors (e.g. (95)). The actual distances over which spread occurs are more readily apparent from such planned experiments than from those in which spread is from naturally occurring foci, especially those that are distant, large or otherwise ill-defined.

Van der Plank (139) has stressed the 'cryptic' errors and interference between plots that complicate the design and analysis of field experiments on pests and pathogens that soon spread beyond the boundaries of areas in which they are allowed to progress unchecked. Particular problems are encountered in experiments on disease gradients and it is advantageous to follow spread from discrete foci planted at typical sites that are not exposed to further infection from elsewhere. This may necessitate establishing isolated plots surrounded by bare ground (e.g. (111)), or by non-susceptible crops (e.g. (127)). Small plots are, however, subject to pronounced edge, positional or exposure effects and growing conditions differ markedly from those in large stands. This justifies the alternative approach of incorporating trials within much larger plantings (22, 37).

Ideally there should be replication within and between sites and in different seasons to obtain reliable and truly representative data. For many diseases this cannot readily be arranged without at least some spread between plots (e.g. (44, 116)), although the risk can be decreased by a careful choice of plot size, shape and orientation, and by ensuring adequate separation. There should be the minimum interface between adjacent plots and these should be arranged across (rather than along) the direction of the winds prevailing during the main period of spread. The effectiveness of such measures in avoiding 'background' contamination from within or outside the experimental area can be determined by establishing otherwise similar plots without infected sources (67, 128).

Enough healthy plants must be exposed at each distance from the infected source to obtain a statistically valid estimate of infection, whether or not seasonal and other conditions facilitate spread. Many 'trap' or 'target' plants are required away from the source, where few infections are to be expected and occasional spread from extraneous sources has a disproportionately large effect. Fewer plants will suffice near the source, unless spread is likely to be so great that almost all plants become infected. Nevertheless, many more plants are required than in comparable experiments on non-systemic pathogens causing discrete lesions or pustules. This raises major problems in assessing spread amongst widely spaced trees or bushes at low density.

Plants should ideally be arranged in concentric circles to follow spread in all directions from a small central source (Fig. 1 *a*). Circular plots are, however, difficult to mark out, cultivate and maintain and plants arranged in squares cannot readily be assigned to definite annuli about a central source (Fig. 1 *c*). A convenient alternative is to plant in staggered rows to form concentric hexagons (Fig. 1 *d*) and so assess spread at different distances from the source in each of six 60° sectors of similar area (127).

Rectangular or cruciform plots have been widely used to follow the spread of aphid-borne viruses of potato from outside sources (91), or from a centrally planted group or strip of infector plants (37, 90, 95). Limitations of the strip design are that equal numbers of plants are exposed at each distance (Fig. 1 *e*) and spread can be followed in only two directions. Hence the size and arrangement of the plots in relation to the prevailing wind greatly influence the proportion of vectors remaining within the experimental area. Vectors inevitably disperse or are swept away, especially when the plants around the source are so few, small, or widely spaced that they present limited catchment surfaces of low profile (127).

The distant spread of some viruses and their vectors has been followed by growing small experimental plots of 'trap' plants at various distances and in different directions from major foci (38, 39). Alternatively, successive batches of potted plants are placed sequentially at each site to provide additional information on season of spread (30, 114), or to avoid secondary spread (111). One difficulty encountered is that potted plants may behave abnormally because they are very exposed or otherwise atypical of those in large stands.

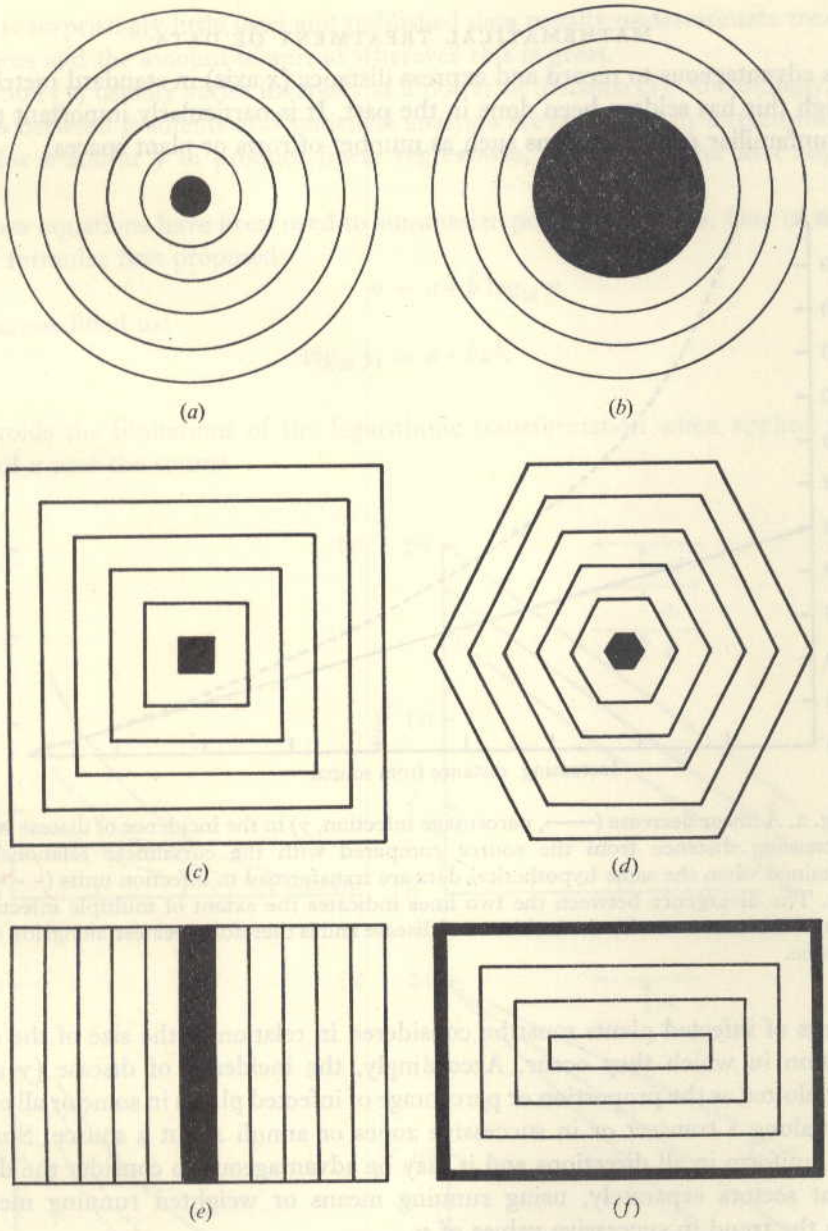

Fig. 1. Diagrammatic representation of various possible arrangements for following spread from the point, area or line sources of infection shown in solid black. Note the great differences between the different designs in the rate of dilution of inoculum with increasing distance from the source. (*a*) Circular plot, point source; (*b*) circular plot, area source; (*c*) square plot, central source; (*d*) hexagonal plot, central source; (*e*) rectangular plot, line source; (*f*) rectangular plot, peripheral source.

MATHEMATICAL TREATMENT OF DATA

It is advantageous to record and express distance (x axis) in standard metric units, although this has seldom been done in the past. It is particularly important to avoid using unfamiliar or vague terms such as number of rows or plant spaces.

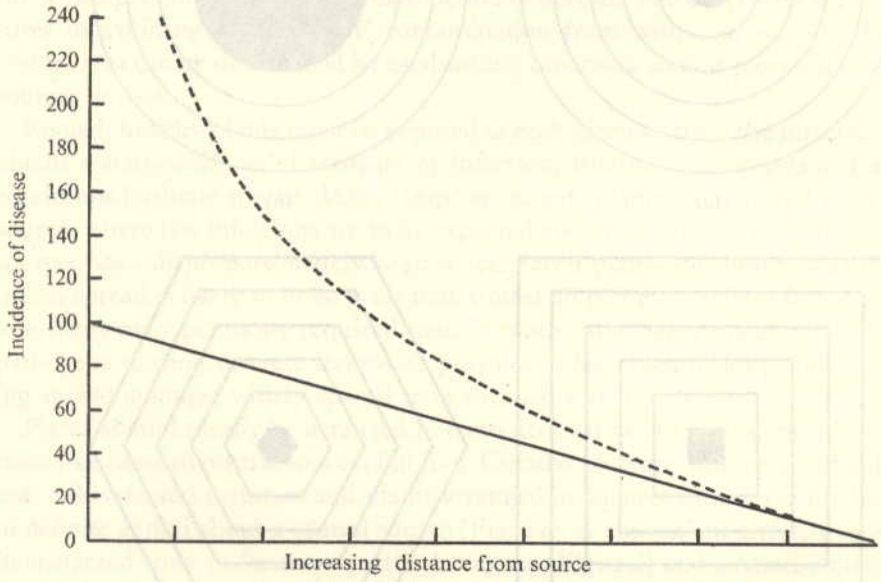

Fig. 2. A linear decrease (——, percentage infection, y) in the incidence of disease with increasing distance from the source compared with the curvilinear relationship obtained when the same hypothetical data are transformed to infection units (- - - -, y_t). The divergence between the two lines indicates the extent of multiple infection (55) which increases with the incidence of disease and is therefore greatest alongside the source.

Counts of infected plants must be considered in relation to the size of the area or population in which they occur. Accordingly, the incidence of disease (y axis) is usually plotted as the proportion or percentage of infected plants in some or all of those present along a transect or in successive zones or annuli about a source. Spread is seldom uniform in all directions and it may be advantageous to consider the data for different sectors separately, using running means or weighted running means to smooth the trend in successive values of y.

As y increases it is inevitable that an increasing proportion of the exposed plants receive more than one infective dose (Fig. 2). The partial extent of such 'multiple infection' is sometimes apparent from meticulous records of early symptoms indicating the initial sites of inoculation (127, 128). The full extent can be estimated mathematically and the appropriate transformation of percentage values of y to infection units y_t has been tabulated and discussed (55, 139). The procedure is of general validity and is of particular importance when values of y exceed 20%. However, the transfor-

mation is surprisingly little used and published data usually underestimate treatment differences and the amount of spread wherever this is great.

Infection (y) usually varies inversely as a power of distance (x). Accordingly, comparisons between gradients and statistical analyses are facilitated by transforming the values for x and/or y to produce linear regressions, preferably after first adjusting y to y_t.

Various equations have been used to summarize published results. One of the two general formulae first proposed:

$$y = a + b \log_{10} x \tag{151}$$

was later modified to:

$$\log_{10} y_t = a + bx^p. \tag{58}$$

This avoids the limitations of the logarithmic transformation when applied to low values of x near the source.

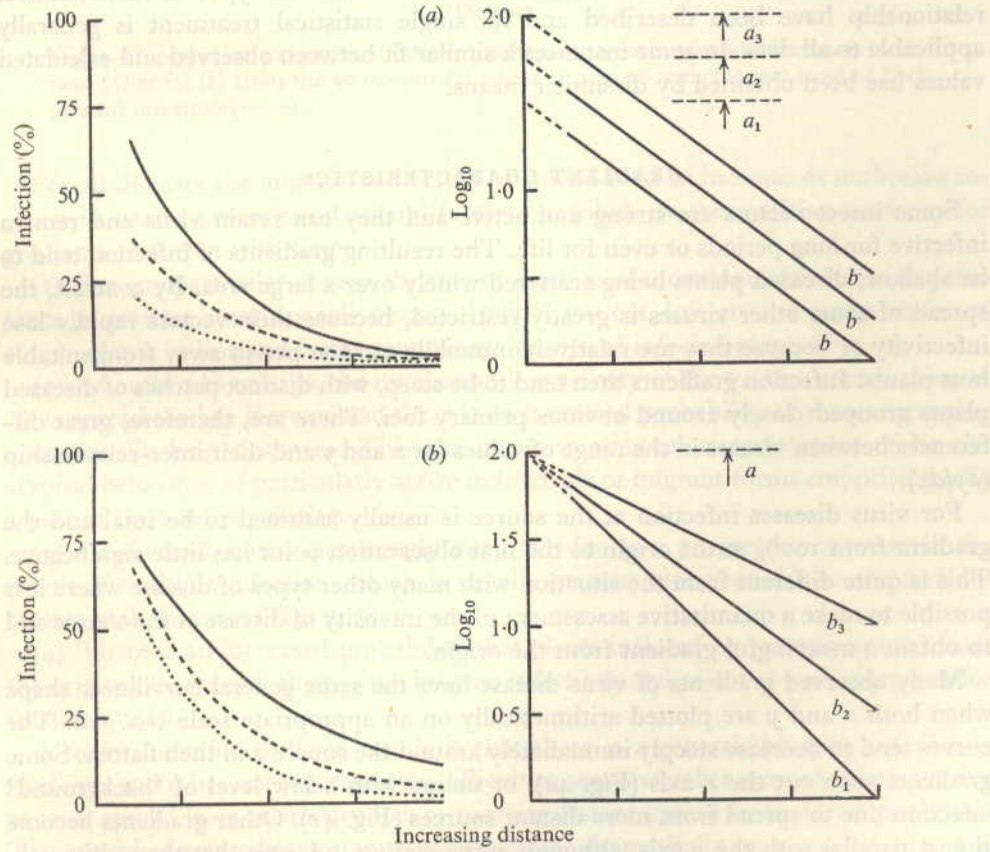

Fig. 3. Three curvilinear relationships (——, - - - -, ...) between infection and distance (left), transformed to straight lines (right) of (*a*), similar slope but different height and (*b*), similar height but different slope, after converting percentage data to logarithms.

The modified equation expresses a linear relationship between the logarithm of disease intensity and a power (p) of distance. The constants a and b vary independently according to the height and slope of the regression line, respectively (Fig. 3). They are, therefore, important parameters indicating the overall level of infection and the rate of change with distance. For various diseases, including some caused by viruses, there is a better approximation to a straight line on plotting $\log_{10} y_t$ against actual values of x (i.e. $p = 1$) than by using the square or square root transformation of x ($p = 2$ or $\frac{1}{2}$).

The general formula was later modified further to log/log form:

$$\log_{10} y_t = a + b \log_{10} x. \tag{56}$$

This also has limitations when $\log x \doteq 0$ but it is consistent with the definition of gradient of disease as 'the slope (b) of the line when the logarithm of the amount of disease is plotted against the logarithm of distance from the source of inoculum' (36). Such a definition is, however, unduly restrictive and conflicts with general use of the term gradient (as in this review) for 'a change in incidence of disease with distance from a source of infection' (46). Moreover, various distinct types of mathematical relationship have been described and no single statistical treatment is generally applicable to all data. In some instances a similar fit between observed and calculated values has been obtained by dissimilar means.

GRADIENT CHARACTERISTICS

Some insect vectors are strong and active and they can retain virus and remain infective for long periods or even for life. The resulting gradients of infection tend to be shallow, diseased plants being scattered widely over a large area. By contrast, the spread of some other viruses is greatly restricted, because their vectors rapidly lose infectivity or because they are relatively immobile or soon perish away from suitable host plants. Infection gradients then tend to be steep, with distinct patches of diseased plants grouped closely around obvious primary foci. There are, therefore, great differences between viruses in the range of values for x and y and their inter-relationship (dy/dx).

For virus diseases infection at the source is usually assumed to be total and the gradient from 100% at the origin to the first observation point has little significance. This is quite different from the situation with many other types of disease where it is possible to make a quantitative assessment of the intensity of disease at the source and so obtain a meaningful gradient from the origin.

Many observed gradients of virus disease have the same general curvilinear shape when both x and y are plotted arithmetically on an appropriate scale (151, 152). The curves tend to decrease steeply immediately around the source and then flatten. Some gradients soon cut the x axis (Fig. 4a), or merge with a low level of 'background' infection due to spread from more distant sources (Fig. 4c). Other gradients become almost parallel with the x axis, although extrapolation indicates that they ultimately reach zero far from the source (Fig. 4b).

Around outbreaks of many diseases there is a distance beyond which spread is so infrequent that infection becomes insignificant or so unimportant that it can be dis-

regarded. This distance has been termed the 'horizon of infection' (137), which is an important concept in epidemiology even though no precise and generally applicable definition is possible. In control measures against widespread and prevalent diseases it may suffice merely to delay the onset and/or decrease the ultimate amount and extent of spread, whereas quarantine, eradication and isolation requirements are more exacting. Moreover, the horizon varies according to the form of the infection gradient and is most circumscribed for 'crowd' diseases that seldom spread far in any considerable amount (136). These were later defined as diseases 'likely to reach epidemic proportions only when the host plants are crowded together into fields' (138).

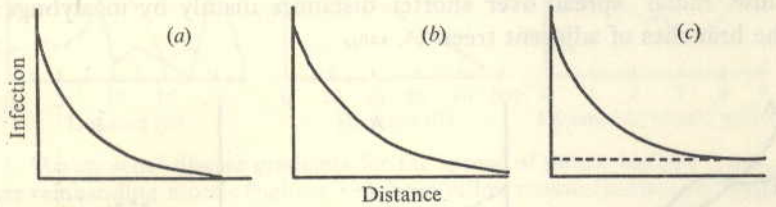

Fig. 4. Hypothetical examples of disease gradients in which infection decreases to zero near (*a*) or far (*b*) from the source, or (*c*) where it merges with the low level of background infection (– – –).

For all diseases the amount and extent of spread tend to increase as outbreaks increase in size or potency and several factors contribute to the resulting tendency for gradients to flatten with time:

(1) For any particular disease the rate of dilution of inoculum with increasing distance is greatest around small discrete 'point' sources, less around several infected source plants in line and least around large groups of infected plants (Fig. 1).

(2) As outbreaks enlarge, the number and/or activity of the vectors contributing to virus spread tend to increase and there is an increased probability of some dispersing exceptionally long distances. This can occur in unusual circumstances or by the atypical behaviour of particularly active individuals or migrant forms comprising only a part of the total population.

(3) Gradients become increasingly distorted due to a progressive increase in the extent of multiple infection, which is usually greatest alongside the source and decreases with distance (Figs 2, 7).

(4) There is an increased probability that plants infected by primary spread from the original source will themselves become infectious and so act as secondary foci for further spread.

A major outcome of these trends is that there is a general 'blurring' of disease gradients and it becomes increasingly difficult to assess whether new infections are due to local spread from secondary foci or to more distant spread from the original ones. The spread of some diseases appears to increase dramatically once a critical level of infection has been exceeded and control then becomes increasingly difficult to achieve (139).

Away from the source, new infections tend to occur singly and they may be diffi-

cult or impossible to distinguish from the low level of 'background' infection due to spread from extraneous sources at even greater distances (56). Nevertheless, the total number of widely scattered infections that occur discontinuously distributed amongst the many plants around the periphery of an outbreak may greatly exceed those occurring at greater density amongst the far fewer plants alongside the source. This may not be apparent from published percentage data and there is a general tendency to underestimate the number and significance of outlying infections. These initiate new outbreaks and have a disproportionate importance in epidemiology. Most new foci of cacao swollen shoot virus, for example, are due to 'jump spread' by wind-borne mealybugs. This is far less frequent but much more difficult to anticipate and control than the slow 'radial' spread over shorter distances mainly by mealybugs walking between the branches of adjacent trees (96, 126).

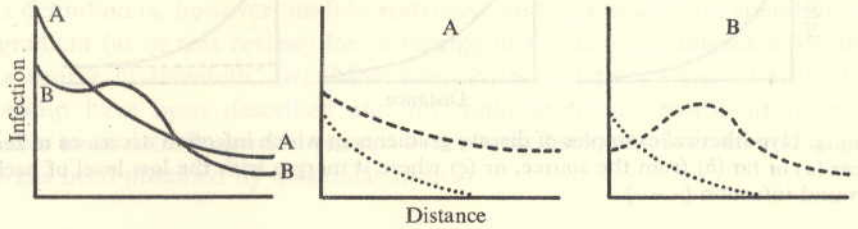

Fig. 5. Two hypothetical gradients for the incidence of disease (left) produced by combining the spread due to active (– – –) and relatively inactive (. . . . .) forms of vectors A (centre) and B (right) of different habits.

Mealybugs, aphids and some other types of vector exhibit advanced polymorphism, with great variation between the different forms in their seasonal abundance and mobility and in their ability to transmit virus (130). Shallow gradients of spread over great distances are due solely to the most mobile forms and their appearance may be restricted to certain clearly defined migration periods. Spread at other times and by less active individuals or forms results in relatively steep gradients over short distances around the source. This explains why the initial patterns of infection by migrants moving considerable distances into or between plantings may be quite different from those due to subsequent local spread by the incoming vectors or their less mobile progeny. Where different forms coexist and each contributes to spread, the observed gradients of infection represent the superimposition of two or more separate distributions (Fig. 5). However there is seldom any discontinuity or inflexion in observed gradients to distinguish distinct zones of spread. These tend to merge imperceptibly and there is considerable uncertainty as to the relative importance in local spread of wind-borne and crawling mealybugs or mites (126, 127) and short- and long-flying forms of certain leafhopper vectors (105). Similarly with the long-winged (macropterous) and short-winged (brachypterous) plant-hopper vectors of maize rough dwarf virus (62). Conflicting claims have also been made on the performance of apterous and alate aphids as vectors (17, 101, 102) and their relative importance seems to differ between viruses and between regions. There is, however, general agreement that in some crops apterous aphids and the relatively immobile forms of other vectors

often reach plants that have been infected already by the more active members of a population.

'False' gradients exhibit a reversal of the initial negative slope with further increase in distance (56). This usually occurs when greater isolation from one source leads to closer proximity to others. Anomalous gradients also occur when barrier crops are

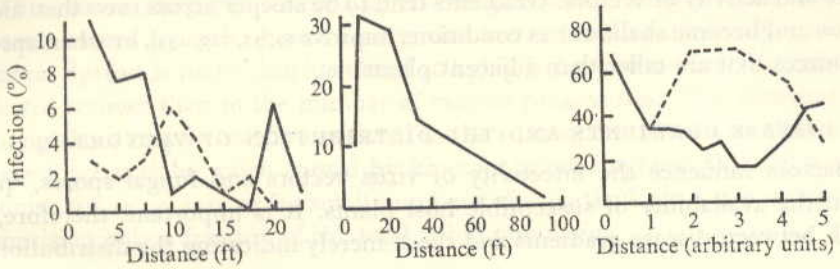

Fig. 6. 'Anomolous' disease gradients for the spread of potato leaf roll (right, ——), pepper veinbanding mosaic (right, - - -), bean yellow mosaic (centre) and cauliflower mosaic in different areas (left, —— and - - -) (91, 111, 61, 16) respectively.

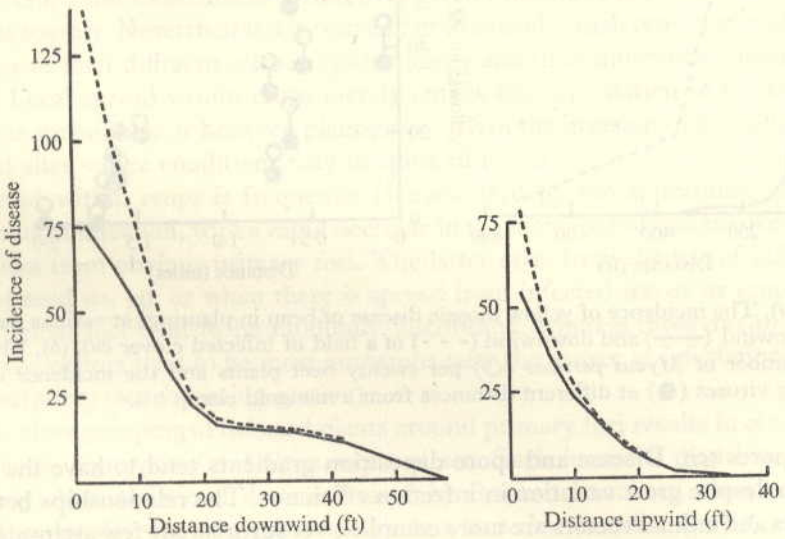

Fig. 7. Observed gradients (——, percentage infection, y) in the incidence of black-currant reversion virus upwind (right) and down-wind (left) of a central source compared with the curves of the same data transformed to infection units (- - -, y_t) to indicate the extent of multiple infection. (127).

used (140) and when vectors leaving an infected source overfly adjacent plants or are blown over them to give an initial 'skip distance' downwind before the zone of maximum infection (Fig. 6). Such gradients have been recorded for the spread of cauliflower mosaic by aphids, but sometimes there is a similar incidence of infection immediately alongside the source and again several plant spaces away (16).

Alate aphids and other types of wind-borne vector tend to be carried downwind rather than upwind. Accordingly the amount and extent of spread and the degree of multiple infection are least in the upwind direction (Figs 7, 8*a*). Gradients downwind are relatively shallow and the horizon of infection is less circumscribed (53, 61, 127).

The amount and extent of spread are further influenced by the size, density and susceptibility of the crop and by temperature and other conditions influencing the abundance and activity of vectors. Gradients tend to be steeper across rows than along them (77, 90) and become shallower as conditions improve (9, 31, 140, 153), or when spread is from sources that are taller than adjacent plants (16).

DISEASE GRADIENTS AND THE DISTRIBUTION OF VECTORS

Many factors influence the infectivity of virus vectors and fungal spores, quite apart from the availability of susceptible host plants. It is important, therefore, to distinguish between disease gradients and those merely indicating the distribution of

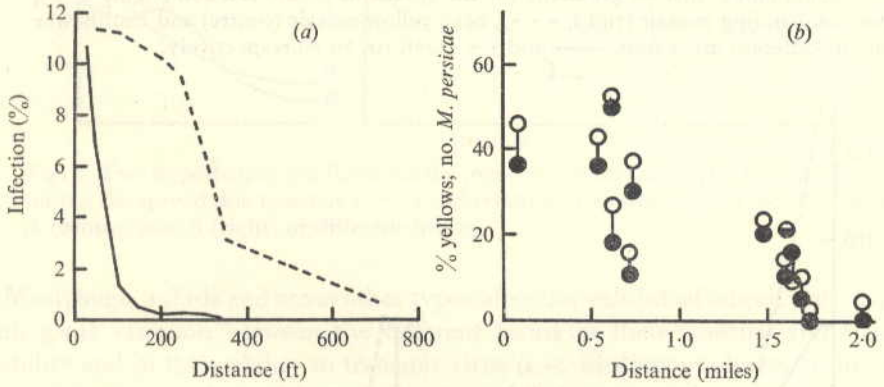

Fig. 8. (*a*), The incidence of yellow mosaic disease of bean in plantings at various distances upwind (——) and downwind (- - -) of a field of infected clover (61). (*b*), The mean number of *Myzus persicae* (○) per twenty beet plants and the incidence of yellowing viruses (●) at different distances from a mangold clamp (18).

vectors or spores (57). Disease and spore deposition gradients tend to have the same general form despite great variation in infection efficiency. The relationships between virus diseases and animal vectors are more complex, yet surprisingly few attempts have been made to relate gradients of virus disease to numbers of vectors as counted on plants or trapped at different distances from a source. There is even less information on the proportion of vectors that are infective in field situations and data on aphids transmitting viruses of citrus (34) and sugar beet (145) indicate great differences in performance.

The simplest situation arises when the vectors entering a crop are already infective, having retained virus throughout the winter or having developed or overwintered on infected plants. This accounts for the similar gradients of infestation by vectors and of disease around sources of persistent or semi-persistent viruses transmitted by thrips (9), aphids (Fig. 8*b*), mites (127) or leafhoppers (106). The initial incidence of barley

yellow dwarf, beet curly top and several other diseases is also related to the influx of infective vectors (80, 93, 103, 115). The later distribution tends to be less distinct because dissimilar factors influence primary deposition and subsequent reproduction (135). Further complications arise when there are seasonal differences in the proportion of incoming vectors originating from infected plants compared with those having developed from overwintering eggs on virus-immune hosts (144).

There are no simple relationships between gradients of infection and infestation for diseases caused by stylet-borne viruses that are not retained for long by their aphid vectors. Spread is more closely related to aphid behaviour and to the distribution of infected sources than to the number of vectors present (146). The distribution of incoming alates may be totally unrelated to the subsequent pattern of disease (5). Elsewhere there may be much spread by itinerant aphid migrants that fail to settle and colonize (32, 35, 40, 122), or by small numbers of a particularly active species or form comprising only a fraction of the total aphid population.

GRADIENTS OF SPREAD WITHIN CROPS

It is seldom possible to distinguish between infections arising from local spread within crops and those due to spread over greater distances between plantings or from outside sources. Nevertheless it is convenient to consider each type of spread separately, because of their different roles in epidemiology and their different ecological connotations. Local spread within crops merely entails the exploitation of existing habitats, whereas spread into or between plantings involves the invasion of new and sometimes distant sites where conditions may be quite different.

Spread within crops is frequently characterized by the appearance of very steep gradients of infection, with a rapid decrease in the incidence of disease over quite short distances from obvious primary foci. The latter arise from the use of infected plants (37), or seed (20, 94), or when there is spread from infected weeds or crop debris (42). Such initial foci tend to be randomly distributed, whereas those due to an influx of infective vectors tend to be most numerous near the source of infestation and around the periphery (see following section).

The close grouping of infected plants around primary foci results in obvious 'pools' of infection that spread and ultimately coalesce. Such localized distributions are particularly characteristic of diseases caused by viruses transmitted non-persistently (16, 20, 37), or by slow-moving nematode vectors (125). Viruses that persist in arthropod vectors can be carried further, but they too cause most infections immediately around the source. This accounts for the obvious patches of diseased plants that are a feature of groundnut rosette (44), barley yellow dwarf (115) and sugar beet yellows (144). Moreover, potato leafroll virus persists far longer in aphids than potato virus *Y*, yet both viruses often spread similarly in small plots (Fig. 9; (19, 64, 153)). These observations support much other work indicating the limited frequency and extent of aphid movement within crops once the initial influx of winged migrants has occurred (15). The continued mobility of at least some alates is restricted by unfavourable weather, or by an early degeneration of the wing muscles that occurs after initial flight and as reproduction begins. Individuals may make only one major flight, during which they

tend to be swept far away from the original source as they leave the relatively still air amongst crops and become exposed to large-scale wind movement and atmospheric turbulence (73).

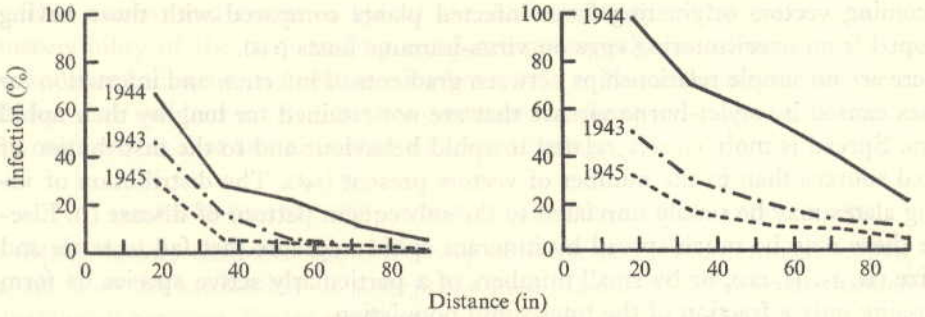

Fig. 9. The local spread of rugose mosaic (left) and leaf roll (right) of potato from a central strip of infectors; summarized data from several sites in each of 3 yr with greatly differing amounts of spread (58).

GRADIENTS INTO AND BETWEEN CROPS AND FROM OUTSIDE SOURCES

Spread into or between crops is a crucial feature in the epidemiology of many virus diseases and particularly those of short-lived crops in regions with a restricted growing season. Diseases of the 'simple-interest' type spread exclusively from outside sources and many 'compound-interest' diseases progress from primary foci started by incoming vectors and enlarged by subsequent local movement or by their progeny (129). The initial influx may be from wild or cultivated plants that are sometimes remote and difficult to locate. It often involves particularly active itinerant individuals and in many instances, a high proportion of adult females that are sexually immature and specially well adapted for dispersal (73).

The factors governing the distant spread of many viruses are linked, therefore, with those that determine the appearance of specialized migrants. These are physiologically and in some instances morphologically distinct from the usual forms that are relatively immobile and soon settle and breed. Migrants often appear as conditions begin to deteriorate because of seasonal factors or overcrowding, or as host plants mature and begin to senesce. Hence there are many gradients of disease due to vectors spreading from old to new plantings or from otherwise deteriorating habitats to those more favourable. This explains the high incidence of infection in market garden and other ephemeral crops grown in close proximity to each other and in overlapping sequence throughout the year (16, 20). Infection is prevalent in many crops grown in tropical or sub-tropical areas where there is virtually no break in the natural growing season or where rain-fed and irrigated crops follow in close succession. Elsewhere there are examples of the seasonal progress of virus diseases across countries or even whole continents as with barley yellow dwarf in North America (21). Other diseases caused by persistent viruses of cereals, legumes or other widely grown crops are likely to spread between the different climatic zones within the continental land masses of Africa (2) and Asia, but this possibility has received scant attention.

The spectacular wind-assisted flights of the leafhopper vector of sugar beet curly top virus result in very shallow disease gradients (Fig. 10) over many miles to and from ephemeral weed hosts in the desert foothills of mountain ranges in California and neighbouring south-west states (12). Flights over low ranges of hills and for several miles along valleys, are referred to as 'local'. Migrations of 30–60 miles are commonplace and spread of curly top virus and/or its vector have been traced beyond 398 miles (11, 51).

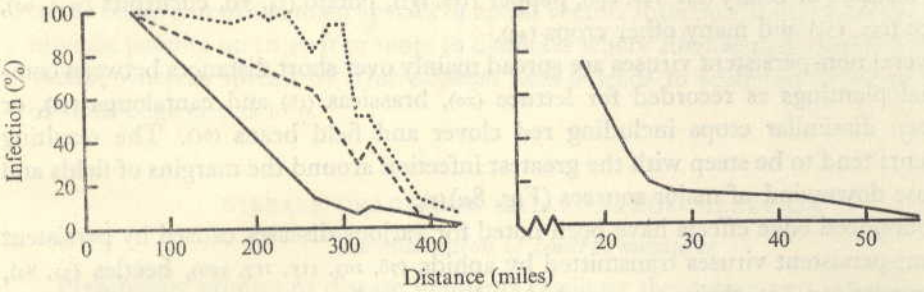

Fig. 10. The overall incidence of beet curly top virus in Idaho fields at different distances from the nearest main breeding ground of the leafhopper vector. Data for crops of field bean (right) and sugar beet in three different seasons (left, ——, - - - and . . . .) (7, 104) respectively.

The leafhopper vector of hoja blanca virus of rice can also remain infective for long periods and occasional spread into Florida, Louisiana and Mississippi is attributed to vectors transported far beyond their usual range by cyclonic or hurricane winds from Cuba (45).

Wind-assisted flight is a regular feature of the life cycle of many aphid and other insect species (73). This results in much virus spread, although the precise distances involved are seldom apparent. Potato leafroll is carried occasionally to remote parts of the Netherlands (66) and sugar beet yellowing viruses can be spread into Scandinavia from more southerly European countries (72). The distant spread of barley yellow dwarf virus has received particular attention in North America (21), where wind conditions and night temperatures are much more favourable for prolonged flights than in England (13).

The eriophyid mite vectors of blackcurrant reversion and wheat streak mosaic viruses can be blown far (86), but they do not survive for long away from host plants. This so limits dispersal that local gradients of mite infestation and virus infection have been recorded within and between plantings (6, 114, 127). Indeed, severe outbreaks of wheat streak mosaic are largely confined to regions where both autumn- and spring-sown crops are grown in overlapping sequence with no break in the cycle of infection (114).

Overwintering sources of infection are particularly important in the epidemiology of many diseases caused by aphid-borne viruses of temperate regions (144). An early survey in England showed yellowing of sugar beet root crops to be most prevalent in districts where biennial seed crops occurred, but within these areas proximity to

individual seed crops did not influence disease incidence (147). This suggests very shallow gradients of infection as recorded within several miles of beet clamps (Fig. 8*b*; (18, 65)).

The spread of non-persistent viruses tends to be very localized around primary foci of infection, whether these are within or alongside crops. Sugar beet mosaic, for example, is mainly restricted to plantings within 100 yards of seed crops (147) and the prevalence of maize dwarf mosaic is closely associated with the distribution of perennial grasses. Nearby wild or garden sources of infection are also important in the epidemiology of virus diseases of celery (141, 148, 149), pepper (110, 113), potato (14, 33), cucurbits (3, 4, 92), lettuce (133, 134) and many other crops (43).

Several non-persistent viruses are spread mainly over short distances between commercial plantings as recorded for lettuce (20), brassicas (16) and cantaloups (92), or between dissimilar crops including red clover and field beans (61). The resulting gradients tend to be steep with the greatest infection around the margins of fields and in those downwind of major sources (Fig. 8*a*)(5).

Pronounced edge effects have been noted for various diseases caused by persistent or semi-persistent viruses transmitted by aphids (78, 103, 115, 117, 120), beetles (31, 84), leafhoppers (107, 142), thrips (9, 25) and plant bugs (29). Incoming insects tend to alight preferentially and accumulate on peripheral plants (37, 87, 93), especially those in sheltered sites on the windward edge (124). The effect is most pronounced with the steepest gradients of infestation when the crop is highly attractive (89), or when the stand has become dense before the influx occurs (88, 91). The deposition and behaviour of vectors are further influenced by air turbulence leading to zones of accumulation in depressions (80) and to leeward of trees, hedges, fences, buildings, windbreaks or the banks of drainage channels (5, 20, 81, 82, 93, 115).

Some gradients into crops are due to the slow movement of nematode vectors from the undisturbed soils of adjacent hedges or headlands. This leads to particularly pronounced edge effects with very steep gradients of infection and infestation (63, 79, 125).

Other edge effects are due to an influx of arthropod vectors from nearby sites where they have survived unfavourable conditions. Irrigated gardens are important in hot arid areas (92, 123). Favourable over-wintering sites elsewhere include adjacent woodland (29), thicket (28), the sheltered banks of drainage channels (143), wasteland (62, 139), urban gardens (14, 33, 90) and market garden or other protected crops (47, 48, 117).

SEASONAL AND REGIONAL DIFFERENCES BETWEEN GRADIENTS

Seasonal, site or regional differences in the rate and distance of spread have been reported for many insect-borne viruses including those of broccoli (31), lettuce (100), potato (19, 37, 69, 95) and sugar beet (27, 147). Aphid-borne viruses of beet spread further and faster in California than in England, where the vectors are fewer and less active (109, 145). Similarly, aphids in Florida spread pepper vein-banding virus much further in the spring than in the autumn, when conditions are cooler and aphids and sources of infection are fewer (111).

Temperature also greatly influences the activity of the thrips vector of spotted wilt virus. Tomato fields in Australia can be almost totally infected by incoming thrips in

warm weather, whereas at other times infection is mainly localized around the periphery (9). There are similar seasonal differences in the distribution of maize streak virus in Rhodesia, where long-flying forms of the leafhopper vector predominate in the main migration period and cause infection throughout susceptible crops. Spread at other times is mainly by short-flying forms and tends to be restricted to the margins of fields (106, 107).

Regional and seasonal differences in the distribution of barley yellow dwarf virus in North America are associated with differences in the predominant strain of virus and in the behaviour of the main species of aphid vector. Infection in oats tends to occur in obvious patches up to 30 ft or more in diameter where *Rhopalosiphum padi* is the main vector, whereas spread by *Macrosiphum avenae* leads to scattered infection without obvious edge effects (103).

DISEASE GRADIENTS AND CONTROL MEASURES

The evaluation of control measures

Preliminary studies of disease gradients facilitate the design and interpretation of field experiments to test the effectiveness of control measures. Those of possible value against diseases that do not spread frequently or far can be assessed in small, compact plots arranged in conventional statistical designs. There is little likelihood of spread between plots and only limited guarding and replication are necessary to obtain valid results.

It is much more difficult to evaluate means of controlling diseases characterized by shallow gradients of infection. Experimental plots in which disease is allowed to spread unchecked (or where control measures are largely unsuccessful) are likely to benefit from proximity to sprayed or other plots in which there is good control. Conversely, the performance of resistant or tolerant varieties, insecticides, roguing or other measures is impaired by spread from plots in which infection is virtually unchecked. Such interference between plots is not usually encountered in other types of field experimentation and leads to an inevitable tendency to underestimate treatment differences whenever these are great and especially when multiple infection occurs.

Control measures that are only partially effective in small plots are likely to be much more successful when generally adopted. Other measures may be almost totally ineffective unless used on a large scale. Innovations of considerable potential significance may be overlooked or discarded on the evidence of their poor performance in small-scale trials.

There is no ready solution to this problem which is seldom fully appreciated and may even be ignored despite the detailed assessment of van der Plank (139). It is advantageous to decrease the interface between plots by increased separation and much can be achieved by using large plots with extensive guarding. Nevertheless, it must be appreciated that for many diseases it is impossible to simulate field conditions in experiments of manageable size. This is a major limitation of field experimentation on disease control and restricts the practical relevance of the results obtained.

Isolation

Information on disease gradients has been widely exploited in developing control measures. This has been necessary because gradients indicate the change of 'infection pressure' with distance and close proximity to major foci greatly enhances the onset, progress and ultimate extent of spread in many crops (Fig. 11*a*; (7, 38, 42, 75, 92, 111)). Isolation has a corresponding impact on the success of control measures and insecticides, resistant varieties, roguing, sanitation or cultural methods that are adequate at suitably remote sites may be totally ineffective where there is much greater exposure to spread from nearby sources. Some degree of isolation is also necessary to exploit fully the advantages of healthy planting material, weed control and other sanitation measures.

The minimum effective isolation distance is not constant for a particular disease but is related to the horizon of infection and varies according to season and to the size, orientation and potency of the sources. Such a concept is seldom understood by administrators responsible for official policy or by growers and extension officers, seeking advice on the suitability of sites for new plantings. It is often naively assumed that spread does not occur beyond a set distance that may be selected quite arbitrarily.

'Crowd' and other diseases that spread mainly or entirely over short distances into crops (and not from foci within them) are those most easily controlled by isolation. This approach can be surprisingly effective, even when practised within individual farms or holdings or where only limited separation is possible. It is also advantageous to make plantings fewer and larger to increase the average distance between them and decrease the proportion of plants in the vulnerable peripheral areas. The control of celery mosaic by removing all wild hosts within 75 ft of plantings (149) has been very fully discussed (136). There are, however, many other examples of control by eradicating nearby weed hosts (3, 4, 28, 111, 120), by isolating plantings (71, 76, 85, 98, 99) or by increasing field size (20, 52, 54).

Planting upwind rather than downwind of major foci increases the effectiveness of isolation from viruses with wind-borne vectors (5, 61, 127). In some other instances secondary spread is avoided by destroying or specially treating the vulnerable peripheral plants after the main influx of vectors has occurred (24, 29). Alternatively, barrier or cover crops of immune species are used to intercept incoming vectors (16, 70, 111, 112). Such measures are mainly effective against non-persistent viruses. These tend to predominate in gardens and small holdings, whereas the main problems in large plantings are caused by persistent and semi-persistent viruses that are less readily controlled by isolation (144). Nevertheless, some success has been achieved by co-ordinated policies designed to eliminate carry-over hosts from entire districts or regions and so break the otherwise continuous cycle of infection (49, 68, 70, 108, 114, 123).

Eradication

Eradication measures have been widely used to control the spread of some virus diseases and in attempts to eliminate others from individual farms or even from whole regions or countries. In several instances efficiency has been greatly improved by applying information gained from gradient studies.

Eradicating only plants found with symptoms is seldom effective, because it is almost inevitable that latent or missed infections are left behind and they eventually become foci from which further spread occurs. Such secondary foci tend to be grouped closely around the primary ones for diseases characterized by steep gradients of infection. They can, therefore, be eliminated by slightly more drastic measures at the outset. For example on 'roguing' Canadian potato crops it is recommended that infected plants are removed and those immediately alongside (8). Diseases that spread rapidly and far from small initial foci are less likely to be controlled by eradication unless the measures are so penal as to be highly unpopular, prohibitively expensive and difficult or impracticable to enforce.

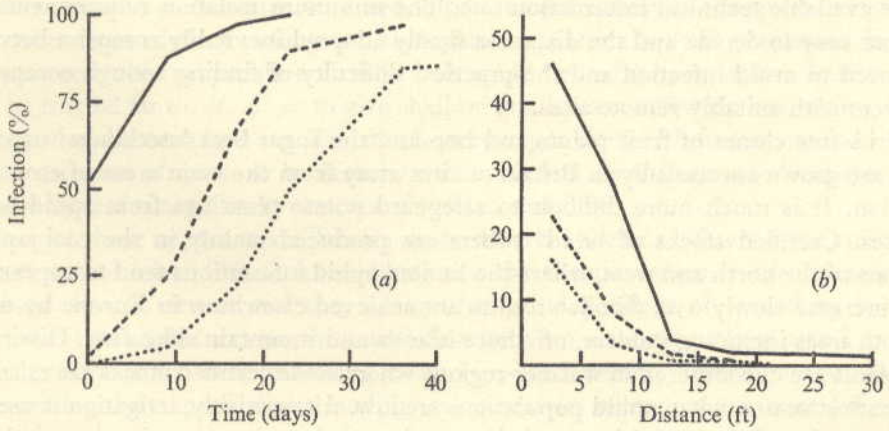

Fig. 11. (*a*), The seasonal increase in percentage of plants infected with watermelon mosaic virus 2 within a field of cantaloups in Arizona. Data for three sites (——, - - -, ...) at increasing distances from the main source of infection (92). (*b*), The incidence of latent and missed infections at different distances around large (——), intermediate (- - -) and small (. . . .) outbreaks of cacao swollen shoot virus in Nigeria (131).

Eradication measures have been widely used to control cacao swollen shoot virus. The most widely adopted practice in Ghana has been to remove only trees with symptoms (60), despite early evidence that only the smallest outbreaks are controlled in this way without further inspections and retreatments (96). More extreme measures were adopted in Nigeria, where the trees with symptoms were removed and all others within 30 yards. This practice was found to be unnecessarily drastic, especially for small outbreaks (131). Comparable results were achieved by treatments based on gradients of latent and missed infections around outbreaks of different size (Fig. 11*b*).

Similar studies may decrease the cost and/or increase the effectiveness of eradication measures used against banana mosaic (1) and peach mosaic (83). Additional information on disease gradients is also likely to facilitate the control of citrus tristeza and plum pox viruses that are now causing increasing concern following spread into new areas (10, 121).

The production and certification of healthy planting material

All attempts at disease control depend upon the availability of healthy stocks of planting material. The selection or production of such material, together with its initial propagation is done mainly in insect-proof conditions, using sterilized soil or potting compost. Further propagation usually has to be done outside to produce sufficient quantities for general distribution.

With some crops and diseases there is little risk of infection during the successive stages of outside propagation. It is usually necessary, however, to take special precautions and ensure at least some degree of isolation from all other potential sources of infection. This is facilitated by officially controlled certification schemes based on the latest available technical information (118). The minimum isolation requirements are seldom easy to decide and the distances finally adopted inevitably comprise between the need to avoid infection and the practical difficulty of finding enough competent growers with suitably remote sites.

Virus-free clones of fruit plants and hop and the sugar beet 'stecklings' used for seed are grown successfully in Britain at sites away from the main areas of crop production. It is much more difficult to safeguard potato plantings from aphid-borne viruses. Certified stocks of 'seed' tubers are produced mainly in the cool upland regions of the north and west, where the limited aphid infestations tend to appear late and increase slowly (132). Similar results are achieved elsewhere in Europe by using remote areas including polders, off-shore islands and mountain slopes (66). Dissimilar problems are encountered in warmer regions where some certified stocks are raised in the hottest season when aphid populations are low. Alternatively, irrigation is used to produce virus-free material out of the usual cropping season or in remote desert areas (59, 119).

With some particularly important and widely grown crops there are various schemes in the same country and extreme isolation is one of the main criteria of eligibility for the highest grade of certificate. 'Elite' strawberry runners in England must be grown at least 5 miles from any other commercial plantings, whereas the isolation requirements for the 'special stock' and 'A' schemes are increasingly permissive and some infection is tolerated.

Isolating propagation material from the main areas of crop production decreases the risk of infection with some diseases but increases the incidence of others, including some that spread from weeds, natural vegetation or totally unrelated crops. For example, the fungus vector of potato mop top virus is widespread in parts of Scotland otherwise suitable for raising 'seed' tubers (74). Moreover, green petal disease is carried into strawberry plantings by leafhoppers from wild and cultivated clovers (97). Arabis mosaic virus has an even wider host range and nursery soils must be checked and found to be free of nematode vectors before they can be used for raising certified fruit or hop plants in England.

COMPARATIVE EPIDEMIOLOGY

Despite similarities in virus structure and means of replication there are important differences in the epidemiology of virus diseases of plants and animals and these are related to host mobility and to the main avenues of infection. The clear gradients of plant virus diseases amongst rooted plants contrast with the much more complex situation within populations of bacteria, algae or animals. The mobility and gregarious nature of higher animals facilitate direct spread by contact as well as by insect and mite vectors including some that are almost immobile. A distinctive feature of mammals as hosts is their tendency to develop a viraemia of limited duration followed by recovery and the acquisition of resistance that may persist for life.

There are also some similarities and important differences in the spread of viruses and other types of plant pathogens. Mycoplasmas that multiply in plants and in leafhoppers resemble propagative viruses with aphid or leafhopper vectors in that they can be carried far (11, 26, 41, 50) to give shallow gradients of infection resembling those due to wind-borne spores (57). The much steeper gradients of infection caused by the splash dispersal of spores or bacteria by water droplets are analogous to local spread of viruses by leaf contact or by vectors of limited mobility.

Despite these apparent similarities quite different factors influence the spread of viruses and of fungi. The latter seldom cause the chronic systemic infections typical of those due to viruses and they are generally independent of spread by vectors. Environmental influences on the interaction between a fungal pathogen and its host differ greatly from those involving host, virus and vector. The numerous factors determining the take-off, flight, landing and infectivity of vectors are more difficult to quantify and assess than those influencing the behaviour of inert air-borne spores.

This complicates attempts to relate gradients of virus disease with the distribution of vectors. It also emphasises the importance of a comprehensive ecological approach to epidemiology as advocated since the earliest work on beet curly top virus in California (23). The few other viruses to have received such detailed attention include cacao swollen shoot and the aphid-borne viruses of sugar beet, potato, brassicas and other market garden crops in Europe and North America. Much further work is required on a wider range of viruses and crops for a fuller understanding of gradients of virus disease and to facilitate the development of new methods of control.

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