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SESSION 2. EPIDEMIOLOGY OF PLANT VIRUSES

PATTERNS OF VIRUS SPREAD

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INTRODUCTION

The literature on the epidemiology of plant virus diseases is extensive and many papers record differences in the incidence of disease within or between plantings. From these reports it is clear that infected plants are seldom randomly distributed within crops and they often occur in discrete groups that are closely related to initial foci of infection. This paper considers the distribution and type of foci encountered and their contribution to subsequent patterns of disease development. The approach is a general one similar to that adopted in previous reviews (Thresh, 1974, 1976, 1980, 1981), which provide full details of the references cited.

INITIAL FOCI OF INFECTION

In considering the initial foci of infection from which outbreaks originate it is convenient to distinguish between crop, weed and wild species and also between remote sources and those occurring within or alongside crop stands. These distinctions are important in analysing observed patterns of spread and in devising effective control measures.

A. Sources Occurring Within Crops

Sources of infection occurring within crops from the outset obviously present the greatest threat and exert the greatest «infection pressure». They can soon lead to major outbreaks of disease and serious losses even if the virus responsible is not spread very efficiently or far.

Crop plant sources

Seed transmission is much commoner than once supposed and several important viruses including tomato mosaic (Broadbent, 1976), lettuce mosaic (Grogan *et al.*, 1952) and peanut mottle (Paguio and Kuhn, 1974) are widely disseminated in commercial seed stocks. Many other viruses of vegetatively-propagated crops are introduced in cuttings, bulbs, tubers or other propagules.

Such primary foci of infection tend to be randomly distributed within crops. There is no obvious grouping or pattern of distribution unless different batches of material have been used of unequal health status. However, subsequent spread within the crop tends to be localised around the initial foci to give expanding «pools» of infection (Thresh, 1976).

There are obvious advantages in improving the health of planting material and this explains the priority given in many countries to developing virus-free stocks of citrus, grapevine, potato and many other vegetatively-propagated crops (Hollings, 1965). Those grown from seed other than tomato and lettuce have received much less attention and this is a major deficiency of current control measures.

Crop plants can behave as weed sources of infection when they develop as «volunteer» seedlings or by regeneration from the debris of previous plantings. The distribution of such foci within crops is not random but related to the cropping history of the site and the previous incidence of infection. Detailed observations are available on the spread of wheat streak mosaic virus from volunteer seedlings (King and Sill, 1959) and on the spread of aphid-borne viruses of potato (Doncaster and Gregory, 1948), sugar beet (Howell and Mink, 1971) and carrot (Howell and Mink, 1977) from crop debris.

Weed sources

Many viruses have a wide host range and infect weeds that can be the main initial sources of infection within crops (Wellman, 1935). Weeds that regenerate vegetatively or in which viruses are seed-borne are particularly important in providing an effective means of survival between growing seasons or for even longer periods. Moreover, viruses that are seed-borne in weeds can be widely disseminated and this is an important feature of viruses that are not otherwise carried far because they have nematode vectors of limited mobility (Murant, 1970), or because they do not persist for long in aphid vectors (Hani, 1971).

B. Sources Alongside Crops

Many viruses are carried into crops by vectors moving from nearby plantings, weeds or natural vegetation. This leads to marked gradients of infection which tends to be most prevalent around field margins (Thresh, 1976). However, such «perimeter» effects do not necessarily mean that infected sources are nearby because incoming vectors accumulate or may be most active on the outside rows, especially to leeward of buildings, hedges and other windbreaks (Lewis, 1969).

Crop sources

Much of the spread between crops is from old to young plantings as reported with viruses of lettuce (Broadbent *et al.*, 1951), brassicas (Pound, 1946) and other vegetables particularly when grown in close proximity in small market garden plots. There is also much spread between early and late-sown cereals

(Slykhuis *et al.*, 1957) and from overwintered plantings of beet and brassicas retained for seed (Watson *et al.*, 1951).

In many other instances spread is from dissimilar crops as recorded from grass leys to cereals (Smith, 1963) from pasture legumes to peas and beans (Hampton, 1967) and from chrysanthemum to tomato (Hollings and Stone, 1979). These examples illustrate the way in which long-lived hosts maintain the cycle of infection. They also emphasise the importance of field size and disposition; losses can often be decreased by an appropriate choice and arrangement of crops to achieve at least some degree of isolation.

Weed/wild plant sources

The weeds or natural vegetation around crops can be the main initial foci. Indeed, lettuce necrotic yellows (Stubbs *et al.*, 1963) and a few other viruses spread exclusively from such outside sources and there is no spread within plantings. Patterns of spread depend on the behaviour and mobility of the vectors and on the number, size and potency of the sources. Gradients of infection due to insect-borne viruses tend to be steeper upwind of the source than downwind (Hampton, 1967; Adlerz, 1974) and particularly steep gradients are encountered where slow-moving nematode vectors introduce virus from adjoining vegetation (Taylor and Thomas, 1968).

C. Distant Sources

Many viruses persist for long periods in mobile vectors that can fly or be blown far and this provides an opportunity for virus spread over considerable distances. However, this has seldom been substantiated because it is difficult to track insect movement and to distinguish between spread from local and distant sources.

The most detailed evidence has been obtained in work on beet curly top (Bennett, 1971), barley yellow dwarf (Bruehl, 1961) and subterranean clover stunt (Gutierrez *et al.*, 1971, 1974). These occur suddenly and over considerable areas soon after a major influx of vectors into regions where they could not have overwintered or developed locally.

Detailed studies over many years have shown that the leafhopper vector of curly top mainly originates from vast stands of weeds in the desert foothills of California and neighbouring states. The major winter and summer breeding grounds have been identified and these contribute enormous numbers of winged adults that periodically migrate and carry virus into crops up to hundreds of kilometres away. Similarly, yellow dwarf is carried into the main cereal-growing areas of Canada and the north-central United States by winged aphids originating from cereal crops already maturing in Texas and adjoining states. The aphids are swept northwards by jet-stream winds and cause serious outbreaks if they reach crops at a vulnerable stage in years when conditions facilitate secondary spread (Duffus, 1980).

Viruses that are carried far are obviously difficult or even impossible to control adequately by isolation and additional measures are required. In some instances planting date and spacing can be manipulated to decrease the vulnerability of crops at the time a major influx of vectors is likely. It may also be possible to decrease secondary spread within crops by timely application of insecticides. Such measures have been largely ineffective against beet curly top and it has been necessary to develop tolerant or resistant varieties. Major efforts have also been made to combat the vectors at source by spraying operations or vegetation changes in the desert breeding grounds.

CONCLUSIONS

This brief account suffices to illustrate that viruses are a diverse and versatile group of pathogens that exploit various strategies to maintain a continuing threat to crop production. Losses will continue and may even increase until far greater resources are allocated to epidemiological studies on spread and control. Inevitably there will be continuing emphasis on locating and eliminating the initial foci of infection which play such a crucial role in determining patterns of spread.

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