The spread of nettlehead and related virus diseases of hop

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INTRODUCTION

Nettlehead was first described in the sixteenth century (Scot, 1574) and it has long been known as a serious and prevalent disease of the hop (*Humulus lupulus* L.) in England and some other countries. However, there is little published information on the pattern and sequence of spread. The observations of Legg (1953, 1955, 1964) and previous workers are difficult to interpret because they were completed before a nematode-borne virus was implicated. Also it is now apparent that at least some of the infection could have been introduced in the planting material.

This review is based on the results obtained in the most recent studies which began after the hop strain of arabis mosaic virus (AMV(H)) was first detected in nettlehead plants (Bock, 1966) and transmitted by the dagger nematode, *Xiphinema diversicaudatum* Micol. (Valdez *et al.*, 1974). In subsequent work AMV(H) has also been associated with two other important hop diseases. The major differences between sites in the type, pattern and sequence of infection can be explained with the information now available. This also permits a more rational and effective approach than hitherto in developing control measures.

HOP DISEASES ASSOCIATED WITH ARABIS MOSAIC VIRUS (AMV(H))

Nettlehead, the severe form of split leaf blotch, and bare bine are three distinct but inter-related diseases (Thresh *et al.*, 1972). Some features of their aetiology are still uncertain, but AMV(H) is undoubtedly involved as it always occurs in affected plants of diverse origin and never in symptomless ones. The diseases are widespread in the main U.K. hop-growing areas. Affected plants occur singly or in patches in many plantings and infection is prevalent at some sites. There has, however, been no systematic survey of hop diseases or estimate of their economic importance.

The losses caused by nettlehead must be great as infected plants are

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virtually worthless. Some areas soon become so seriously affected that they have to be replanted prematurely, which is expensive and disrupts production. The worst affected sites are usually abandoned, with the consequent major expense of setting up new supporting posts and wirework elsewhere.

Severe split leaf blotch disease halves the yield of Fuggle (Legg, 1959) and bare bine decreases crop weight and/or quality in other varieties (Thompson & Neve, 1971; Thresh, unpublished). The aggregate effects of these diseases are likely, therefore, to be just as great as those of nettlehead, which is far more damaging but much less prevalent. The available evidence suggests that AMV is currently more important in hop in England than in any other known host.

THE SPREAD OF ARABIS MOSAIC VIRUS IN HOP

Recent work on nettlehead and related diseases has concentrated on the role of AMV(H). This spreads in hop in various ways and each is important in epidemiology. Nematodes are responsible for local spread between plants, whereas AMV(H) is disseminated over greater distances and to new sites in seeds, cuttings and rooted plants.

Seed transmission

AMV(H) occurs in up to half the seedlings raised from the seed of infected hop plants and there are occasional instances of nettlehead being seed-borne. This provides an important and effective means of dissemination as many seeds are scattered widely at harvest and by birds, or when the cones of unwanted and wild hops shatter and the seeds blow (Thresh & Ormerod, 1974). Germination takes place in the following spring and young seedlings occur commonly in all plantings, despite the routine use of herbicides and defoliants. Growth is particularly profuse where seeds penetrate the deep cracks and fissures of untilled land. There are opportunities for any nematodes present to feed on the roots and acquire AMV(H), even though only a small proportion of the seedlings survive for long.

Dissemination in infected plants

Hop varieties are propagated vegetatively and the extensive movement of infected cuttings and rooted plants is a major factor in disseminating viruses within and between farms. Growers give insufficient attention to the health of the many stocks raised within hop-producing areas. None qualifies for the official "A plus" certification scheme and only the best are symptomless and free of AMV(H).

The "A plus" scheme was started to encourage propagation from carefully selected stocks of the best available health status at isolated sites, mainly in East Anglia. However, growers have been slow to change traditional practices and detailed surveys established that only about one third of all 1968-70 plantings were of "A plus" origin (Thresh &

Ormerod, 1971). The use of locally produced uncertified material has continued, despite the now well-known risks of spreading viruses and verticillium wilt.

Nematode transmission

AMV(H) is transmitted by *X. diversicaudatum* in much the same way as are other strains of AMV. Valdez *et al.* (1974) obtained infective nematodes from hop soils where nettlehead was spreading. AMV(H) was also transmitted by nematodes from a woodland site, but only after they had first fed on the roots of infected hop plants. Adults and larvae remained infective for 36-44 and 29-36 weeks, respectively, when kept in moist soil without host plants.

Transmission rates are sometimes low, even when up to fifty nematodes are transferred to each small "bait" plant. The performance of *X. diversicaudatum* as a vector is also impaired by its slow movement through soil, estimated at one site to be only 30 cm per year (Harrison & Winslow, 1961). These limitations are partially offset by the ability of nematodes to remain infective for several months, enabling them to retain virus between successive hop plantings.

Spread in hop is also facilitated by the stability of the *X. diversicaudatum* populations encountered. Adults are long-lived, their reproduction rate is low and populations are correspondingly slow to respond to changes of crop, or even to bare fallowing (McNamara & Pitcher, 1977). The roots of a well-established hop plant exploit several cubic metres of soil, and samples containing only one vector per 200 ml represent about 12,000 per root system. Densities up to 300 per litre have been found beneath hop and there are abundant opportunities for AMV(H) to be spread by nematodes moving short distances between the intermingled roots of adjacent plants. Root density and virus spread are greater along the rows than across them when plants are spaced at 1 m within rows 2 m apart. Spread is particularly rapid when AMV(H) is first introduced to sites where non-infective vectors are already widely distributed. The virus moves more rapidly in roots than *X. diversicaudatum* can travel in soil and nematodes act mainly as the crucial link between adjacent root systems (Fig. 1).

PATTERNS OF SPREAD

In early observations on the spread of nettlehead and split leaf blotch diseases there were great differences between sites in the onset, distribution and sequence of infection. The slowly-spreading patches of disease in many plantings suggested transmission by a soil-inhabiting vector. Elsewhere, the widely scattered distribution of infected plants was attributed to spread by flying insects (Legg, 1964). There was rapid spread at some sites but in others infection appeared soon after planting and then failed to increase.

A reassessment of these and subsequent observations is possible with

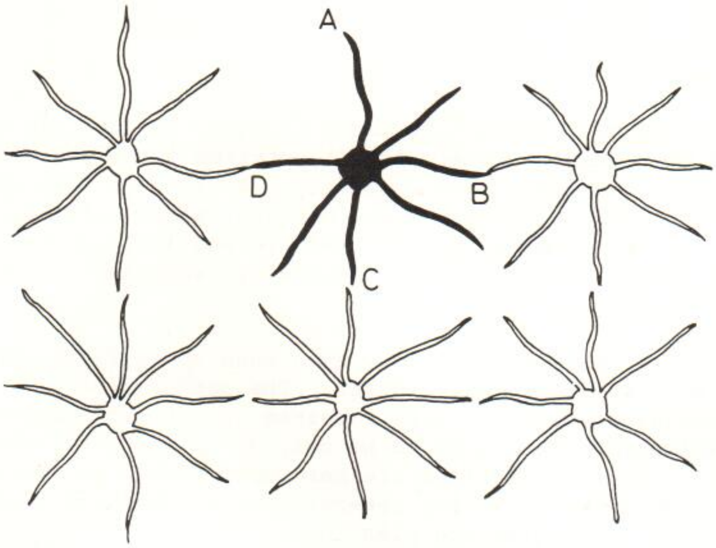

Figure 1. Diagrammatic representation of the root systems of adjacent hop plants. Nematode vectors introducing AMV(H) at A will be slow to reach B, C or D, whereas the virus will move more rapidly through the roots to reach additional vectors near the roots of adjoining plants. Actual root systems are much more complex, especially at rectangular spacings.

the additional information now available. Differences between sites are largely explicable by differences in their previous cropping history and/or in the health status of the planting material used. These are the main factors influencing the distribution of infected plants and the occurrence and infectivity of *X. diversicaudatum* populations.

Sites where the nematode vector is absent remain free of AMV(H) unless the virus is introduced in the planting material. Infection then tends to be randomly distributed, with no further spread (Fig. 2, a and b).

At sites where vectors are present and already infective at the time of planting there is spread to even the healthiest stock within 2 years (Fig. 2, e). However, the situation is worse if AMV(H) is also introduced in the planting material because infection is then present from the outset and not restricted to the nematode-infested areas (Fig. 2, f).

The health status of the planting material is particularly important at sites where vectors are present but not infective at the outset. Rapid spread occurs if AMV(H)-infected plants are introduced to the area (Fig. 2, c), whereas uninfected material remains trouble-free until

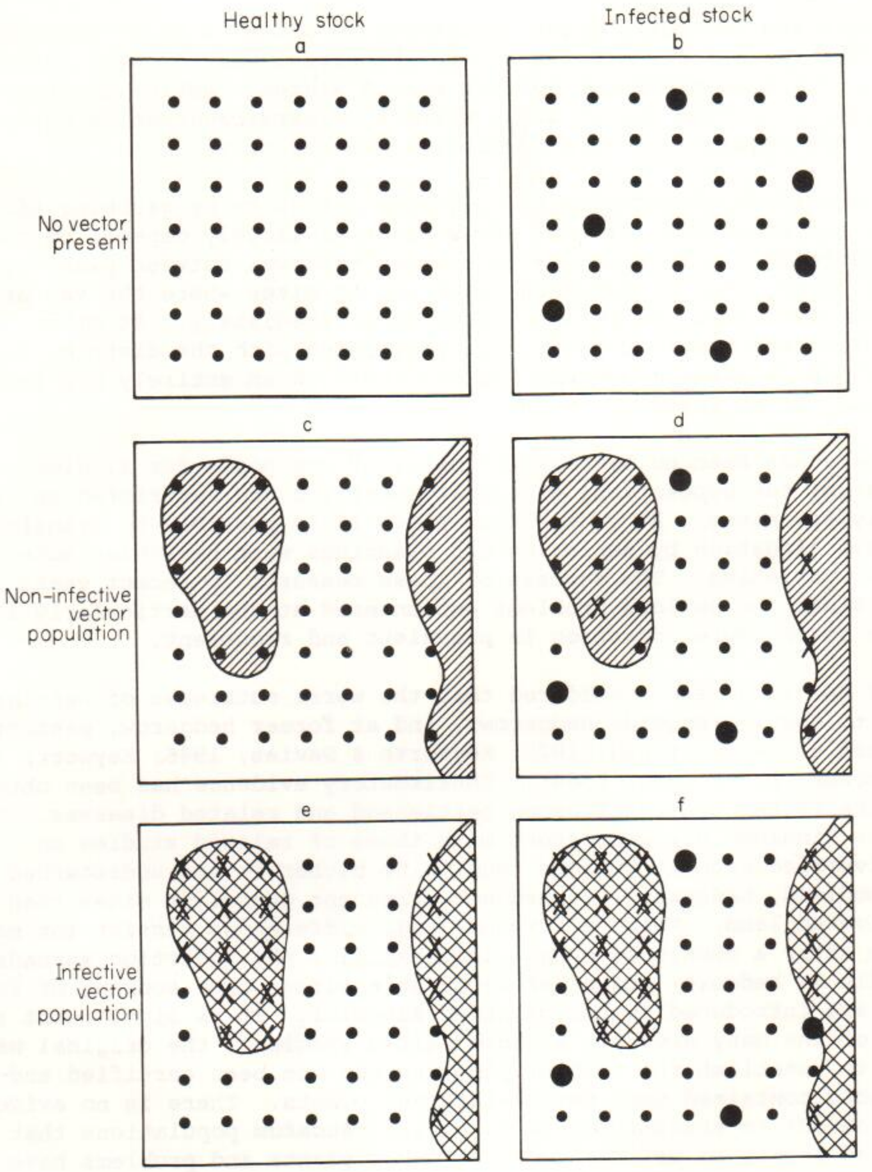

Figure 2. Diagrammatic representation of the situation where healthy (left) and AMV(H)-infected stocks (right) of planting material are used at sites where the nematode vector (*X. diversicaudatum*) is absent (top) and where the populations are non-infective (centre) or infective (bottom) at the outset. The distribution of the nematode vector is indicated by cross-hatching. Spread occurs from AMV(H)-infected plants with nematodes around their roots (crosses) and not from infected plants in uninfested soil (large circles).

there is spread from infected seedlings introduced naturally (Fig. 2, d).

There are obviously great advantages in using "A plus" certified material for all new plantings. Nevertheless, many growers continue to use uncertified plants of dubious health status. AMV(H) is often introduced in this way to sites where *X. diversicaudatum* is absent or where the populations were previously non-infective.

The outcome of attempts to eliminate infection by grubbing affected sites and replanting with AMV-free material largely depends on the incidence of *X. diversicaudatum* and the interval between plantings. There is no risk of infection recurring at sites where the vector is absent, even when the replanting is done immediately. At other sites infection may recur in patches corresponding with the distribution of infective *X. diversicaudatum,* unless there is an entirely hop-free interval of at least 18 months.

There has been no systematic survey of hop soils for *X. diversicaudatum,* but populations are often localized and restricted to relatively few sites. At vector-free sites it is possible to transform the disease situation by replacing old plantings with healthier material of better varieties. The success of these measures in recent years has emphasized the serious problems encountered at the particularly intractable sites where infection is prevalent and recurrent.

It has long been considered that the worst outbreaks of nettlehead tend to occur alongside hedgerows, and at former hedgerow, pasture or orchard sites (Duffield, 1925; Keyworth & Davies, 1946; Keyworth & Hitchcock, 1948; Legg, 1964). Confirmatory evidence has been obtained in more recent observations on nettlehead and related diseases. These latest findings are consistent with those of related studies on *X. diversicaudatum.* Numbers tend to be higher in the undisturbed soil of woodland, hedgerow, orchard and permanent grassland sites than in cultivated land. Moreover, these local differences persist for many years after a change of crop. This explains why infection spreads so rapidly at hedgerow and other favourable sites, once sources of infection are introduced in the planting material. It is significant that at each of the many severely affected sites examined, the original material used to establish the initial planting had not been certified and probably contained some AMV(H)-infected plants. There is no evidence that AMV(H) is transmitted by *X. diversicaudatum* populations that have not had access to wild or cultivated hop plants and problems have not been encountered where only certified stocks have been used at completely new sites, even where *X. diversicaudatum* is present.

PROSPECTS FOR CONTROL

Until quite recently growers could be given little advice on controlling nettlehead other than to use healthy planting material. The information now available together with the introduction of virus-tested clones of greatly improved health status and performance enable far more specific measures to be advocated. Moreover, facilities have been provided by the Agricultural Development and Advisory Service for assessing hop soils for *X. diversicaudatum*. These developments enable growers to be much more discriminating than hitherto in selecting stocks and sites for all new plantings.

Fumigation and fallowing procedures have been developed for controlling vector populations or rendering them non-infective (McNamara *et al.*, 1973). This makes it possible to replant even the most severely affected sites with little risk of reinfection. Present losses can be greatly decreased if current recommendations are adopted on a sufficiently large scale. Any increase in productivity will strengthen the position of English hop growers, who are now under extreme pressure due to increasing production costs and competition from foreign imports.

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