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Transmission of the hop strain of arabis mosaic virus by *Xiphinema diversicaudatum**

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SUMMARY

Hop plants became infected with the hop strain of arabis mosaic virus (AMV(H)) when grown in hopfield and woodland soil in which infected plants had been growing. Infection occurred in soil infested with the dagger nematode *Xiphinema diversicaudatum*, but neither in uninfested soil nor in soil previously heated to kill nematodes. *X. diversicaudatum* transferred direct from hop soils transmitted AMV(H) to young herbaceous plants and to hop seedlings; some of the hop seedlings developed nettlehead disease. A larger proportion of plants was infected using *X. diversicaudatum* obtained from a woodland soil and then given access to the roots of hop or herbaceous plants infected with AMV(H). AMV(H) was transmitted by adults and by larvae, in which the virus persisted for at least 36 and 29 wk, respectively.

Difficulties were encountered in detecting AMV(H) in infected hop plants, due partly to the delay in virus movement from roots to shoots. Infection of hop shoots was seldom detected until the year after the roots were infested and sometimes nettlehead symptoms did not appear until the third year. Isolates of arabis mosiac virus from strawberry did not infect hop. The results are discussed in relation to the etiology and control of nettlehead and related diseases of hop.

INTRODUCTION

Nettlehead has long been a severe and prevalent virus disease of the hop (*Humulus lupulus* L.) in England and it occurs elsewhere in Europe and in Tasmania. Infection spreads slowly, often recurs at the same sites in successive plantings and tends to be particularly prevalent alongside hedgerows, where hedges have been removed and after orchard crops or permanent pasture (Keyworth & Davies, 1946; Keyworth & Hitchcock, 1948).

These features suggest that infection is soil-borne, but early attempts to confirm this were unsuccessful. Hop plants remained symptomless when grown in soil collected from around the roots of hop plants affected by nettlehead disease. Herbaceous

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hosts inoculated with sap of infected hop plants failed to show symptoms of any of the viruses then known to be transmitted by nematodes. Moreover, the first hop soils sampled contained few individuals of the dagger nematode (*Xiphinema diversicaudatum* Micol.) which is the vector of strains of arabis mosaic virus (AMV) occurring in raspberry, strawberry and other crops (Jha & Posnette, 1959; Harrison & Cadman, 1959).

Our transmission experiments followed the detection of an unusual strain of AMV in nettlehead-infected and some other hop plants and the recovery of substantial numbers of *X. diversicaudatum* from soils where nettlehead and severe split leaf blotch diseases were spreading (Bock, 1966; J. J. M. Flegg & R. S. Pitcher, unpublished).

MATERIALS AND METHODS

Sources of Xiphinema diversicaudatum

The hop soils and *X. diversicaudatum* used at first were from farms near Headcorn or Horsmonden, Kent, where nettlehead disease was spreading. Later samples were taken from the Rosemaund Experimental Husbandry Farm, Preston Wynne, Hereford.

The average population density of *X. diversicaudatum* in most hop soils is low. Accordingly, a dense population from woodland soil at High Halstow, Kent, was used for most of the experiments requiring large numbers of individually checked nematodes. Early tests by J. J. M. Flegg (unpublished), and our own, established that this population did not transmit AMV unless first fed on infected plants.

Bait plants and containers

Field soil was brought carefully to the laboratory and stored at 5–10 °C in closed polyethylene bags kept in an unheated gauze-house. The nematodes were extracted as required, often after several months' starvation. Alternatively, virus-infected plants were grown in the soil to obtain stocks of infective *X. diversicaudatum*. Infected hop plants were usually grown in wooden boxes (25 l capacity) lined with polyethylene sheeting. The herbaceous source plants *Chenopodium quinoa* Willd., *C. amaranticolor* Coste and Reyn. or *Nicotiana clevelandii* Gray were grown in plastic containers (800 ml capacity).

Bait plants were grown in the 25 l wooden boxes or in clay pots (20 ml capacity), plastic tubes (40 ml), egg cups (20 ml) or ice-cube moulds (10 ml). All plants initially infested in 10–40 ml of soil were later transplanted to larger pots of steamed soil.

Nematode extraction

A modification of Cobb's decanting and sieving technique (Flegg, 1967) was used to assess populations and to obtain nematodes for transmission tests. Identification and transfer began after 3 h extraction through nylon sieves and was completed within 24 h to obtain viable nematodes.

Detection and identification of AMV(H)

AMV(H) is associated with nettlehead and related diseases of hop (Bock, 1966; Thresh & Pitcher, 1971), in which symptom expression is inconsistent. Some AMV(H)-infected hop plants never develop symptoms and others remain symptomless for long periods, especially in hot weather or under glasshouse conditions. Symptom expression in herbaceous hosts is equally indefinite and all isolates of AMV yet obtained from hop cause slighter symptoms in herbaceous plants than isolates from strawberry and other hosts. If symptoms do appear they are slow to develop and often preceded or obscured by those of prunus necrotic ringspot virus, which occurs throughout all the older commercial English hop varieties. Consequently a serological method was used to detect AMV(H) in sap from the young leaves and shoots of all bait plants. Specific precipitation lines developed in agar gels within 24–48 h when tested against suitable dilutions of antisera prepared against either hop or strawberry isolates of AMV.

AMV could not be detected serologically in the roots of bait plants, which were tested by sap inoculations to young plants of *C. amaranticolor*. Those that became infected developed a characteristic vein-net leaf symptom within 2–3 wk in spring or autumn. At other times, reliable symptoms developed only when the inoculated indicator plants were kept in a growth chamber at 16–18 °C and lit for 16 h per day (Valdez, 1971, 1972*b*).

RESULTS

Infection with AMV in boxes and pots of infested soil

Eighteen boxes of hop or woodland soil infested with *X. diversicaudatum* were planted with pairs of AMV(H)-infected hop plants. These were symptomless plants cv Early Prolific, except for three boxes planted with nettlehead-affected plants cv Fuggle. After 6 months these infectors were replaced by pairs of healthy bait plants cv Fuggle. AMV(H) was not detected serologically in the shoots of any of the bait plants tested after 4 months. The plants were allowed to become dormant in an unheated, insect-proof gauze-house and were retested when growth resumed. AMV(H) was then detected serologically in the shoots of ten plants growing in infested soil. The infected plants were retained for 3–6 yr and remained symptomless throughout. No infection occurred in the three boxes of soil that had been heated to 60 °C to kill all nematodes. However, a plant became infected in one of three boxes of heated soil that had been re-infested with *X. diversicaudatum*.

In other experiments, healthy hop bait plants (cv Fuggle or seedlings) were grown in boxes or pots of soil collected from the Slade Hop Yard, Rosemaund. In three experiments sixteen of fifty-three plants became infected with AMV(H) when grown in soil from around the roots of AMV(H)-infected plants showing symptoms of severe split leaf blotch. No infection occurred in the twelve plants grown in soil from around healthy control plants. AMV(H) was first detected in the bait plants by serology in the second or third year of growth. All the seedlings remained symptomless, whereas infected Fuggle plants developed split leaf blotch.

Fifteen of sixty-five hop seedlings also became infected with AMV(H) in field

soil from around the roots of several different nettlehead plants. There was no infection in the six seedlings grown in otherwise comparable soil that had been heated to 60 °C. Again, AMV(H) was not detected in the shoots of the bait plants until the second or third year. Some of the infected plants then developed a slight vein-clearing and upward rolling of the leaves, which is a feature of nettlehead disease, but only one plant developed typical nettlehead symptoms, which included small enations on the undersides of the leaves.

Transmission by Xiphinema diversicaudatum *from hop soils*

X. diversicaudatum extracted from hop soils, transmitted AMV(H) to the roots of small bait plants (Table 1). Experiments 1 and 4 were concluded when AMV(H) was detected in the roots of *C. quinoa*, *N. clevelandii* or hop seedlings. In Expts 2, 3 and 5 the hop roots were not tested and AMV(H) was first detected in the shoots produced after the first dormant period. Six of the twelve AMV(H)-infected hop plants developed conspicuous nettlehead symptoms within 2–3 yr. All other plants remained symptomless.

Table 1. *The transmission of arabis mosaic virus (hop strain) to hop seedlings and herbaceous hosts by* Xiphinema diversicaudatum *from hop nettlehead sites*

	Nematodes		Seedling bait plants		
Expt	Source	No./plant	Container	Species	Infection*
1	Horsmonden	30	Egg cups	*C. quinoa*	10/20 (R)
		30	Egg cups	Hop	2/20 (R)
2	Horsmonden	50	Tubes	Hop	6/12 (T)
		0	Tubes	Hop	0/8 (T)
3	Horsmonden	50	Tubes	Hop	1/12 (T)
		0	Tubes	Hop	0/20 (T)
4	Hereford	50	Tubes	Hop	1/14 (R)
		0	Tubes	Hop	0/6 (R)
		50	Tubes	*N. clevelandii*	2/11 (R)
		0	Tubes	*N. clevelandii*	0/6 (R)
5	Hereford	50	Tubes	Hop	5/28 (T)
		0	Tubes	Hop	0/12 (T)

* The proportion of bait plants infected with AMV, shown by testing roots (R) or shoot tips (T).

Comparatively few of the plants became infected in these and previous experiments with *X. diversicaudatum* from or in hop soil, so the probability of transmission by individual nematodes must have been very low. Presumably few of the nematodes had acquired virus or they were seldom able to transmit. Additional evidence was obtained in the following experiments, in which transmissions were obtained readily after nematodes from the woodland site had been given access to infected sources.

Transmission by woodland Xiphinema diversicaudatum

Groups of *X. diversicaudatum* froom woodland soil were transferred to small bait plants after access to the roots of AMV(H)-infected source plants grown in large boxes or plastic containers (Table 2, Expts 1–3 and 4–6, respectively). Adults and

larvae were kept separate in Expt 1 which was concluded when AMV(H) was detected in the roots of all the infested bait plants. There was no infection in uninfested controls or in plants infested with nematodes direct from woodland soil. In Expts 2–4 the roots of the hop bait plants were not tested, but AMV(H) was detected in the new shoots produced after the first dormant period. One of the plants infected with AMV(H) by nematodes from a nettlehead source developed conspicuous nettlehead symptoms in the second growing season. All other plants remained symptomless.

Table 2. *Transmissions to hop seedlings and herbaceous hosts of arabis mosaic virus (hop strain) by* Xiphinema diversicaudatum *given access to infected source plants*

			Seedling bait plants		
Expt	AMV-source*	Infestation†	Container	Species	Infection‡
1	Symptomless hop (> 17 wk)	50 (A)	Egg cups or pots	*C. quinoa*	30/30 (R)
		50 (L)		*C. quinoa*	20/20 (R)
	None	100 (A)		*C. quinoa*	0/20 (R)
	None	0		*C. quinoa*	0/40 (R)
	Symptomless hop (> 17 wk)	50 (A)		Hop	20/20 (R)
		50 (L)		Hop	17/17 (R)
	None	100 (A)		Hop	0/10 (R)
	None	0		Hop	0/30 (R)
2	Nettlehead hop (> 96 wk)	50 (A,L)	Tubes	Hop	14/18 (T)
	Symptomless hop (> 96 wk)	50 (A,L)		Hop	1/23 (T)
	None	50 (A,L)		Hop	0/35 (T)
3	Symptomless hop (96 wk)	50 (A,L)	Tubes	Hop	8/12 (T)
	None	50 (A,L)		Hop	0/8 (T)
4	Nettlehead (12 wk)	50 (A,L)	Egg cups	Hop	7/14 (T)
5	Nettlehead hop (8 wk)	60 (A,L)	Cube moulds	*C. quinoa*	6/15 (R)
		60 (A,L)		Hop	3/14 (R)
6	*N. clevelandii* (4 wk)	50 (A,L)	Tubes	*N. clevelandii*	11/20 (R)
	C. quinoa (4 wk)	50 (A,L)		*N. clevelandii*	8/10 (R)
	C. amaranticolor (4 wk)	50 (A,L)		*N. clevelandii*	5/10 (R)
	None	50 (A,L)		*N. clevelandii*	0/20 (R)

* The AMV (H)-infected sources and the period spent in infested soil before the nematodes were extracted and transferred to bait plants.

† Number of adults (A), larvae (L) or mixtures (A,L) per bait plant.

‡ The proportion of infested plants that became infected with AMV (H), as shown by testing roots (R) or shoot tips (T).

In Expt 6 the roots of *N. clevelandii* plants were readily infected with AMV(H) by nematodes transferred from infected *N. clevelandii*, *C. quinoa* and *C. amaranticolor*. AMV(H) was also transmitted from hops to the roots of *C. quinoa* plants and hop seedlings (Expts 1–5). Two of the seven AMV(H)-infected hop seedlings in Expt 4 eventually developed conspicuous nettlehead symptoms. All other plants remained symptomless.

Effect of number of Xiphinema diversicaudatum *on the transmission of AMV(H) and nettlehead*

Table 3 summarizes the transmissions achieved by different numbers of nematodes obtained from around the roots of nettlehead-diseased hop plants grown for a year in boxes of woodland soil.

Single adult nematodes transmitted AMV(H) to the roots of two of eight *C. quinoa* plants, but not to hop seedlings or to *C. amaranticolor*. Using greater numbers of nematodes, plants of all three species were infected, but the *C. amaranticolor* plants grew badly and few became infected, even with 100 nematodes per plant.

Table 3. *Effect of number of* Xiphinema diversicaudatum *on the transmission of arabis mosaic virus (hop strain) and nettlehead**

Nematodes† per plant	*Chenopodium amaranticolor*	*Chenopodium quinoa*	Hop	
			Roots	Tops‡
Seedling bait plants infected with AMV(H), out of eight				
1 (A)	0	2	0	0
5 (A)	1	4	3	5 (1N)
10 (A)	2	—	5	6 (1N)
25 (A,L)	3	7	7	8 (4N)
50 (A,L)	2	8	5	8 (3N + 1LP)
100 (A,L)	2	8	7	7 (2N)
0	0	0	0	0
100 (A) non-infective	0	0	0	0

* Bait plants were infested in egg cups and transferred to larger pots after 3 wk. *Chenopodium* spp. were tested 5 wk later and hops after 17 wk (roots) and *c.* 48 wk (tops).

† Adults (A) or adults and larvae (A,L).

‡ The number of AMV(H)-infected hop plants with nettlehead (N) or line pattern (LP) symptoms is given in parentheses.

The hop plants were re-potted after samples of the roots had been tested. No leaf symptoms developed until growth resumed after dormancy; AMV(H) was then detected in the shoots of thirty-four plants, including twenty-seven which had already shown root infection. One of the AMV-infected plants developed a line-pattern in the leaves, nine others had developed conspicuous nettlehead symptoms within 12 months and two more developed nettlehead in the following year.

Persistence of AMV(H) in starved Xiphinema diversicaudatum

The persistence of AMV(H) in starved nematodes was tested using *X. diversicaudatum* from boxed woodland soil in which nettlehead plants had been grown for at least a year. The plants and all roots were then removed with great care to avoid leaving fragments behind. The soil was then crumbled, mixed and stored in a closed polyethylene bag in an unheated gauze-house. At intervals, nematodes were extracted and transferred to the roots of small *C. quinoa* bait plants grown in egg cups. Adults and larvae were transferred in separate batches on three occasions. The roots of bait plants were tested 5 wk after infestation.

The proportion of plants infected declined as the period of starvation increased (Table 4). The low transmission after 25 wk was probably due to the poor growth of these bait plants, rather than to any sudden decrease in the infectivity of the nematodes.

AMV(H) was transmitted by larvae after 29 wk and by adults after 36 wk, but not after 36 and 44 wk, respectively. These are longer periods than those reported previously for other strains of AMV. The nematodes may have died in the later stages of two such experiments (Jha & Posnette, 1961; Harrison & Winslow, 1961). AMV persisted for 16 wk in a third experiment, but longer periods were not considered (Taylor & Thomas, 1968).

Table 4. *Persistence of arabis mosaic virus (hop strain) in* Xiphinema diversicaudatum *in fallow soil*

Starvation period (wk)	Stages of nematode*	Infection in *C. quinoa*	
		Number	%
0	A, L3, L4	9/10	90
8	A, L3, L4	8/10	80
25	A, L3, L4	3/12	25
29	A	7/16	44
29	L3, L4	3/8	37
32	A, L3, L4	3/8	37
36	A	2/15	13
36	L3, L4	0/15	0
44	A	0/12	0

* 50 nematodes per plant, adults (A) and/or larval stages 3 (L3) and 4 (L4).

Intervals between infestation of the roots and the detection of AMV(H) in the shoots

Viruses tend to move slowly from the roots to aerial parts (Fulton, 1941) and a delay before virus becomes systemic is a feature of nematode transmission. Usually AMV(H) could be detected in the roots of hop seedlings and herbaceous plants soon after infestation with infective nematodes. However, leaf symptoms appeared slowly and virus could not be detected in the aerial parts for several months. There was an even longer delay when hop seedlings or rooted cuttings were planted in infested soil in pots or in hop gardens, where virus was never detected in the aerial parts until the second year, when the first symptoms also appeared.

The movement of virus was investigated further in experiments with hop seedlings and chenopodiaceous plants. These were infested with infective *X. diversicaudatum* and later growth was stimulated by repotting in fresh soil and by periodic pruning.

The first experiment was started in January 1970 and AMV(H) was detected in the young leaves of *C. quinoa* plants after 22 wk, but not after 19 wk or earlier. Later experiments were started in the autumn and AMV(H) was first detected in *C. quinoa* after 15 wk and in *C. album* and *Atriplex patula* L. after 16 wk (Valdez, 1971).

AMV(H) was not detected in hop shoots 21 wk after infestation, but it was detected readily 19 wk later in shoots produced after dormancy. The results of this and previous experiments suggested that AMV(H) does not become systemic in hop until

the plants have been dormant. However, in a further test AMV(H) was detected after 27 wk in plants that were infested in September 1970 and grown continuously, with additional heat and light (Valdez, 1971).

The inability of a strawberry isolate of AMV to infect hop

Strains of AMV that cause conspicuous symptoms in herbaceous hosts have never been isolated from hop. Moreover, all attempts to infect hop with such a strain from strawberry have been unsuccessful, using either infective nematodes or mechanical inoculation with highly infective sap or concentrated and partially purified preparations.

Neither the roots nor shoots of hop plants became infected when grown for 2 yr in boxes of soil from a site in Hampshire where AMV and strawberry latent ringspot virus (SLRV) occurred in strawberry. The soil contained numerous *X. diversicaudatum*, and cucumber bait plants became infected with AMV and/or SLRV within a few weeks.

In two other experiments *X. diversicaudatum* failed to transmit a strawberry isolate of AMV from petunia to the roots of small hop seedlings growing in egg cups or very small clay pots, each receiving 100 adults or larvae. The nematodes were recovered at the end of one of the experiments and shown to be still infective by fresh transfers to the roots of *C. quinoa* plants (Valdez, 1971).

DISCUSSION

Recurring difficulties have been encountered in demonstrating that nettlehead disease is soil-borne and more recently problems arose in confirming the role of *X. diversicaudatum* as a vector of AMV(H). The soil used by early workers may not have contained this nematode and some of our experiments were terminated before the virus had invaded the aerial parts or before it caused symptoms or could be detected there. Other (unpublished) experiments were compromised when AMV(H) was shown to be seed-borne and infection was found in stocks of seed from parent plants in which no infection had been detected earlier in the season. The presence of an unusual strain of AMV in hop and the masking of nettlehead symptoms that occurs, particularly in hot weather, have long caused special problems and impeded progress.

Nevertheless, AMV(H) has now been transmitted readily by *X. diversicaudatum* extracted from woodland and hop soils and between herbaceous hosts, between hop plants and from hop to herbaceous hosts. Moreover, a proportion of our hop bait plants developed typical symptoms of nettlehead disease. Transmission seemed to be facilitated by using very young bait plants grown in small containers (Valdez, 1972*b*). The number of nematodes in relation to the amount of root and soil must have been greater in these circumstances than in much previous work. However, there has been no critical comparison of containers in our work or previously. Further information is required on this aspect of inoculation technique, which may explain why certain viruses are sometimes transmitted under laboratory conditions by nematode species that are not the usual vectors (Fritzsche & Kegler, 1967; Valdez, 1972*a*).

Meanwhile, our results contribute to an understanding of the etiology of nettlehead and related diseases.

Legg (1964) suggested that nettlehead disease was caused by two viruses, of which one was soil-borne and seemed to predispose plants to nettlehead disease. This virus is now considered to be AMV(H) (Bock, 1966). The existence and identity of a second virus remains uncertain. It cannot be prunus necrotic ringspot virus, as suggested by Bock (1966, 1967), because all our hop plants that developed nettlehead were free of this virus. Prunus necrotic ringspot virus was also absent from many other hop plants with nettlehead disease, including seedlings and meristem tip clones that became infected on exposure in the field, or after mechanical inoculation with concentrated partially-purified virus preparations from hop plants with nettlehead. Polyhedral particles typical of the nepovirus group are the only ones common to purified preparations from such diverse sources. Hence nettlehead may be caused by AMV(H) together with a second nepovirus not yet characterized or isolated and less readily transmitted by *X. diversicaudatum*. This would explain why few of the plants infected with AMV(H) in our experiments developed nettlehead. The precise role of AMV(H) in the etiology of nettlehead and split leaf blotch diseases remains undetermined, although it seems likely that the causal agents of both diseases are transmitted by *X. diversicaudatum*. However, the existing information, together with the initial results of our field trials (Thresh & Pitcher, 1971; Thresh, Pitcher, McNamara & Ormerod, 1972) should help hop growers to avoid or decrease losses caused by nematode-transmitted viruses.

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