

The transmission of two strains of arabis mosaic virus from England by populations of *Xiphinema diversicaudatum* (Nematoda : Dorylaimoidea) from ten countries

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SUMMARY

The ability of twelve populations of *Xiphinema diversicaudatum* from ten countries to transmit two strains of arabis mosaic virus from England (AMV) was tested using a standard laboratory procedure. Eight of the twelve populations were efficient vectors of AMV type-British strain (AMV-T). A population from USA transmitted the virus at a rate intermediate between these eight efficient populations and one from Spain which transmitted AMV-T infrequently. Spanish nematodes did not transmit a second strain of virus (AMV-W) and French and Italian nematodes only infrequently transmitted AMV-W. However, AMV-W was relatively frequently transmitted by nine other populations of *X. diversicaudatum*. It is concluded that most populations of *X. diversicaudatum* have the ability to become virus vectors and that non-infective populations have not previously had access to virus. *Petunia hybrida* and *Chenopodium quinoa* virus-source and bait plants were used with AMV-T and AMV-W respectively and AMV-T was transmitted by substantially more of the nematodes from eight of the populations than was AMV-W. In a separate test AMV-T was more frequently transmitted when *P. hybrida* rather than *C. quinoa* plants were used. Differences in transmission between the two strains of AMV were much larger than the differences when the two plant species were compared. Therefore, the differences may be inherent in the specificity of the relationships between AMV-T and AMV-W and their vector, *X. diversicaudatum*.

RÉSUMÉ

Transmission de deux souches anglaises du virus de la mosaïque arabis par des populations de Xiphinema diversicaudatum (Nematoda : Dorylaimoidea) provenant de dix pays

L'aptitude de douze populations de *Xiphinema diversicaudatum* provenant de dix pays à transmettre deux souches anglaises du virus de la mosaïque arabis (AMV) a été testée en utilisant des procédures de laboratoire standards. Huit de ces douze populations se sont montrées des vecteurs efficaces de la souche de « type britannique » de l'AMV (ou AMV-T). Une population des USA transmettait le virus à un taux intermédiaire entre les huit populations efficaces et une population espagnole qui transmettait irrégulièrement l'AMV-T. Cette population espagnole ne transmettait pas la seconde souche du virus (AMV-W), et les populations française et italienne la transmettaient irrégulièrement. Cette souche AMV-W est transmise par contre avec une bonne fréquence par les neuf autres populations de *X. diversicaudatum*. Il est conclu de ces observations que la plupart des populations de *X. diversicaudatum* sont capables de devenir vecteurs de virus et que les populations inactives n'avaient pas été auparavant en contact avec le virus. *Petunia hybrida* d'une part et *Chenopodium quinoa* d'autre part ont été utilisés comme sources de virus et plantes-tests pour l'AMV-T et l'AMV-W, respectivement; chez huit des populations, l'AMV-T a été transmis par un nombre nettement plus grand de nématodes que ne l'a été l'AMV-W. Une expérience particulière a démontré que l'AMV-T était transmis avec une fréquence plus élevée si *P. hybrida* était utilisé au lieu de *C. quinoa*. Les différences dans la transmission étaient beaucoup plus grandes entre les deux souches de l'AMV qu'entre les deux plantes utilisées. Ces différences sont donc peut-être dues à la spécificité des relations entre l'AMV-T et l'AMV-W, d'une part, et leur vecteur, *X. diversicaudatum*, d'autre part.

Arabis mosaic virus (AMV; Smith & Markham, 1944) and its vector *Xiphinema diversicaudatum* (Micoletzky, 1927) Thorne, 1939 are widely distributed in Europe (Martelli, 1975, 1978; Murant, 1970; Novak & Lanzova, 1975; Saric & Velagic, 1980); also, the virus has been reported from Canada, Japan and New Zealand (Iwaki & Kamuro, 1974; Stace-Smith in Murant, 1970; Thomas & Proctor, 1972). There are several reports of variation between populations of *X. diversicaudatum* in their ability to transmit AMV (Brown & Taylor, 1981;

Brown & Trudgill, 1983; Dalmaso, Munck-Cardin & Legin, 1972; Martelli, 1975, 1978). In Britain, where there are two serologically distinguishable strains of AMV, in an extensive survey only 17 of 325 (5%) populations of *X. diversicaudatum* were found to be naturally infected with AMV (Taylor & Brown, 1976).

The ability of four populations of *X. diversicaudatum* from Britain to transmit two serologically distinguishable strains of AMV was examined, also, similarly populations from six other European countries, New Zealand

and USA were examined and compared. Some aspects of the virus transmission procedures which might influence transmission of the viruses by the nematodes also were examined and the results are reported here.

Materials and methods

Populations of *X. diversicaudatum* used in the study were from *Sambucus nigra* L., Dundee, Scotland; *Lolium perenne* L., Ilkley, England; Scrubland, Aylesford, England; deciduous woodland, High Halstow, England; *Ribes nigrum* L., Kostinbrod, Bulgaria; *Rosa* sp., the Var region, France; *Rubus idaeus* L., Lombardi region Italy; *Prunus armencia* L., Alexandra, New Zealand; *Fragaria* × *ananassa* Duch., Sandefjord, Norway; *Vitis vinifera* L., Cazalegas, Spain; *Triticum spelta* L., Holziken, Switzerland and *Prunus persica* L., San Diego, USA. The population from France came from a glasshouse whereas all the others came from field biotopes. All populations were kept as breeding colonies in a heated glasshouse at the SCRI with *Rosa* sp., *R. idaeus* and *F. × ananassa* as host plants and the populations were bait-tested and found to be free from infection with any detectable nepoviruses.

The strains of virus used were the type-British strain (AMV-T; Harrison, 1958) and a strain transmitted by *X. diversicaudatum* from High Halstow, England (AMV-W; Clark, 1976). Both viruses were propagated in *Chenopodium quinoa* Willd. plants in a heated glasshouse at the SCRI.

VIRUS TRANSMISSION PROCEDURES

The procedures used were those described by Brown and Trudgill (1983). Experiments were done with 25 cm³ plastic pots maintained in temperature controlled cabinets (Taylor & Brown, 1974) and with three-week-old seedlings of *Petunia hybrida* Vilm. or *C. quinoa* used as manually infected sources of AMV-T and AMV-W respectively. Groups of c. 35 virus-free nematodes, mainly adults and fourth-stage juveniles, were given access to these virus-source plants for four weeks. They were then extracted, counted and in groups of two or five placed in clean 25 cm³ pots in which were planted one *P. hybrida* or three *C. quinoa* virus free bait plants. After four weeks the nematodes were extracted and counted.

The roots of the virus-source and bait plants were washed to remove any nematodes and/or virus that may have become entangled with or be adhering to the roots. Root galls, indicative of nematode feeding, were counted and the roots tested for virus by comminuting them and rubbing the resultant suspension onto the leaves of *C. quinoa* assay plants. The aerial parts of the bait plants were frozen (−20°) and some of those in which virus had been detected in the roots were subsequently tested

for systemically translocated virus. Virus from some of the *C. quinoa* assay plants was used in serological tests to confirm its identity.

P. hybrida and *C. quinoa* were compared as virus-source and as bait plants using the procedures described above with AMV-T and groups of two and five *X. diversicaudatum* from the Scottish, Aylesford and High Halstow populations.

Nematodes from the Scottish, French and Italian populations were used in a separate experiment to examine their ability to acquire AMV-T from plants which previously had been infected with AMV-T by nematodes from these same populations. The effect of consecutive transmission of the virus to acquisition from and resultant transmission to further plants by these nematodes also was examined. Nematodes were infected as before and groups of five then were given access to virus-free bait plants. After four weeks they were extracted, counted and discarded; the root galls were counted and approximately half of each bait plant root system was excised and the plant transferred to a clean 25 cm³ pot. The excised portion of root was tested for the presence of virus and those bait plants which had had virus detected in the excised portion of their roots were used as virus-source plants in the subsequent test. This procedure was repeated until virus was not detected in any of the bait plants used with *X. diversicaudatum* from the French and Italian populations (Tab. 3).

The percentage of nematodes transmitting virus were estimated by using the maximum likelihood estimator of Gibbs and Gower (1960).

Results

TRANSMISSION OF AMV-T

AMV-T was transmitted by nematodes from all the populations tested. The results from the groups of two nematodes indicated that c. 75 % or more of the individuals in the populations from Scotland, Ilkley, Aylesford, High Halstow, Bulgaria, New Zealand, Norway and Switzerland transmitted AMV-T (Tab. 1). In contrast only c. 25 % of the nematodes from the USA and 2 % from the Spanish populations transmitted the virus.

TRANSMISSION OF AMV-W

Except for the Spanish population, AMV-W was transmitted by all the *X. diversicaudatum* populations (Tab. 1). The results with the groups of two nematodes indicated that c. 20 % of the nematodes from the Scotland, Ilkley, Aylesford, High Halstow, Bulgaria, Switzerland and USA populations transmitted AMV-W whereas c. 30 % of the nematodes from the New Zealand and Norway populations but only c. 4 % from the French and Italian populations transmitted virus. In general with groups of two and five nematodes similar

Table 1

The transmission, by groups of two and five *Xiphinema diversicaudatum* from twelve populations of two strains of arabis mosaic virus

Population	Numbers of nematodes per replicate							
	2		5		2		5	
	AMV-T*		AMV-W*		AMV-T		AMV-W	
	Numbers of transmissions**				Estimated percentages of nematodes transmitting virus****			
Bulgaria	25/25	12/12	9/24	na	> 80	> 39	18	na
England								
Ilkley	24/25	12/12	9/25	13/15	80	> 39	20	33
Aylesford	24/25	12/12	9/25	4/7	80	> 39	20	16
High Halstow	23/25	12/12	10/25	12/15	72	> 39	23	28
France	na***	na	1/25	0/6	na	na	2	< 3.6
Italy	na	na	1/25	0/10	na	na	2	< 1.4
New Zealand	24/25	12/12	15/25	4/10	80	> 39	37	9.7
Norway	24/25	12/12	13/25	6/7	80	> 39	31	32
Scotland	23/25	12/12	9/25	14/15	72	> 39	20	42
Spain	0/20	1/15	0/20	0/15	< 2.5	1.4	< 2.5	< 1.4
Switzerland	24/25	12/12	10/25	8/10	80	> 39	23	28
USA	12/25	9/12	9/25	7/9	28	24	20	26

* AMV-T, type-British strain, AMV-W, strain transmitted by *X. diversicaudatum* from High Halstow, England.

** Numerator is the number of bait plants infected, denominator is the number tested.

*** na : Not available.

**** See Gibbs and Gower (1960).

Table 2

A comparison of *Petunia hybrida* and *Chenopodium quinoa* as the test plant in experiments testing the transmission of arabis mosaic virus (type - British strain) by groups of two and five *Xiphinema diversicaudatum* from three populations

Population	Numbers of nematodes per replicate							
	2		5		2		5	
	<i>P. hybrida</i>		<i>C. quinoa</i>		<i>P. hybrida</i>		<i>C. quinoa</i>	
	Number of transmissions				Estimated percentages of nematodes transmitting virus**			
England								
Aylesford	24/25*	12/12	21/25	12/25	80	> 39	60	39
High Halstow	23/25	12/12	19/25	14/25	72	> 39	51	42
Scotland	23/25	12/12	19/25	14/25	72	> 39	51	42

* Numerator is the number of bait plants infected, denominator is the number tested.

** See Gibbs and Gower (1960).

proportions of nematodes transmitted virus within each population.

COMPARISON OF *P. hybrida* AND *C. quinoa* AS VIRUS-SOURCE AND BAIT PLANTS

When groups of two *X. diversicaudatum* from the

Scottish, Aylesford and High Halstow populations were used with *P. hybrida* as the AMV-T source and as the bait plant *c.* 75% of the nematodes transmitted virus (Tab. 2), a value similar to that obtained previously (Tab. 1). However, when *C. quinoa* was used as the virus-source and bait plants the mean percentage of

Table 3
The transmission of arabis mosaic virus (type - British strain) in consecutive tests with groups of five *Xiphinema diversicaudatum* from three populations using virus-source plants infected with virus in each preceding tests by nematodes from the respective populations

Populations	Test							
	1		2		3		4	
France	3/20*	(3.2**)	3/22	(2.9)	2/18	(2.3)	0/12	(< 1.7)
Italy	2/20	(2.1)	0/15	(< 1.4)	na***	(na)	na	(na)
Scotland	20/20	(> 45)	14/15	(42)	13/13	(> 40)	15/15	(> 42)

* Numerator is the number of bait plants infected, denominator is the number tested.

** Estimated percentage of nematodes transmitting virus. See Gibbs & Gower (1960).

*** na : Not available.

nematodes from the three populations transmitting virus was 54 %. This is a larger ratio of transmission than was obtained for AMV-W with these populations when *C. quinoa* was used as the test plants (Tab. 1 & 2).

VIRUS-SOURCE PLANTS INFECTED WITH AMV-T BY *X. diversicaudatum*

X. diversicaudatum from the Scottish population frequently transmitted AMV-T whereas nematodes from the French and Italian populations did so only infrequently (Tab. 3). The use of AMV-T source plants which had been naturally infected by nematodes from a given population did not influence the frequency of transmission of virus by nematodes from the same population.

Discussion

Except for a population from Spain, all *X. diversicaudatum* populations transmitted AMV-W and AMV-T. As these populations came from diverse geographical locations it is likely that most populations of *X. diversicaudatum* can transmit these two viruses. In Britain only a few populations were found to be naturally infective with AMV (Taylor & Brown, 1976) and it is probable that the non-infective populations had not had access to AMV. The virus has an extensive host range (Murant, 1970) and it is unlikely that any *X. diversicaudatum* population, after having access to AMV, can become free of the virus due, for example, to changes in the plant community of the nematodes biotope.

Most populations examined were efficient vectors of AMV-T and AMV-W but populations from France and Italy transmitted AMV-W only infrequently and a Spanish population did not transmit AMV-W and infrequently transmitted AMV-T. Brown and Taylor (1981) and Brown and Trudgill (1983) found that populations of *X. diversicaudatum* from France and Italy infrequently transmitted AMV-T and strains of strawberry latent ringspot virus. Populations of *X.*

diversicaudatum from southern and western Europe may be less efficient vectors of AMV than those from northern Europe. However, more populations need to be examined to determine if these differences are consistent among populations of *X. diversicaudatum* from these areas.

Populations of *X. diversicaudatum* vary considerably and they may be grouped according to their measurements (Brown & Topham, 1985). The reproductive capacities of females from different *X. diversicaudatum* populations also differ (Brown, 1985). Populations used in the present study are representative of many of these morphometric groups, and, of populations with differing reproductive capacities. These differences however do not correspond with differences in the ability of populations to transmit AMV-T and AMV-W.

Maintaining virus cultures in the glasshouse for several years by consecutive manual inoculations to herbaceous host plants resulted in apparent loss of transmissibility of some aphid transmissible viruses (Koike, 1979). The isolate AMV-T used in the experiments reported here has been cultured by this method for c. 25 years (Murant, pers. comm.), apparently without any deleterious effect on its transmissibility by nematodes from the *X. diversicaudatum* populations studied. Furthermore, successive tests in which bait plants infected with virus by nematodes were used as the source plants did not enhance transmission by Scottish, French and Italian nematodes, the results with these populations being similar to those reported by Brown and Trudgill (1983).

C. quinoa has a smaller root system than *P. hybrida*, but this difference is probably insufficient to account for the rate of transmission of AMV-W being much less than that of AMV-T. It is more likely that the difference in transmission rate is inherent in the specificity of the relationships between AMV-T and AMV-W and their vector nematode, *X. diversicaudatum*.

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