# Differential transmissibility of arabis mosaic and strains of strawberry latent ringspot viruses by three populations of *Xiphinema diversicaudatum* (Nematoda : Dorylaimida) from Scotland, Italy and France

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## SUMMARY

The ability of three populations of Xiphinema diversicaudatum to transmit arabis mosaic virus (AMV) and three strains of strawberry latent ringspot virus (SLRV) was tested in laboratory experiments. X. diversicaudatum from Scotland readily transmitted the type strains of AMV and SLRV from Britain but did not transmit two strains of SLRV from Italy. A population of X. diversicaudatum from Italy transmitted all four viruses, but only with a small frequency. X. diversicaudatum from France did not transmit a strain of SLRV from Italy, transmitted the SLRV from Britain only infrequently, and transmitted AMV with a frequency intermediate between that of the Scottish and Italian populations. Anatomical and morphological studies showed the three populations were all X. diversicaudatum but that the Italian and French populations were significantly smaller than the Scottish. Electron microscope examination of thin sections through the oesophagus and odontophore indicated that infrequent or non-transmission of virus was related to lack of retention of virus within the nematodes.

## Résumé

Différences de transmissibilité du virus de la mosaïque de l'arabis et de souches du « latent ringspot virus » du fraisier par trois populations de Xiphinema diversicaudatum (Nematoda : Dorylaimida) originaires d'Écosse, d'Italie et de France

L'aptitude de trois populations de Xiphinema diversicaudatum à transmettre le virus de la mosaïque de l'Arabis (AMV) et trois souches du virus des taches annulaires (SLRV), a été testée au laboratoire. Une population écossaise a transmis facilement les souches anglaises de l'AMV et du SLRV, mais pas du tout une souche italienne du même SLRV. Une population italienne de X. diversicaudatum a transmis ces quatre virus, mais avec un faible pourcentage de réussite. Une population française n'a pas transmis le SLRV d'Italie et seulement avec difficulté le SLRV d'Angleterre ; son aptitude à transmettre l'AMV s'est révélée intermédiaire par rapport à la population d'Écosse et à celle d'Italie. L'étude anatomique et morphologique indique qu'il s'agit bien de trois populations de X. diversicaudatum, cependant les indívidus d'Italie et de France sont significativement un peu plus petits que ceux d'Écosse. L'examen en coupe mince en microscopie électronique, au travers de l'œsophage et de l'odontophore, indique que dans les cas où la transmission du virus n'a été obtenue que rarement ou pas du tout, il n'y a pas de rétention du virus dans le nématode.

Xiphinema diversicaudalum has been shown to be a vector of arabis mosaic (AMV) and strawberry latent ringspot viruses (SLRV) which affect a range of crops in Britain, France and Italy (Harrison & Cadman, 1959; Corte, 1966; Jha & Posnette, 1959; Lamberti *et al.*, 1980; Lister, 1964; Scotto La Massese, Marenaud & Dunez, 1973). Trudgill, Brown and Robertson (1981) reported that X. diversicaudatum from Scotland was an efficient vector of the type strains of AMV and SLRV whereas Dalmasso, Munck-Cardin and Legin (1972) and Martelli (1975) suggested that some populations of X. diversicaudatum may differ in their ability to transmit some isolates of AMV. Trudgill and Brown (1978) described a procedure for

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determining the frequency with which viruses are transmitted by longidorid nematodes. Using these procedures, and as part of a study of the intraspecific variability in X. diversicaudatum, the abilities of a Scottish, an Italian and a French population of X. diversicaudatum to transmit the type strains of AMV and SLRV from Britain and two Italian strains of SLRV were compared.

# **Materials and Methods**

## Nematodes

Populations of X. diversicaudalum from Sambucus nigra L. near Dundee, Scotland; from raspberry (Rubus idaeus L.), Lombardi region, Italy and from glasshouse roses (Rosa sp.), Var region, France, were maintained in a heated glasshouse at the SCRI with Rosa sp., Rubus idaeus L. and Fragaria  $\times$  ananassa Duch. as host plants.

# VIRUSES

The strains of virus used were : AMV, type strain (Harrison, 1958); SLRV-T, type strain (Lister, 1964); SLRV-Ip and SLRV-Ir Italian strains, from Prunus persica L. and Rubus idaeus L. respectively. The four strains of virus were propagated in herbaceous plants at the SCRI. Gel-diffusion serological tests (using anti-serum to SLRV-T) showed that SLRV-Ip, SLRV-Ir and SLRV-T were related antigenically but were not identical (Fig. 1A). Therefore, SLRV-T, SLRV-Ip and SLRV-Ir are considered to be strains of one virus. In the first experiment with X. diversicaudatum from Scotland and Italy the transmission of all four viruses was compared. However, in succeeding experiments the viruses used were those obtained from bait plants infected by the Italian population of X. diversicaudatum. This was done because we wished to use virus isolates recently transmitted by nematodes, and partly because we wished to determine whether the Italian nematodes were selecting the viruses so that the frequency with which they were transmitted was changed. The possible influence of the bait plant species on the frequency of transmission of these virus isolates by the Scottish nematodes was also examined.

# VIRUS TRANSMISSION PROCEDURE

Three-week-old seedlings of Chenopodium quinoa Willd. (used for SLRV strains) or Petunia hybrida

Vilm. (used for AMV) were transplanted into 25 ml pots, manually inoculated with virus and used as source plants from which groups of c. 35 virus-free nematodes could acquire virus. The pots were maintained in temperature controlled cabinets (Taylor & Brown, 1974) at 18° and with a minimum daylength of 16 hr. After four weeks the nematodes were extracted, counted and hand-picked in groups of two or five into new 25 ml plastic pots containing one *P. hybrida* or three *C. quinoa*, virus-free, bait plants. After four weeks access to the bait plant root systems the nematodes were re-extracted and counted.

The root systems of the source and bait plants were examined for root galls which were indicative of nematode feeding activity and tested for virus by comminuting the roots and rubbing the extract onto the leaves of *C. quinoa* assay plants. The aerial parts of the bait plants were frozen ( $-20^{\circ}$ ) and those from plants in which virus had been detected in the root systems were subsequently tested for the presence of systemically translocated virus. Virus from some of the *C. quinoa* assay plants was used in serological tests to confirm the identity of the viruses transmitted.

### INGESTED AND RETAINED VIRUS

The presence of virus in nematodes from the source plants was tested for in two ways. Several nematode bodies were tested for ingested virus, within the intestine, using immunosorbent electron microscopy (ISEM) as described by Roberts and Brown (1980). The heads taken from these nematodes were fixed in 3 % glutaraldehyde, postfixed in 1 % osmium tetroxide, sectioned and examined with an electron microscope for virus particles retained within the odontophore (Taylor & Robertson, 1970).

# MORPHOLOGY AND MORPHOMETRICS

The morphology and morphometrics of ten female and five male X. diversicaudatum, taken from each population, were examined. Specimens were heat killed and fixed in triethanolamine formalin (Courtney, Polley & Miller, 1955) and processed to glycerol by a slow replacement method.

## Results

## VIRUS TRANSMISSION

An experiment with AMV, SLRV-T, SLRV-Ip

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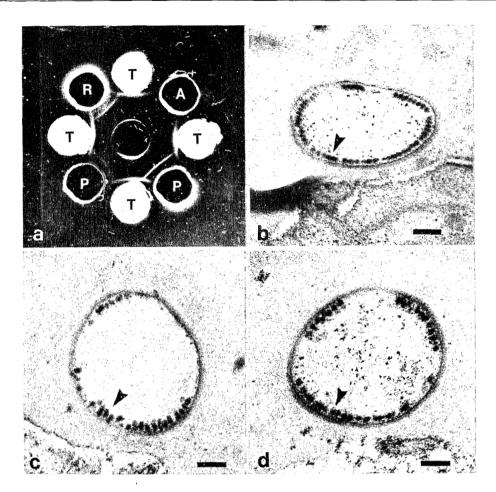


Fig. 1. a : Immunodiffusion test showing antigenic relatedness of three strains of strawberry latent ringspot virus from Britain and Italy (T : type strain from Britain; P : peach strain from Italy; A : arabis mosaic virus, type strain and R : raspberry strain from Italy) using SLRV-T antisera. b : Arabis mosaic virus particles (arrow) adsorbed to the oesophageal lining in a Scottish *Xiphinema diversicaudatum*. c & d : Strawberry latent ringspot virus particles (arrow; type strain) adsorbed to the oesophageal lining in a Scottish *X. diversicaudatum* respectively. (In b, c and d bar represents 100 nm).

and SLRV-Ir showed that X. diversicaudatum from Scotland fed on the source and bait plants and that replicated groups of two or five nematodes readily transmitted AMV and SLRV-T but did not transmit SLRV-Ip or SLRV-Ir (Tab. 1). Using the maximum likelihood formula (Gibbs & Gower, 1960) it was estimated that the proportion of nematodes transmitting AMV and SLRV-T, in the test with two nematodes per replicate, was 0.6 and 0.3 respectively. In contrast, similar groups of X. diversicaudatum from Italy, which also had ample opportunity to transmit virus, transmitted all four virus isolates but

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only a very small proportion of the nematodes acted as vectors ( < 0.03, Tab. 1).

The results from a subsequent experiment which used four different species of bait plants confirmed that SLRV-Ip and SLRV-Ir were not transmitted by X. diversicaudatum from Scotland (Tab. 2). The results also showed that, even though they appeared to be less good as hosts for the nematodes, C. quinoa and Gomphrena globosa L. were infected with SLRV-T more readily than Rubus idaeus L. cv. Malling Jewel or Fragaria  $\times$  ananassa Duch. cv. Cambridge Favourite.

Table	1
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The transmission of arabis mosaic virus and three strains of strawberry latent ringspot virus by X. diversicaudatum from Italy and Scotland

Virus	Source plants							
	Nei used	matodes recovered	Root galls	Ner used	natodes recovered	Root galls	Virus recovered*	P**
			(X. d)		<i>utum</i> from Scot	land)		
AMV	40	33	35	$\frac{2}{5}$	$\begin{array}{c} 1.2\\ 3.4\end{array}$	$\begin{array}{c}1.1\\3.6\end{array}$	$rac{26}{31}$ 16/16	$0.598 \\ > 0.426$
SLRV-T	40	37	31	$\frac{2}{5}$	$\begin{array}{c} 1.4 \\ 1.5 \end{array}$	1.6 2.4	$16/31 \\ 15/16$	$\begin{array}{c} 0.304 \\ 0.426 \end{array}$
SLRV-Ip	40	40	25	5	1.2	2.6	0/20	
SLRV-Ir	40	33	30	5	1.8	3	0/20	
Controls (virus free)				40	29	30	0/10	
			· (X.	diversicau	<i>datum</i> from It	aly)		
AMV	35	32	28	$\frac{2}{5}$	$0.9 \\ 2$	1.1 3.3	1/35 0/15	0.014 < 0.013
SLRV-T	35	32	29	2 5	$\begin{array}{c} 0.9 \\ 2.3 \end{array}$	$^1_{2.8}$	1/35 0/15	0.014 < 0.013
SLRV-Ip	35	31	24	$\frac{2}{5}$	$\begin{array}{c} 0.9 \\ 1.1 \end{array}$	$\begin{array}{c} 0.9 \\ 3 \end{array}$	$2/35 \ 2/16$	$\begin{array}{c} 0.021 \\ 0.026 \end{array}$
SLRV-Ir	35	29	33	$\frac{2}{5}$	$1 \\ 1.8$	1 2.9	1/33 3/15	$\begin{array}{c} 0.015 \\ 0.044 \end{array}$
Control (virus free)	—			5	2.8	2.1	0/15	0.013

\* Numerator is the number of bait plants infected, denominator is the number tested. \*\* P, the estimated proportions of nematodes transmitting virus calculated using the equation of Gibbs and Gower (1960).

## Table 2

The transmission, by X. diversicaudatum from Scotland, of three strains of strawberry latent ringspot virus from C. quinoa virus source-plants to C. quinoa, G. globosa, R. idaeus and F.  $\times$  ananasa bait-plants.

Virus	Source-plant				Bait-plant			
	Ner used	natodes recovered	Root galls	Plant species	Nen used	natodes recovered	Root galls	Virus recovered*
SLRV-T	c. 40	c. 30	42	C. quinoa	5	1.8	2.8	10/10
				G. globosa	5	1.7	2.1	8/10
				R. idaeus	5	4	3.5	1/10
				F.~ imes~ananasa	5	4	4.4	1/10
SLRV-Ip	c. 40	c. 30	37	C. quinoa	5	2.6	3.5	0/10
				G. globosa	5	1.7	3.2	· 0/10
				R. idaeus	5	3.8	2.4	0/10
				F. $ imes$ ananasa	5	3.6	5.2	0/10
SLRV-Ir	c. 30	c. 30	43	C. quinoa	5	2.5	3.4	0/10
				G. globosa	5	2.7	2.2	0/10
				R. idaeus	5	2.7	2.1	0/10
				F.~ imes~ananasa	5	4	5.4	0/10
Control (virus free)				C. quinoa	c. 40	26	43	0/10

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

# Table 3

The transmission, by X. diversicaudatum from Italy and Scotland, of isolates of arabis mosaic virus	
and three strains of strawberry latent ringspot virus which had been transmitted	
by X. diversicaudatum from Italy.	

Virus		Source plants			Bait plants			
	Nei used	natodes recovered	Root galls	Ne: used	matodes recovered	Root galls	Virus recovered*	P**
			(X. d)	iversicaud	atum from Scot	land)		<u> </u>
AMV	36	24	32	$\frac{2}{5}$	$\begin{array}{c} 1.1 \\ 2.7 \end{array}$	$\begin{array}{c} 1.6 \\ 5.6 \end{array}$	$\frac{16}{19} \\ 15/15$	0.603 > 0.418
SLRV-T	36	23	13	$\frac{2}{5}$	$\begin{array}{c} 1.2 \\ 2.9 \end{array}$	na*** na	$rac{17}{25} \ rac{12}{12}$	0.434 > 0.392
SLRV-Ip	36	22	10	30	16.6	na	0/5	< 0.007
SLRV-Ir	36	26	11	30	18.0	na	0/5	< 0.007
			(X.	diversicat	<i>udatum</i> from It	aly)		
AMV	30	30	42	$2 \\ 5$	$\begin{array}{c} 1.3 \\ 2.0 \end{array}$	$2.1 \\ 5.8$	$1/22 \\ 0/15$	0.023 < 0.013
SLRV-T	30	27	10	2 5	$\begin{array}{c} 1.4 \\ 2.7 \end{array}$	1.2 na	$0/24 \\ 3/15$	$< \begin{array}{c} 0.021 \\ 0.044 \end{array}$
SLRV-Ip	30	25	9	$2 \\ 5$	$\begin{array}{c} 0.8 \\ 1.5 \end{array}$	na na	$2/25 \\ 1/14$	$\begin{array}{c} 0.041 \\ 0.015 \end{array}$
SLRV-Ir	30	24	8	$\frac{2}{5}$	$\begin{array}{c} 1.0\\ 2.3\end{array}$	na na	$2/25 \\ 1/12$	$\begin{array}{c} 0.041\\ 0.017\end{array}$

Numerator is the number of bait plants infected, denominator is the number tested.
\*\* P, the estimated proportions of nematodes transmitting virus calculated using the equation of Gibbs & Gower (1960).
\*\*\* Data not available.

 Table 4

 The transmission, by X. diversicaudatum from France and Scotland, of isolates of arabis mosaic virus

and two strains of strawberry latent ringspot virus which had been transmitted

by X. diversicaudatum from Italy.

Virus		Source plants		Bait plants				
	Nei used	natodes recovered	Root galls	Ne: used	matodes recovered	Root galls	Virus recovered*	P**
			(X. d)	iversicaude	atum from Scot	land)		
AMV	36	25	22	$\frac{2}{5}$	1.6 $3.5$	$1.9\\3.8$	$\frac{18}{20}$ $\frac{12}{12}$	0.684 > 0.392
SLRV-T	35	32	8.2	$\frac{2}{5}$	0.9 2.3	0.6 na***	9/20 10/12	$0.258 \\ 0.301$
SLRV-Ip	34	27	11	2	1	0.9	0/40	< 0.013
			(X. d)	liversicaud	<i>latum</i> from Fra	ance)		
$\operatorname{AMV}$	36	22	29	<b>2</b>	1	2.4	10/40	0.134
SLRV-T	38	26	14	$^{2}$	1.1	2.0	4/40	0.051
SLRV-Ip	40	29	8	<b>2</b>	1.4	2.1	0/40	< 0.013
Control (virus free)				27	6.6	17	0/10	< 0.004

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

\*\* P, the estimated proportions of nematodes transmitting virus calculated using the equation of Gibbs & Gower (1960).

\*\*\* Data not available.

When the first experiment was repeated, using the viruses transmitted by the Italian X. diversicaudalum, similar results were again obtained (Tab. 3); the Italian population transmitting all four viruses with a small frequency and the Scottish population readily transmitting AMV and SLRV-T but not transmitting SLRV-Ip or SLRV-Ir. In a second experiment with three of the ,,transmitted" isolates of virus, X. diversicaudatum from France did not transmit SLRV-Ip (< 0.013), only a small proportion transmitting AMV (0.13) was less than that obtained with the Italian in the two previous experiments (Tab. 4).

INGESTED AND RETAINED VIRUS

Virus particles were detected, using ISEM, in every nematode body examined from the Scottish, Italian

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and French populations exposed to AMV, SLRV-T or SLRV-Ip (Tab. 5). No virus particles were detected in nematodes not exposed to virus-source plants. When thin sections through the heads of the same nematodes were examined with an electron microscope, virus particles were detected only in one of two Scottish nematodes exposed to AMV. Virus particles were also detected in two of four Scottish nematodes exposed to SLRV-T and in one of three French nematodes exposed to SLRV-T (Tab. 5; Fig. 1 B, C & D). In each instance virus particles were retained on the cuticular lining at the anterior end of the cesophageal lumen.

## MORPHOLOGY AND MORPHOMETRICS

No significant anatomical differences were apparent between X. diversicaudatum specimens taken from the three populations used in the virus transmission experiments. But, male and female specimens from

### Table 5

The proportion of nematodes from three populations exposed to three viruses in which virus particles were detected by immunosorbent electron microscopy and by examination of thin sections through the nematode odontostyle and oesophagus.

Virus	X. diversi- caudatum population	Virus particles detected by immuno- sorbent electron microscopy	Virus particles within the odontostyle or oesophagus
AMV	Scotland	4 /4	1/2
	Italy	4 /4	0/3
	France	4 /4	0/2
SLRV-T	Scotland	4/4	2/4
	Italy	4/4	0/4
	France	4/4	1/3
SLRV-Ip	Scotland	4/4	0/4
	Italy	4/4	0/4
	France	4/4	0/4

### Table 6

Morphometric mean values calculated from female *Xiphinema diversicaudatum* from Dundee, Scotland; Lombardi Region, Italy and Adrets, France.

		Scottish	Italian	French
n .		10	10	10
Length	$\mathbf{m}\mathbf{m}$	5.22	4.24a	4.3a
a		84.4a*	75.3	79.5a
b		10.4a	9.03	9.38a
c		110	95a	84.7a
c'		1.02a	1.07a	1.32
V		44a	43a	43a
Odontostyle	μ	136	125a	124a
Odontophore	μ	79.1	74a	75a
Tail	μ.	47.5a	44.6a	50.9a

\* The means in each row bearing the same letter are not significantly different at the probability level p = 0.01.

the Scottish population were significantly larger than specimens from the Italian and French populations. However, the French specimens had significantly longer tails than the Scottish and Italian specimens (Tab. 6).

# Discussion

Using a standard test procedure designed to assess the efficiency of longidorid nematodes as virus vectors (Trudgill & Brown, 1978) it was found that Scottish, French and Italian populations of X. diversicaudatum differed markedly in their ability to transmit a strain of AMV and three strains of SLRV. These differences did not appear to be related to differences in the opportunity nematodes had to acquire and transmit the viruses or to be affected following transmission by the Italian nematodes; nor were they due to the populations being different species as the three populations were anatomically similar, differing only in some of their respective morphometrics.

A few nematodes were examined with the electron microscope for the occurrence of virus particles within their feeding apparatus. The results indicated that in those instances where little or no virus was transmitted, there was correspondingly little or no virus at the sites of retention within the nematodes.

Other workers have reported differences in the transmission of AMV by populations of X. diversicaudatum. Dalmasso, Munck-Cardin and Legin (1972) reported that three populations of X. diversicaudatum from France transmitted AMV with differing effectiveness and Martelli (1975) reported that a Polish population of X. diversicaudatum, unlike a French population, was unable to transmit an isolate of AMV from grapevine. However, these reports did not indicate whether there were morphological differences between the nematode populations or the extent of the differences between the virus isolates or the frequency with which the different AMV isolates were transmitted by the different X. diversicaudatum populations.

The results obtained from the present study confirm that populations of X. diversicaudalum can differ in their ability to transmit the type strain of AMV. Furthermore, differences were also found to occur in the transmission of the type strain of SLRV. In addition, two strains of SLRV from Italy were found to be transmitted only infrequently and only by X. diversicaudatum from Italy. These differences in the transmission of viruses may be a consequence of geographical separation leading to subtle changes

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developing between populations of X. diversicaudatum which affect the specificity of virus retention and virus transmission.

The results reported here support the view that there is specificity between nepo-viruses and their nematode vectors. Harrison (1964) suggested that serologically distinctive forms of nepo-viruses had different specific nematode vectors e.g. Longidorus elongatus was the vector of the type strain of tomato black ring virus (TBRV) and L. attenuatus was the vector of a serologically different strain of TBRV. Brown and Taylor (1981) further suggested that the degree of specificity may differ between populations of a nematode vector species e.g. three geographically separated isolates of TBRV and three strains of raspberry ringspot virus being transmitted more frequently by a population of L. elongatus from Scotland than by a population from England. The present results further support the suggestion that serologically distinctive strains of nepo-viruses have specific nematode vectors and shows that for Xiphinema species the specificity of the relationship can differ between populations of the same nematode and strains of the same virus.

Note: The work reported here is part of a more comprehensive study examining intraspecific variation in X. diversicaudatum involving populations of the nematode from several European countries, New Zealand and the United States of America. Other investigations include morphometric variability, population sex ratios, reproductive rates, hybridization and the transmission of viruses including transmission by hybrids. It is anticipated that these investigations will be reported upon completion of these studies.

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