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Biological characteristics of maize dwarf mosaic potyvirus from Spain

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Abstract

Two isolates of maize dwarf mosaic virus (MDMV-Sp and MDMV-Sp1) obtained from maize in the northeast of Spain were studied. Both isolates induced similar reactions on 6 sorghum cultivars, johnsongrass and oat (cv. Clintland), with the exception of MDMV-Sp which produced a different reaction on one sorghum cultivar. Thirty-three grass species were tested as possible hosts (16 previously untested) and 18 were found to be susceptible. Among those, eight were previously unidentified hosts for MDMV: *Aegilops ovata, A. ventricosa, Avena barbata, Bromus alopecurus, B. diandrus, B. fasciculatus, Echinaria capitata* and *Lolium rigidum.* Both isolates were transmitted from maize to maize nonpersistently by *Rhopalosiphum maidis, R. padi, Schizaphis graminum* and *Sitobium avenae.* The virus was not seed-transmitted in Mo17 and B73 maize inbred lines. Pinwheels, scrolls and short curved laminated aggregates were observed in the cytoplasm of maize cells infected by MDMV-Sp or MDMV-Sp1. In addition, laminated aggregates were observed in cells infected by MDMV-Sp1.

Introduction

Maize dwarf mosaic is the principal viral disease of maize in northeastern Spain. Disease incidence was higher (17%) in the locality of Lleida than in the locality of Girona, 250 km away (lower than 1%) (Achon et al., 1995). Recently, we reported that the disease was caused by maize dwarf mosaic potyvirus (MDMV), and characterized an isolate designated MDMV-Sp (Achon et al., 1994). The homology between the 3′ terminal regions of the viral RNAs of MDMV-Sp and MDMV-A from Illinois (USA) is in the range of variability found between strains of other potyviruses. Currently there is limited information available on biological characteristics of MDMV strains from USA and from other countries where this virus is present. Strains of MDMV from Ohio (USA) have been differentiated on the basis of host response in maize inbreds, by the rate of transmission by *Acryrthosiphom pisum* and *Myzus persicae* (Louie and Knoke, 1975) and serologically (Lenardon et al., 1993). Studies dealing with host range have mainly been done with strain A or isolates not characterized at the molecular level (Antignus, 1987; Gáborjányi and Duons, 1991; Kerlan et al., 1974; Persley et al., 1985; Rosenkranz 1977, 1980, 1983, 1987; Tosic and Ford, 1972; Tosic et al., 1990).

This paper reports the biological characterization of MDMV-Sp (Achon et al., 1994), and of one additional MDMV isolate from the same area (MDMV-Sp1), in order to increase our understanding of the epidemiology of MDMV in northeastern Spain. The two isolates have identically sized coat proteins which are indistinguishable serologically. The genomic RNAs are also very similar, a probe specific for the 3′-terminal 1.5kb of MDMV-Sp, hybridising with the genomic RNA of MDMV-Sp1 (Achon, unpublished).

Materials and methods

Virus isolates. The virus isolates were MDMV-Sp (Achon et al., 1994) and MDMV-Sp1. Both isolates were obtained from naturally infected maize plants

from two localities in northeastern Spain (Girona and Lleida). Virus isolates were propagated by mechanical inoculation on to maize plants cv. G4507 (Funk's).

Mechanical transmission. The inoculum used for all experiments was prepared by triturating young-infected leaves (from plants inoculated 12–20 days earlier) in a mortar with a pestle in 2 volumes of either dH_2O or 0.05M Na-K phosphate buffer pH 7 plus 1% β-mercapthoethanol (Achon, 1993). The triturate was applied with the pestle to test plants previously dusted with 600-mesh Carborundum.

Host range studies. Sorghum seeds of cvs. TX2786, BTX389, Atlas and Rio were supplied by the United States Dept. of Agriculture, Griffin, Georgia. Cv. TX2786 was also suppied by Dr. R. W. Toler, Texas University. Oat cv. Clintland was obtained from National Small Grains Collection, Aberdeen, Idaho. Grass seeds were supplied either by the Germoplasm bank, Madrid, Spain or by Dr. J. Recasens, University of Lleida, Spain. Seedlings were mechanically inoculated at the 3–4 leaf stage. Sorghum cvs, *Sorghum halepense* and oat cv. Clintland were inoculated at the same time. At least 10 seedlings of each cv. were inoculated with each virus isolate and two to five left uninoculated as checks. The test was repeated twice. Grass species of the same genus were inoculated at the same time. With few exceptions, at least 21 seedlings of each grass species were inoculated with each virus isolate and five to seven left uninoculated. In each inoculation experiment, at least 10 seedlings of maize cv. G-4507 were also inoculated to test the infectivity of the virus source. Plants were scored for symptoms for 4 weeks at 3-day intervals. All grasses that remained symptomless were back-assayed to maize (cv. G-4507). For the back assay, leaf tissue samples (inoculated and younger leaves) from all symptomless plants of a species were combined to prepare the inoculum. Depending on the availability of seeds and their viability, differences between virus isolates were re-assayed.

Aphid transmission. The four species of aphids were field-collected, cloned and reared on *Triticum durum* cv. Mexa and G-4507 maize. The virus source was maize that had been mechanically inoculated 12–20 days earlier. Late instar apterous aphids, starved 1–2 h, were given a 1 min access period on detached healthy or infected leaves. Aphids were then transferred to G-4507 maize seedlings in the one leaf stage (10 aphids per plant) for an inoculation access period of 16 h after which they were killed by spraying the plants with insecticide. At least 25 seedlings were inoculated with each aphid species under study. The test was repeated at least twice. Plants were rated for symptoms 7–20 days later.

Statistical analysis of aphid transmission studies. One experimental unit was one plant inoculated with ten inoculative aphids. The variable, transmission, had an assumed binominal distribution and was analyzed with logistic regression. Aphid transmission was compared by means of the log of their relative transmission (RT); this is the ratio of plants that were infected to plants that were not infected. The results were back transformed to get the proportion infected, and reported as median relative transmission (median RT = $e^{(meanLnRT)}$). Aphid species were sorted by their mean RT. Comparisons between adjacent species were performed with two-tailed *t*-tests.

Seed transmission. Maize inbred lines Mo-17 and B-73 were field-grown and hybrids were obtained by crossing. Five hundred and twenty-five plants of each maize inbred were inoculated at the 5 leaf stage, with the inoculum prepared with equal amounts of leaves infected with MDMV-Sp and MDMV-Sp1. Seeds from both infected hybrid and inbred lines were sown in sterilized soil in an insect-proof greenhouse. Virus detection on seedlings was by symptons, by back inoculation to maize and by DAS-ELISA (Clark and Adams, 1977) using a polyclonal antiserum against MDMV-Sp1 (Achon, 1993).

Electron microscopy. Healthy and infected maize leaves were embedded in Lowcryl K4M resin or in London resin white (LR white) as described by Pinner et al. (1993). Samples were sectioned with an ultramicrotome fitted with a 45° glass knife and sections were picked up on parlodion-coated 400 mesh cooper grids and stained with lead citrate for 1 min. Sections were examined in a Jeol 1200 electron microscope.

Immunogold labelling. Leaf samples were fixed and embedded with the same resin as above according to the method of Wells (1985). Samples were sectioned as above and sections were picked up on parlodion coated-gold grids. These were floated on MDMV-Sp1 antiserum diluted 1:100 in 10 mM Tris, pH 7.4, 0.9% sodium chloride, 0.05% polyethyleneglycol (MW 20K) and 3% bovine serum albumin and then

Table 1. Comparative reaction of differential sorghum cultivars, oat and Johnsongrass to maize dwarf mosaic virus isolates MDMV-Sp and MDMV-Sp1

	Inoculated with MDMV isolates:				
	Sp[a]	bam[b]	Sp1	bam	Symptoms[c]
A. sativa L.					
cv. CLINTLAND	0/52	0/40	0/52	0/40	–
Sorghum bicolor (L.) Moench					
cv. ATLAS	34/36		27/31		MNn
cv. RIO	32/34		31/33		MPN(n)
cv. BT398	33/35		35/35		MP
cv. TX2786	0/34	10/69	13/24		MPN
cv. NECTAR	21/23		23/23		M(PN)
cv. DORADO	19/20		20/20		M(PN)
Sorghum halepense (L.) Pers	35/38		37/39		M
Zea mays L.					
cv. G-4507	38/40		39/40		M

[a] Number of symptomatic plants/total number of plants inoculated.
[b] Number of symptomatic plants/total number of plants inoculated in back assays to G-4507 maize (bam).
[c] M = mosaic; N = necrosis of old leaves; n = necrosis of young leaves; P = purple lesions; ( ) = on some plants.

on goat anti-rabbit serum labelled with gold particles diluted 1:20 in the same buffer as above. Sections were stained with uranyl acetate and lead citrate for 10 and 2 min respectively.

Results

Host range. The two isolates induced similar reactions on the set of sorghum cultivars, oat and *Sorghum halepense* (Table 1), with the exception of the symptomless reaction produced by isolate MDMV-Sp on cv.TX2786 of sorghum. Table 2 summarizes the susceptibility of 33 native grass species of Spain to isolates MDMV-Sp and MDMV-Sp1. Special focus was placed on the genera *Aegilops, Avena* and *Bromus. Leptochloa dubia* does not occur in the area but was included because it is susceptible to MDMV (Tosic and Ford, 1972). Eighteen grass species were found to be susceptible to one or both isolates. Among these, 15 species were common hosts to both isolates. Sixteen of the species were previously unknown with regard to susceptibility to MDMV. The following six are newly identified hosts to both isolates: One source of *Aegilops ventricosa, Bromus alopecurus, B. diandrus, B. fasciculatus, Echinaria capitata* and *Lolium rigidum.* Two differential hosts were found, both symptomless, *Aegilops ovata* and *Avena barbata.* All maize hybrids tested were susceptible to both isolates.

Aphid transmission. The four species of aphids transmitted both isolates of MDMV in a non-persistent manner (Table 3). *Schizaphis graminum* and *Rhopalosiphum maidis* were the most efficient vectors, whereas *Sitobium avenae* was the least efficient. For all four species of aphids no significant differences ($p = 0.91$) were found between transmission rates for the two isolates.

Seed transmission. No symptoms of virus infection were observed on seedlings grown from seeds from infected inbred or hybrid maize plants (6336 seeds). No virus was detected when 33 of these seedlings were tested either by back inoculation to maize or by ELISA.

Electron microscopy. Pinwheels, scrolls and short curved laminated aggregates were observed in ultrathin-sections of leaves infected with isolates MDMV-Sp and MDMV-Sp1 (Figure 1A and B). In cross sections examined, MDMV-Sp1 appeared to produce fewer scrolls than MDMV-Sp. In addition, laminated aggregates were observed in cells infected with isolate MDMV-Sp1 (Figure 1B and 2A). This type of morphology was seen more clearly in sections which were cold embedded (Figure 2A). Individual virus particles were found in the cytoplasm of infected cells (Figure 2A and 2B) and in virus bundles. These were labelled with anti-MDMV serum (Figure 2C). No other structures were labelled with the antiserum.

Table 2. Reaction of native grass species to maize dwarf mosaic virus isolates MDMV-Sp and MDMV-Sp1

Species	Growth habitat[a]	Inoculated with MDMV isolates: Sp[b]	bam[c]	Sp1	bam	Symptoms[d]
Aegilops ovata L.	A	0/42	32/47	0/105	0/117	–
A. triuncialis L.	A	0/21	0/21	0/40	0/50	–
A. ventricosa[1] Tauscha	A	21/21	20/21	37/42	49/50	mo
A. ventricosa[2] Tauscha	A	0/21	0/21	0/41	0/50	–
Avena barbata Lk.	A	0/21	8/20	0/21	0/21	–
A. longiglumis Durieu	A	–	–	0/21	0/21	–
A. fatua L.	A	0/21	0/21	0/21	0/21	–
A. sterilis L.	A	0/21	0/21	0/21	0/21	–
A. sativa L. cv. SALADIN	A	0/60	0/42	0/60	0/62	–
Bromus alopecurus Poiret	A	5/21	8/24	8/21	7/24	mM
B. diandrus Roth	A	0/21	1/21	0/21	14/43	–
B. fasciculatus C. Presl.	A	0/21	1/21	0/21	3/30	–
B. rubens L.	A	14/21	20/21	20/21	19/21	mo
B. squarrosus L.	A	0/21	0/21	0/21	0/21	–
B. sterilis L.	A	0/21	1/21	0/21	4/21	–
B. tectorum L.	A	–	–	0/21	17/21	–
Dactylis glomerata L.	P	0/21	0/21	0/21	0/21	–
Digitaria sanguinalis (L.) Scop.	A	21/24		24/24		M
Echinaria capitata (L.) Desf.	A	0/21	11/30	0/21	4/27	–
Echinochloa crus-galli (L.) Beauv.	A	3/21		5/20		M
Elymus caninus (L.) L.	P	0/21	0/15	0/21	0/15	–
E. curvifolius (Lange) Melderis	P	0/21	0/15	0/21	0/15	–
E. elongatus (Host) Runemark	P	0/21	0/15	0/21	0/15	–
Hordeum murinum subsp. *leporium* L.	A	0/21	0/20	0/21	0/20	–
H. murinum subsp. *murinum* L.	A	0/21	0/20	0/21	0/20	–
H. vulgare L. cv. DOBLA	A	0/21	0/20	0/21	0/20	–
Leptochloa dubia (N.B.K.) Ness	A	14/36		15/36		M
Lolium rigidum Gaud.	A	0/20	14/14	0/20	14/14	–
Panicum capilare L.	A	20/21		20/20		M
Paspalum dilatatum Poiret	P	13/17		14/17		M
Phalaris canariensis L.	A	39/40	26/26	38/42	21/26	mM
Phleum phleoides (L.) Karsten	P	0/17	0/21	0/16	0/21	–
Setaria verticillata (L.) Beauv.	A	17/20		14/17		M
Triticum aestivum (L.) cv. ANZA	A	0/21	0/20	0/21	0/21	–
Zea mays L.						
cv. AD-640	A	45/57		43/57		M
cv. AE-703	A	26/32		42/67		M
cv. FUTURO	A	40/45		48/56		M
cv. M-770	A	46/50		47/49		M
cv. MOLTO	A	54/56		54/57		M
cv. P-3183	A	52/59		51/59		M
cv. XL-72	A	42/56		48/56		M

[a] Abbreviations: P = perennial species, A = annual species.
[b] Number of symptomatic plants/total number of plants inoculated. –: no tested.
[c] Number of symptomatic plants/ total number of plants inoculated in back assays to G-4507 maize (bam).
[d] M = mosaic; m = mild; mo = mottle;
[1] and [2] mean different source of this species.

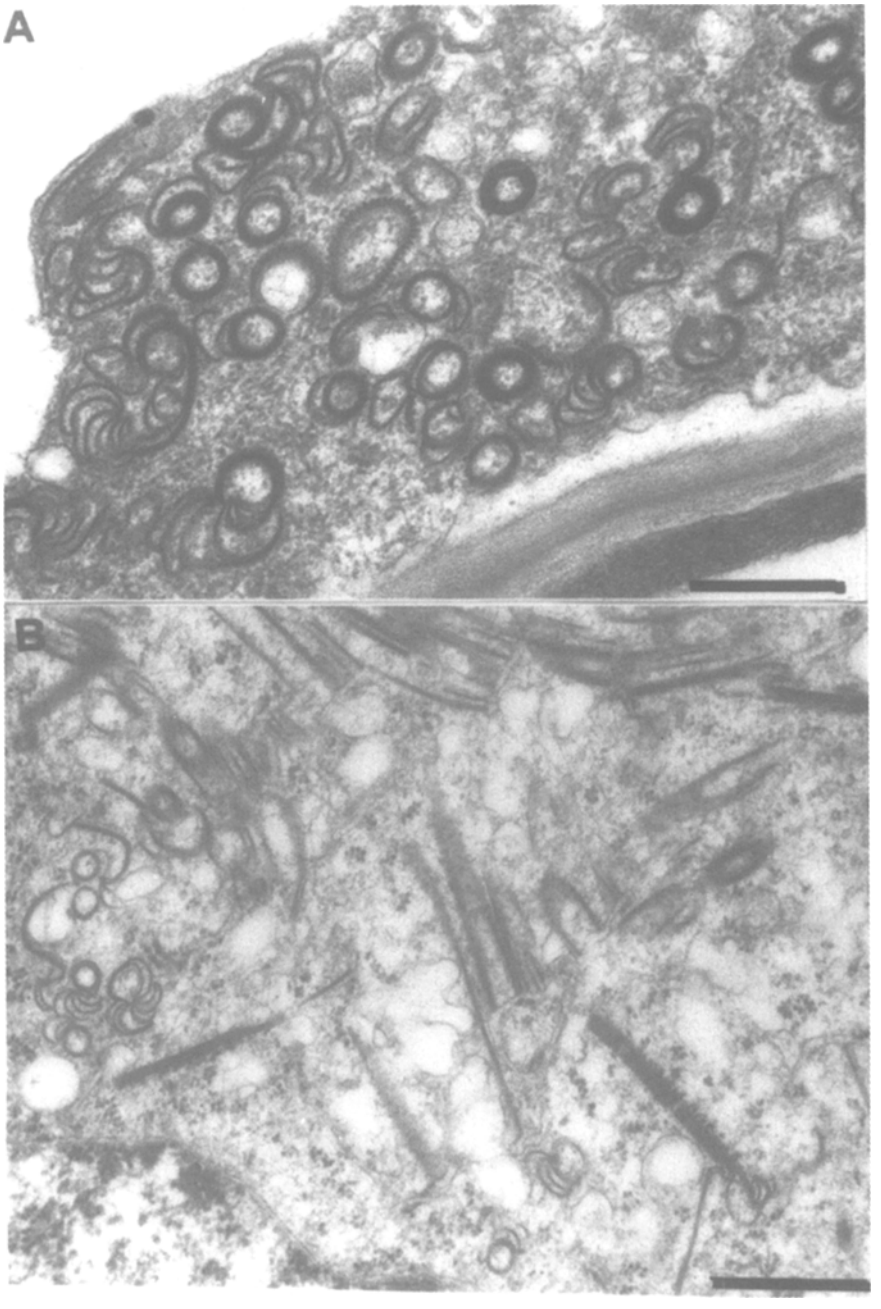

Figure 1. Cylindrical inclusions induced by maize dwarf mosaic virus (MDMV). (A) Pinwheels, scrolls and short curved laminated aggregates induced by MDMV-Sp isolate. (B) Pinwheels, scrolls, short curved laminated aggregates and laminated aggregates induced by MDMV-Sp1 isolate. Bars: 500nm.

Neither virus isolate produced specific inclusions apart from cylindrical inclusions.

Discussion

Results obtained in this study with sorghum cultivars which can differentiate among four viruses (for a review, see Shukla et al. (1992)) have, in general,

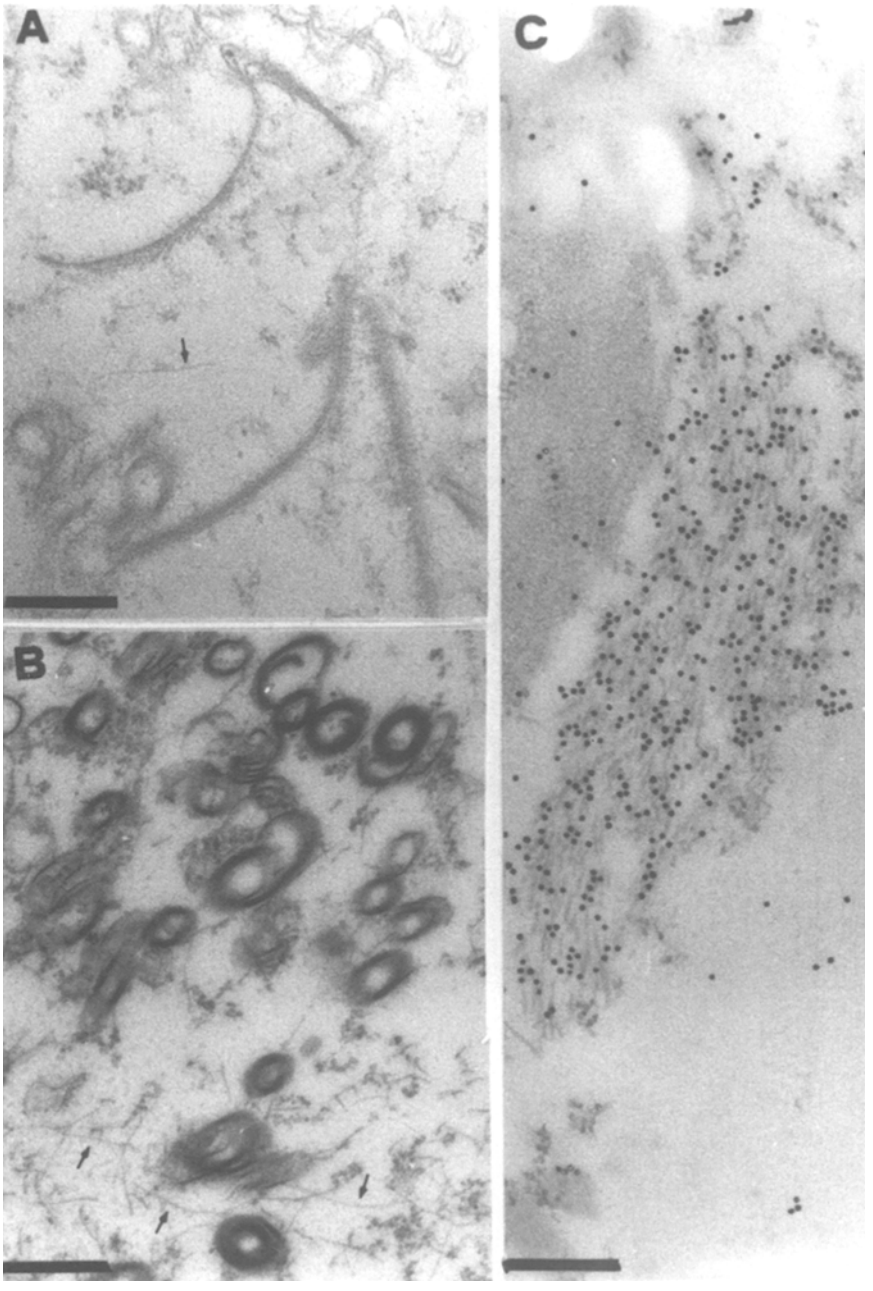

Figure 2. Cylindrical inclusions and virus particles scattered and in bundles in the cytoplasm of mesophyl cells infected with maize dwarf mosaic virus (MDMV). (A) Pinwheels, laminated aggregates and individual virus particles (arrow) in cold embedded section of tissue infected by MDMV-Sp1. (B) Pinwheels, scrolls, short curved laminated aggregates and scattered virus particles (arrows) in normal embedded section of tissue infected by MDMV-Sp1. (C) Bundles of virus particles immunogold labelled with MDMV-Sp1 antiserum in a section of tissue infected by MDMV-Sp1. Bars: 500nm.

corroborated those in the literature (Tosic et al., 1990; Persley et al., 1985), with the exception of the symptomless reaction induced by isolate MDMV-Sp on cv. TX2786 of sorghum. This sorghum cultivar is infected by strains of johnsongrass mosaic virus (IGMV), MDMV and one strain of sugarcane mosaic virus (SCMV) but not by strains of sorghum mosaic virus (SrMV) (Tosic et al., 1990). The symptoms induced

Table 3. Aphid transmission of maize dwarf mosaic virus isolates MDMV-Sp and MDMV-Sp1 and logistic regression analysis

Species	Virus isolates		Median RT[y]
	MDMV-Sp	MDMV-Sp1	
Schizaphis graminum (Rondani)	37/81[x]	40/83	0.88 a[z]
Rhopalosiphum maidis (Fitch)	20/58	21/57	0.55 a
Rhopalosiphum padi (L.)	84/370	85/379	0.29 b
Sitobion avenae (Fabrius)	5/85	4/50	0.09 c

[x] Number of symptomatic plants/total number of plants inoculated.
[y] Median relative transmission = $e^{(meanLnRT)}$.
[z] Values followed by the same letter are not significant different at $p \leq 0.05$.

by other isolates of MDMV are mosaic and systemic necrosis (Tosic et al., 1990; Persley et al., 1985). The symptomless reaction induced on cv. TX2786 by isolate MDMV-Sp may indicate that this cultivar is not capable of differentiating among MDMV, JGMV, SCMV and SrMV.

There is litle information about susceptibility of *Aegilops* species to MDMV. Tosic and Ford (1972) documented a low susceptibility of *A. cylindrica* to a single isolate from the USA. In our study *A. ventricosa* from different regions of Spain showed variable responses to the two isolates. One source of this species was infected by both isolates and the other was not infected by either of them. This may be due to population variability of *A. ventricosa*. *A. ovata* was a host of MDMV-Sp, but not of MDMV-Sp1.

Tosic et al. (1990) reported that MDMV does infect *Avena* after testing a single cultivar of this genus. Gáborbányi and Duons (1991) reported that one isolate of MDMV infected *Avena sativa* and our study indicated that *A. barbata* was a host of MDMV-Sp but not of MDMV-Sp1. Further tests with other species of this genus are needed to thoroughly understand its susceptibility to MDMV.

A common host of MDMV isolates from the Mediterranean Basin is *Bromus rubens* (Kerlan et al., 1974; Antignus et al., 1987), and our study confirmed this grass as a common host of MDMV isolates from Spain. In contrast, this is not a host of MDMV isolates from the USA (Tosic and Ford, 1972). *Bromus squarrosus* which is a host of MDMV isolates from the USA (Rosenkranz, 1987), is not susceptible to MDMV isolates from Spain. The susceptibility of *B. tectorum* to infection by isolates of MDMV from the USA (Tosic and Ford, 1972; Rosenkranz, 1983), from Hungary (Gáborbányi and Duons, 1991) and from France (Kerlan et al. 1974) has been tested; only the French isolate did not infect this grass. Species of the *Bromus* genus, along with *Echinaria capitata* and *Lolium rigidum* could be important over-wintering hosts, together with *Sorghum halepense* and *Paspalum dilatatum*, and could serve as reservoirs of MDMV, playing a significant role in the epidemiology of MDMV in Spain.

The species of aphids studied here were also tested for transmission of MDMV by other researchers. The high efficiency of *S. graminum* in transmitting MDMV has been reported previously (Louie and Knoke, 1975). We found low transmission efficiency in the case of *S. avenae* which could explain why this aphid does not transmit strains D and F of MDMV (Louie and Knoke, 1975) nor an isolate from France (Kerlan et al., 1974). Thongmeearkom et al. (1976) reported that *Rhopalosiphum padi* was a more efficient vector of MDMV than *R. maidis*. In this study rates of transmission of *R. padi* were lower than *R. maidis* and this aphid was as efficient a vector of MDMV as *S. graminum*. Studies of the presence of aphids on maize in northeastern Spain in the period 1983–1993 showed that the most abundant species of aphids in spring were *S. avenae* (36%) and *R. padi* (17%); *R. maidis* and *S. graminum* were present at less than 1% in the same period (Pons et al., 1989; Pons et al., 1994). Although MDMV-Sp isolates were transmitted less efficiently by *R. padi* and *S. avenae*, these species are probably the most important in spreading MDMV in the field.

Lesemann et al. (1992) found a relative uniformity in the morphology of cylindrical inclusions (CI) induced by 5 isolates of MDMV. All 5 produced pinwheels and scrolls, and, possibly, short curved laminated aggregates. One isolate from the USA induced another type of inclusions, needle-like. This type was first described by Krass and Ford (1969). Those authors did not detect any differences in the

morphology of CIs among MDMV-A, MDMV-B and SCMV-H, all of them producing pinwheels, scroll and needle-like inclusions. In contrast, Lesemann et al. (1992) showed that MDMV-B produced scrolls and laminated aggregates. The results obtained in our study confirmed that MDMV isolates produced short curved laminated aggregates. Isolate MDMV-Sp1 produced, in addition, aggregate laminates, and this type could be observed more clearly when samples were cold embedded. This could indicate that laminated aggregates are unstable (Langenberg and Schroeder, 1973). Given that isolate MDMV-Sp1 induced the four types of CI described in potyviruses (Edwarson and Ko, 1984), and that it induced similar reactions in sorghum cultivars to other isolates of MDMV from the USA and from Europe, it is clear that the morphology of CIs must be used in combination with other tests.

Our results indicated that the isolates of MDMV in this study are not transmitted through seed. However, since the rate of seed transmission is lower than 0.2% (Hill et al., 1974) or 0.4% (Shepherd and Holdeman 1965), the number of seeds assayed would have been insufficient to detect transmission. Rates of seed transmission have been reported to be as low as 0.006% (Mikel et al., (1984) or 0.007% (Williams et al., 1968)) or, indeed non existent (Panayotou 1981).

This work illustrates biological properties of MDMV isolates from the same area, one of them characterised at the molecular level, and the importance of host range in detecting variability among isolates or even between strains. Further studies at the molecular level will help to examine the causes of isolate variability.

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