Use of a Monoclonal Antibody to Detect the Stolbur Mycoplasmalike Organism in Plants and Insects and to Identify a Vector in France

A. FOS, J. L. DANET, L. ZREIK, M. GARNIER, and J. M. BOVE, Laboratoire de Biologie Cellulaire et Moléculaire, Institut National de la Recherche Agronomique et Université de Bordeaux II, Domaine de la Grande Ferrade, B.P. 81-33883 Villenave d'Ornon, France

ABSTRACT

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A monoclonal antibody (MA 2A10), specific for the mycoplasmalike organism (MLO) associated with tomato stolbur, was used to detect the MLO in plants and insects by double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) and/or immunofluorescence. All solanaceous plants showing stolbur symptoms reacted with the monoclonal antibody; some nonsolanaceous plants, such as celery, strawberry, bindweed, and periwinkle, that were naturally infected with MLOs also reacted with MA 2A10. Eleven hopper species tested positive by DAS-ELISA with MA 2A10. One of these, *Hyalesthes obsoletus*, reacted frequently and produced high ELISA values; this species transmitted the MLO to periwinkle, tomato, eggplant, and tobacco plants in experimental studies.

Stolbur, also called big bud, is an important worldwide mycoplasmalike (MLO) disease of tomatoes (*Lycopersicon esculentum* Mill.) and other solanaceous plants (14). It is found in Europe, the Middle East, India, and Africa as well as in the United States, China, and Australia. The symptoms of stolbur are characteristic and affect floral parts of the plant in particular (6). In 1987, we produced for the first time a monoclonal antibody (MA) specific for the tomato stolbur MLO (7). Using immunofluorescence (IF) and double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA), we showed that MA 2A10 recognized all stolbur isolates whether or not they induced virescence in periwinkle flowers (7). We also demonstrated that the MLOs present in symptomatic eggplant (*Solanum melongena* L.) and bindweed (*Convolvulus arvensis* L.) reacted with MA 2A10. These results confirmed that bindweed, a perennial plant, is a reservoir of the stolbur MLO, as was suspected by Savulescu and Ploaie in Czechoslovakia (22) and by Marchoux et al in France (12).

The role of insects in the propagation of the disease was investigated as early as 1945 (23), and several planthopper species were suspected to be involved in the transmission of stolbur MLO. The cixiid *Hyalesthes obsoletus* Signoret was thought to be the vector in Russia, Yugoslavia, Bulgaria, Romania, and Czechoslovakia (2,9,18,21,22). In Czechoslovakia, *Aphrodes bicinctus, Euscelis plebejus*, and several *Macrosteles* species were also reported to be possible vectors of the disease (3,19,20,24), whereas *Orosius argentatus* was suspected as a vector in Australia (8) and in India. In France, no insect vector of stolbur MLO has been clearly identified so far. Marchoux et al (13) and Moreau and Leclant (17) could not transmit the disease with *H. obsoletus*, and only low populations of this insect were associated with diseased fields. However, the role of *H. obsoletus* in stolbur transmission could not be specifically excluded.

In this paper we report that *H. obsoletus* is a vector of tomato stolbur in southern France and that other leafhopper species carry the MLO and may be capable of transmitting it. We also report the occurrence of the tomato stolbur MLO in symptomatic solanaceous plants other than tomato and in some nonsolanaceous plant species.

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MATERIALS AND METHODS

Plant material. All healthy or MLO-infected periwinkle (*Catharanthus roseus* (L.) G. Don) plants were grown in a greenhouse at 25 C during the day and 20 C at night.

The initial periwinkle plant infected with tomato stolbur MLO was obtained in 1972 from J. Giannotti (INRA, Saint-Christol-les-Alès, France). The strain has since been maintained in periwinkle plants by graft-inoculation. The periwinkle plant infected with the stolbur strain from Yugoslavia (original strain was from pepper), as well as those infected with apple proliferation, were obtained from E. Seemuller (Biologische Bundensanstalt, Heidelberg, Germany). Periwinkle plants infected with *Spiroplasma citri* were obtained from M. J. Daniels (John Innes Institute, Norwich, England) in 1976; the spiroplasma was transmitted by the leafhopper *Euscelis plebejus* (Fall) injected with a culture of *S. citri* from Israel. Periwinkle plants infected with the citrus greening bacteriumlike organism (BLO) or with the MLO of witches'-broom disease of lime were obtained by dodder transmission of the respective organisms from infected sweet orange (greening BLO) and lime (witches'-broom MLO) seedlings. Periwinkle plants infected with aster yellows were obtained from R. F. Whitcomb (USDA, Beltsville, Maryland, USA). Those infected with clover phyllody, cabbage chloranthy, or apricot chlorotic leafroll were also obtained from J. Giannotti. Periwinkle plants infected with hydrangea phyllody or gladiolus phyllody were obtained from G. T. N. De Leeuw (Baarn, Netherlands). Periwinkles infected with lavandin decline were received from M. T. Cousin (INRA, Versailles, France).

The MLO-infected solanaceous or nonsolanaceous plants were collected in fields in southeastern France (Avignon area and Bouches-du-Rhône) and in southwestern France (Dordogne and Lot-et-Garonne).

Antibodies and serological assays. The production of MAs specific for the MLOs of stolbur and clover phyllody (MA 2A10 and MA 2H4, respectively) and the immunofluorescence assays were described previously (7).

DAS-ELISA was done as described by Clark and Adams (5) with a concentration of immunoglobulins of 10 μg/ml in carbonate buffer for coating the ELISA plates and an 800-fold dilution of the alkaline phosphatase conjugates. The plant extracts were obtained by grinding 1 g of midribs, peduncles, fruit axes, or root tissues in 2 ml of PBS buffer with a mortar and pestle. The extract was

filtered through four layers of cheesecloth, and 150 μl was placed in each well of the DAS-ELISA plate.

Insect capture and testing. Insects were captured on sticky yellow traps placed within or near stolbur-infected tomato fields or were captured with an aspirator (D-vac, Ventura, CA). The species were identified, and insects collected with the aspirator were tested in parallel for the presence of the stolbur and/or clover phyllody MLOs by DAS-ELISA with MA 2A10 and MA 2H4, respectively. One to 10 insects of a given species were ground in 300 μl of PBS buffer with a glass homogenizer, and 150 μl of the homogenate was used in each well of the DAS-ELISA plates.

Experimental transmissions. *H. obsoletus* insects captured with the aspirator were placed singly or in groups of 12 on healthy periwinkle, tomato, tobacco, eggplant, pepper, or celery plants until the insects died. Immediately after their death, they were collected and tested by DAS-ELISA for the presence of the stolbur MLO, as described above.

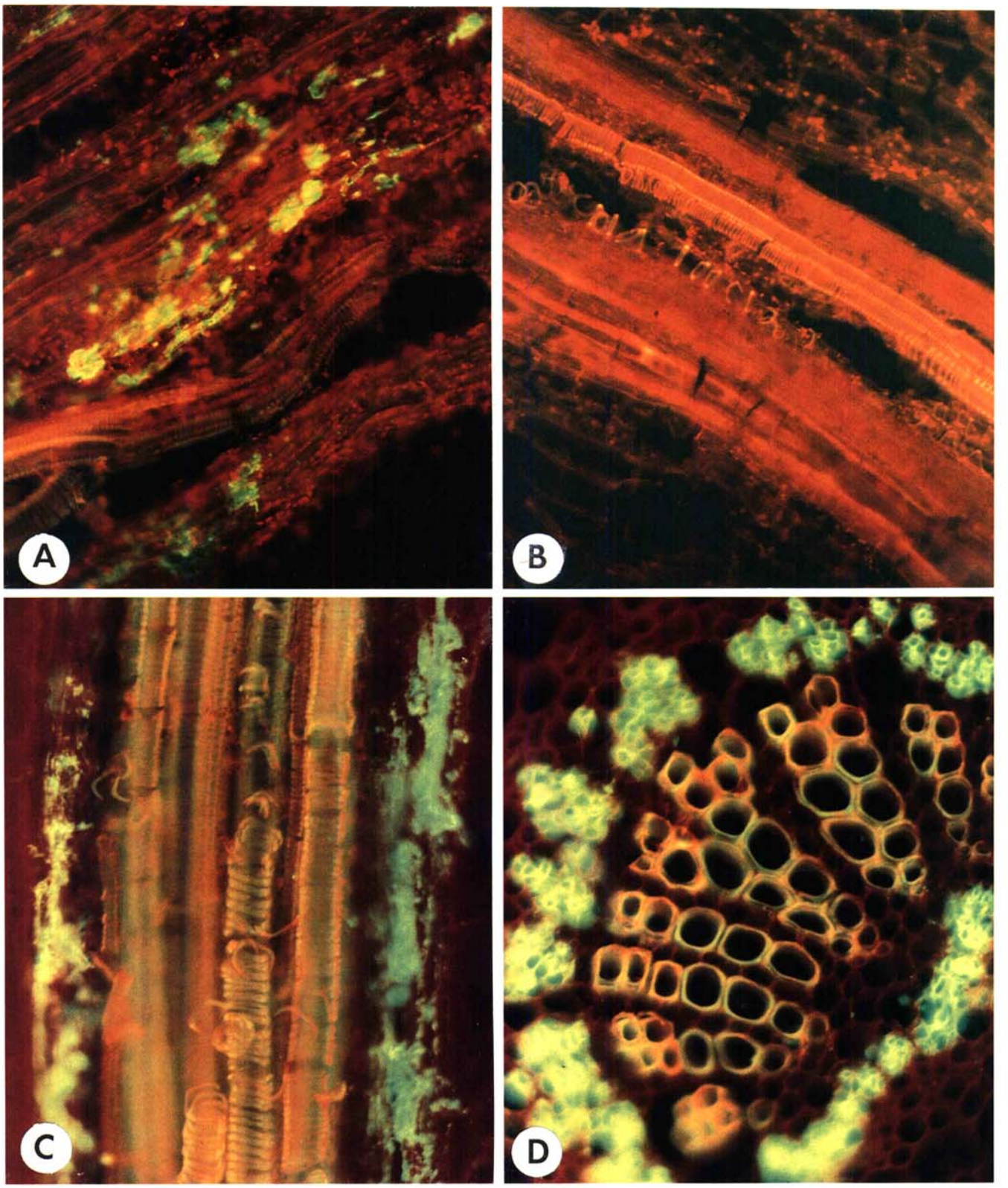

Fig. 1. Immunofluorescence on longitudinal sections of leaf midribs from **(A)** stolbur-infected tomato, **(B)** healthy tomato, and **(C)** stolbur-infected tobacco with monoclonal antibody 2A10; **(D)** transverse section of leaf midrib from stolbur-infected tobacco. (×1,250)

The plants were maintained in the greenhouse for 3 mo. Symptoms were recorded visually and appeared within 3–4 wk after insect inoculation. The symptomatic and nonsymptomatic plants were tested for the presence of stolbur MLO by IF and DAS-ELISA.

RESULTS

Specificity of MA 2A10 for stolbur MLO. The ability of MA 2A10 to specifically detect the stolbur MLO has been reported (7). These data as well as more recent studies have shown that IF and DAS-ELISA with MA 2A10 gave positive reactions, whether the stolbur strain was from southwestern or southeastern France or from Yugoslavia. A positive reaction was also observed with periwinkle plants dodder-infected from lavandin (*Lavandula officinalis* × *L. latifolia*) plants affected by decline in southeastern France. Negative reactions were obtained with leaf midribs of healthy periwinkle plants or periwinkle plants infected with one of the following agents: *Spiroplasma citri*, the BLO associated with citrus greening disease, or the MLO of apple proliferation, clover phyllody, aster yellows, cabbage chloranthy, witches'-broom disease of lime, hydrangea phyllody, gladiolus phyllody, or apricot chlorotic leafroll.

Detection of stolbur MLO in plants. The presence of stolbur MLO in naturally infected field-grown plants as well as in experimentally infected periwinkle plants was investigated by IF and DAS-ELISA with MA 2A10. All cultivated solanaceous plants tested (tomato, pepper, eggplant, and tobacco) showing stolburlike symptoms, as well as two wild solanaceous plants (*Solanum dulcamara* L. and *Lycopersicon hirsutum* Humb. & Bonpl.), gave positive IF reactions regardless of the plant organ used. Leaf midribs of infected tomato plants showed a positive IF (Fig. 1A) whereas leaf midribs from healthy tomato plants showed no fluorescence (Fig. 1B). Plant tissues with a positive IF did not necessarily yield a positive DAS-ELISA (Table 1). Whereas all tomato organs tested reacted positively in DAS-ELISA, only roots of pepper and fruit axes of eggplants were positive in DAS-ELISA. None of the tobacco tissues used reacted positively in DAS-ELISA, despite a strong IF reaction (Fig. 1C and D). Leaf midribs of the wild solanaceous species were positive in both DAS-ELISA and IF (Table 1). Symptomatic, field-infected nonsolanaceous plants (periwinkle, bindweed, celery, and strawberry) also gave positive reactions with MA 2A10 (Table 2).

Detection of stolbur MLO in insects. Planthoppers, froghoppers, treehoppers, and leafhoppers were collected in southeastern and southwestern France; some species were captured in only one location (Table 3). All insects were tested singly or in groups of five to 10 with MA 2A10 and MA 2H4.

The species that gave a positive DAS-ELISA with stolbur-specific MA 2A10 are listed in Table 4; all except *Macrosteles* sp. had negative reactions to MA 2H4. Among the planthoppers, both *H. obsoletus* and *Laodelphax striatellus* gave positive assays, but only one *L. striatellus* tested positive, despite the high number of insects used; also, the OD was very low. *H. obsoletus*, however, gave highly positive DAS-ELISA reactions. Of 54 *H. obsoletus* insects captured in southwestern France and 56 captured in southeastern France and tested individually, 12 (22%) from the first location and 22 (39%) from the second reacted positively with MA 2A10; most values were higher than 1.5. During 1988 and 1989, *H. obsoletus* was difficult to find. Recently, however, we discovered that high numbers of this insect were present on bindweed but only in specific sites, such as farm roads, where soil had not been cultivated. For instance, of 181 *H. obsoletus* individuals captured on bindweed at a certain location on 6 June and 3, 17, and 23 July, 44 (24.5%) gave a positive DAS-ELISA. The other insects giving good ODs in DAS-ELISA were *Macrosteles* sp., *Balclutha* sp., and *Zyginidia scutellaris*, but the number of positive insects was low. *Macrosteles* sp. was the only one that gave a positive DAS-ELISA with MA 2H4.

Experimental transmission of tomato stolbur MLO. Table 5 summarizes the results of experimental transmissions with 23 insects to various receiver plants of the tomato stolbur MLO using *H. obsoletus* captured in July 1990 and July 1991 on bindweed growing in stolbur-affected areas. Each insect was caged on a young plant until it died, then was tested for the presence of the stolbur MLO by DAS-ELISA. Of the 23 insects, eight were not infected by the stolbur MLO. One insect survived for 5 days on a periwinkle plant and was able to transmit the MLO to the plant, as manifest by stolbur symptoms (virescent flowers); as expected, the DAS-ELISA reaction was highly positive (OD >2). Nine of the 12 insects tested on tomato plants were positive by DAS-ELISA, and seven of these transmitted the MLO to the

Table 1. Detection of the tomato stolbur MLO in field-collected solanaceous plants by means of DAS-ELISA and immunofluorescence in phloem tissue

Plant	Symptoms	Part tested	ELISA (av. OD at 405 nm)	Immunofluorescence
Tomato	None	Leaf midribs	0.018	No
	Stolbur	Leaf midribs	0.319	Yes
		Fruit axis	0.525	Yes
		Roots	1.564	Yes
Pepper	None	Leaf midribs	0.015	No
	Stolbur	Leaf midribs	0.043	Yes
		Fruit axis	0.002	Yes
		Roots	0.839	Yes
Eggplant	None	Leaf midribs	0.022	No
	Stolbur	Leaf midribs	0.040	Yes
		Fruit axis	0.121	Yes
		Roots	0.011	Yes
Tobacco	None	Leaf midribs	0.010	No
	Stolbur	Leaf midribs	0.005	Yes
		Flower peduncles	0.040	Yes
		Roots	0.060	Yes
Solanum dulcamara	None	Leaf midribs	0.010	No
	Proliferation	Leaf midribs	0.337	Yes
Lycopersicon hirsutum	None	Leaf midribs	0.021	No
	Small leaves	Leaf midribs	>2	Yes

Table 2. Detection of the tomato stolbur MLO in field-collected nonsolanaceous plants by means of DAS-ELISA and immunofluorescence in phloem tissue

Plant	Symptoms	Part tested	ELISA (av. OD at 405 nm)	Immunofluorescence
Periwinkle	None	Leaf midribs	0.015	No
	Small flowers, with or without virescence	Leaf midribs	>2	Yes
Bindweed	None	Leaf midribs	0.011	No
	Witches'-broom	Leaf midribs	0.288	Yes
		Roots	0.005	Yes
Celery	None	Leaf midribs	0.023	No
	Porcelain disease	Leaf midribs	0.632	Yes
Strawberry	None	Leaf midribs	Not done	No
	Yellow, stunted	Leaf midribs	Not done	Yes

plants. Three insects placed on tobacco plants and two insects placed on eggplants also transmitted the stolbur MLO to the plants. The presence of stolbur MLO in the symptomatic insect-inoculated periwinkle, tomato, eggplant, and tobacco plants was confirmed by DAS-ELISA and IF (*data not shown*). The asymptomatic plants were also tested and gave negative results for both IF and DAS-ELISA. Another successful transmission of the stolbur MLO to periwinkle was obtained with 12 insects put simultaneously on a single plant; the insects survived for as long as 3 days, but only two carried the MLO and gave DAS-ELISA readings with ODs above 2.

DISCUSSION

Stolbur disease has been studied for many years because it produces important losses in Solanaceae cultures. However, studies had to rely exclusively on plant symptoms because no specific reagents for the detection of stolbur MLO were available. We have used for the first time a monoclonal antibody (MA 2A10) that is specific for the stolbur MLO to investigate the host range as well as the transmission of the MLO. We have shown that IF is the best technique to detect the stolbur MLO in plants, as it is not dependent on the organ or plant species used. DAS-ELISA was found to be a reliable technique for the detection of stolbur MLO in insects; high OD readings were obtained with a single insect, and no nonspecific reactions were observed. The positive reaction with MA 2H4 obtained with *Macrosteles* sp. is not surprising, as several species of this genus have been reported to be vectors of the clover phyllody MLO (20). DAS-ELISA can also be used with plants, provided the technique is first evaluated in comparison with IF to determine whether ELISA inhibitors are present in the plant tissue to be examined.

Many previously described strains of stolbur (C, M, SM, P, Ma, and para-stolbur) were distinguished by the symptoms they produced in various graft-inoculated solanaceous plants and in periwinkle plants infected by dodder transmission (1,11,16). Unfortunately, these strains have since been lost, and only strains infecting periwinkle (with or without virescence) are now available, as well as stolbur strains from different geographic origins or from different solanaceous plants. All plants showing stolbur symptoms reacted with MA

Table 3. Hoppers captured in southern France on sticky yellow traps or with an aspirator during 1988–1990

Type	Family Subfamily	Scientific name
Planthoppers	Cixiidae	*Tachycixius pilosus* (Olivier 1791)
		Oliarus sp. Stål 1862
		Hyalesthes obsoletus Signoret 1865
	Delphacidae	*Laodelphax striatellus* (Fallén 1826)
		Delphacidae sp. Leach 1815[a]
	Dictyopharidae	*Dictyophara europeae* (Linnaeus 1767)[b]
Froghoppers	Cercopidae	*Philaenus spumarius* (Linnaeus 1758)
		Cercopis sanguinolenta (Scopolli 1763)[b]
Treehoppers	Membracidae	*Ceresa bubalus* (Fabricius 1794)[b]
Leafhoppers	Cicadellidae	
	Macropsinae	*Macropsis* sp. Lewis 1834
	Agalliinae	*Agallia* sp. Curtis 1833
		Austroagallia sp. Evans 1935[a]
	Idiocerinae	*Idiocerus* sp. Lewis 1834
	Iassinae	*Iassus lanio* (Linnaeus 1761)
	Aphrodinae	*Aphrodes* sp. Curtis 1833
	Typhlocybinae	*Zyginidia scutellaris* (H.S. 1838)
		Empoasca sp. Walsh 1862
		Erythroneura flammigera Fitch 1851[b]
		Eupterix aurata (Linnaeus 1758)[b]
	Deltocephalinae	*Aconurella prolixa* (Lethierry, 1885)[a]
		Allygus sp. Fieber 1875
		Balclutha sp. Kirkaldy 1900[b]
		Cicadella viridis (Linnaeus 1758)[b]
		Deltocephalus publicaris (Fallén 1806)[a]
		Elymana sulphurella (Zetterstedt 1828)[a]
		Euscelis sp. Brullé 1832
		Euscelidius sp. Ribaut 1942[b]
		Exitianus sp. Stål 1855[b]
		Fieberiella florii (Stål 1864)
		Grypotes staurus Ivanoff 1885[a]
		Macrosteles sp. Fieber 1866
		Mocydia crocea (H.S. 1837)[b]
		Neoaliturus fenestratus (H.S. 1834)
		N. haematoceps (Mulsan & Rey 1855)[a]
		Placotettix taernliatifrons (Kirschbaum 1868)[a]
		Psammotettix confinis (Dahlbom 1850)
		P. striatus (Linnaeus 1758)
		Recilia sp. Edwards 1862

[a]Captured only in southeastern France.
[b]Captured only in southwestern France.

Table 4. Insect species giving a positive DAS-ELISA with stolbur-specific MA 2A10 during 1988–1990

Species	No. of times present in 193 captures	No. positive/ no. tested	ELISA (OD range at 405 nm) MA 2A10	MA 2H4[a]
Hyalesthes obsoletus	37	12/31	0.140–>2	0–0.005
Laodelphax striatellus	78	1/38	0.107	0–0.012
Ceresa bubalus	18	1/6	0.257	0–0.008
Aphrodes sp.	20	2/16	0.1–0.7	0–0.008
Zyginidia scutellaris	128	9/81	0.1–0.503	0–0.023
Neoaliturus fenestratus	2	1/2	0.106	0
Balclutha sp.	29	1/23	0.497	0–0.018
Macrosteles sp.	30	3/17	0.240–0.610	0.750
Mocydia crocea	32	2/20	0.190–0.241	0
Eucelis sp.	58	1/31	0.102	0
Psammotettix sp.	74	8/60	0.170–0.250	0–0.021

[a]Specific for clover phyllody.

Table 5. Experimental transmission of the tomato stolbur MLO with 23 individual *Hyalesthes obsoletus*

Test plant	Insect survival (days)	ELISA[a] (OD at 405 nm)	Symptoms of stolbur
Periwinkle	5	>2	Yes
	5	0.024	No
Pepper	2	0.038	No
	3	0.011	No
	3	0	No
Tomato	3	0.001	No
	1	0.001	No
	1	>2	No
	1	>2	No
	1	0	No
	2	0.416	Yes
	1	>2	Yes
	3	>2	Yes
	2	>2	Yes
	2	0.974	Yes
	3	0.471	Yes
	2	0.238	Yes
Celery	5	0.004	No
Tobacco	2	>2	Yes
	2	>2	Yes
	6	0.741	Yes
Eggplant	2	0.718	Yes
	2	1.600	Yes

[a]With stolbur-specific MA 2A10.

2A10, indicating that they are all serologically related, if not identical. This observation stands in contrast to MAs specific for the aster yellows MLO, which recognized a New Jersey strain but no other eastern or western aster yellows strain in the United States (4).

Our results have shown that plant families other than the Solanaceae can be infected with the stolbur MLO. One is celery affected by porcelain disease, which was found to be transmitted by *Macrosteles divisius* (15). Strawberries showing stunting and yellowing are also infected with stolbur MLO but are rarely seen in the fields in southern France. Our results show that the MLO associated with lavandin decline is also serologically related to the stolbur MLO. Leclant (10) reported that lavandin was a host plant for *H. obsoletus*; large amounts of *H. obsoletus* larvae were found on lavandin roots in southeastern France.

Although several insect species carry the stolbur MLO, not all are vectors. To be transmitted, the MLO should multiply in the insect and reach the salivary glands. The low ODs obtained in DAS-ELISA with some insects may reflect only gut infection by the MLO. We succeeded in transmitting the MLO to periwinkle, tomato, eggplant, and tobacco with *H. obsoletus*. In spite of the relatively high proportion of *H. obsoletus* individuals found to be contaminated (25%) and the high efficiency of transmission obtained, the percentage of stolbur in tomato fields is generally around 5%. This is probably because *H. obsoletus* is rarely found in tomato fields but is captured essentially on bindweed, a perennial plant now confirmed to be a reservoir of the MLO. Indeed, we have shown that bindweed, a widely distributed weed, was often infected with the stolbur MLO in southern France, and therefore bindweed in conjunction with *H. obsoletus* is likely to play an important role in the epidemiology of the disease in southern France. The ability of other insect species to transmit the MLO may explain why the percentage of tomato plants infected with the stolbur MLO can be as high as 80% in certain years, well above the usual 5%.

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