Chapter 12

Aphid-Transmitted Viruses

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General Introduction

Four aphid-borne viruses infect beans. They are bean common mosaic virus (BCMV), bean yellow mosaic virus (BYMV), cucumber mosaic virus (CMV) and alfalfa mosaic virus (AMV). This chapter will review the geographical distribution, economic importance, host range, physical properties, purification, transmission, epidemiology, symptomatology, and control measures reported for this group of bean viruses, except AMV, which has been included in the miscellaneous group of viruses.

Bean Common Mosaic Virus

Introduction

Bean common mosaic was one of the first virus diseases reported in the world, when Iwanoski (88) observed it in the Soviet Union. Since then, this seed-borne virus has been reported in nearly every country of the world. It is economically important throughout Africa, Europe, North America and Latin America (1, 2, 4, 34, 37, 38, 39, 40, 41, 42, 43, 45, 46, 47, 48, 50, 51, 52, 54, 62, 66, 67, 68, 86, 93, 96, 97, 98, 99, 100, 110, 111, 112, 113, 114, 118, 138, 139, 146, 164, 169).

Plant infection may reach 100% in fields, and yield losses are reported to range from 35-98% (28, 31, 64, 77, 169). Hampton (77) reported that pod number per plant was reduced 50-64% and seed yield per plant was reduced 53-68%, depending upon the virus strain. Gálvez and Cárdenas (64) reported that yield losses varied from 6-98%, depending upon the cultivar and time of infection.

The host range for BCMV is more limited than that reported for BYMV, but still includes: *Phaseolus vulgaris, P. limensis, P. acutifolius* var. *latifolius, P. angularis, P. aconitifolius, P. calcaratus, P. mungo, P. coccineus, P. atropurpureus, P. radiatus, P. aureus, P. lunatus, P. polyanthus, Vigna sesquipedalis, V. sinensis, Vicia faba, Crotalaria spectabilis, Canavalia ensiformis, Lupinus alba, Nicotiana clevelandii,*

Macroptilium lathyroides, Pisum sativum, Medicago sativa, Dolichos lablab, Trifolium pratense and *Rhynchosia minima* (21, 68, 91, 92, 103, 118, 130, 137, 169). *Sesbania exaltata* and *Macroptilium atropurpureum* are reported to be symptomless hosts (103). *Chenopodium quinoa, Gomphrena globosa, Tetragonia expansa* and cultivars of *Phaseolus vulgaris* serve as local lesion indicators to various strains of BCMV (21, 123, 130, 134, 135, 141, 155, 157, 166).

BCMV was called bean virus 1 and *Marmor phaseoli* Holmes by earlier workers (169). Common names frequently used for bean common mosaic virus in Latin America include mosaico común and mosaico comum.

Symptomatology

Bean common mosaic virus may incite three types of symptoms: mosaic, systemic necrosis (black root), or local lesions, depending upon the cultivar, time of infection, strain and environmental conditions. Mosaic symptoms appear in systemically infected cultivars and may cause a mottling, curling, stunting and malformation of primary leaves (Fig. 1), especially if the primary infection occurred through contaminated seed. The trifoliate leaves express leaf curling and malformation and a mosaic of yellow and various shades of green (Fig. 2). Infected leaves may appear narrower and longer than uninfected leaves, and leaf tips curl downwards and deform the leaf (Fig. 3).

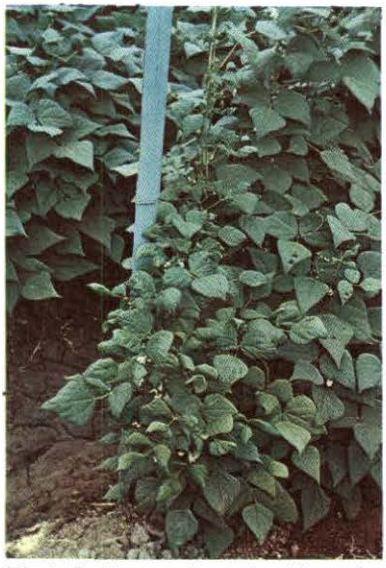

Fig. 1- Curling, stunting and malformation of leaves infected by BCMV.

Fig. 2- Leaf mosaic symptoms induced by BCMV infection.

Fig. 3- Leaf curling and malformation induced by BCMV infection.

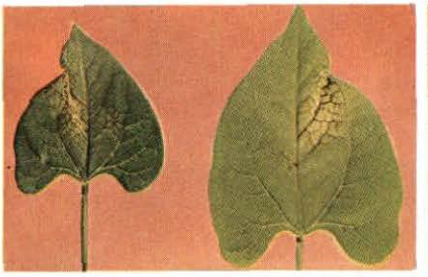

Fig. 4- Initial leaf symptoms of black root reaction induced by BCMV.

Fig. 6- Black root induced necrosis in vascular system of bean pods.

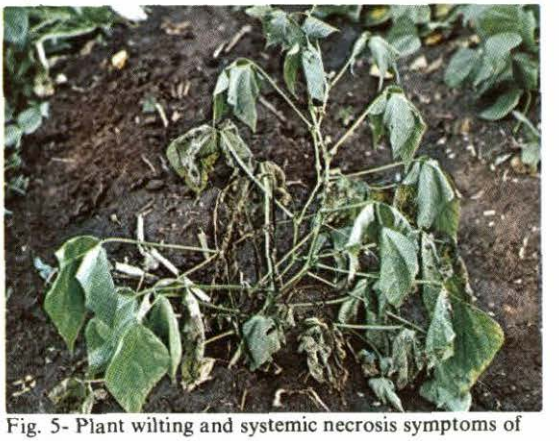

Fig. 5- Plant wilting and systemic necrosis symptoms of black root.

Systemically infected plants may have smaller pods which contain fewer seeds than pods from uninfected plants. Infected pods occasionally may be covered with small dark green spots and mature later than uninfected pods (167, 169). Symptoms of systemic mosaic are expressed more clearly at moderate temperatures between 20° - 25°C.

Systemic necrosis or black root symptoms may appear in cultivars possessing resistance (hypersensitive I gene) to systemic mosaic and which are infected by necrosis-inducing strains at low temperatures (20°C) or other strains at high temperatures (26° - 32°C). Infection may reach 40-100%, and occurs from aphids which transmit BCMV particles from susceptible beans or other hosts to resistant plants.

Symptoms initially appear as leaf lesions (Fig. 4) or in the plant apex and young trifoliates which wilt, become dull green and then black (Fig. 5). Eventually the entire plant wilts and dies. A chararacteristic necrosis (reddish-brown to black) of the vascular system may be evident in leaves, stems, roots and pods (Fig. 6) (55, 80, 81, 82, 169). Bean southern mosaic virus, the necrosis strain of bean yellow mosaic virus and a strain of bean rugose mosaic virus also are able to induce systemic necrosis symptoms (35, 38, 169).

Local lesions may appear on leaves of cultivars resistant to systemic mosaic infection. These lesions may be induced by mechanical inoculation or aphid transmission. They are evident as reddish to dark brown necrotic lesions or spots (Fig. 7) of varying size and frequency, depending upon the cultivar, strain, and environmental conditions. Cultivars which are known local lesion hosts include Great Northern U.I. 31 and 123, Pinto U.I. 111, Potomac, Stringless Green Refugee, Plentiful and Monroe (123, 130, 134, 135, 141, 155, 157, 166).

Physical Properties and Purification

BCMV particles can be observed easily with the electron microscope in crude sap or partially purified preparations. The flexible and filamentous virus particles are 730-750 nm in length and 12-15 nm in width (26, 36,109). These particles are similar in morphology to those produced by bean yellow mosaic virus, see Fig. 12. Cytoplasmic inclusions also are easily observed in preparations and may be present as filaments, lamellates and pinwheels (Fig. 8) (36, 79). Virus particles are transported throughout the phloem and can be detected in upper plant parts within 24-48 hours and in the root system within 60 hours after inoculation (58, 59, 60, 61).

Fig. 8- (above) Cytoplasmic inclusions or pinwheels (25,000 X) produced by BCMV.

Fig. 7- (left) Local lesions produced by BCMV in inoculated bean leaves.

BCMV particles are inactived in sap at 56° to 65°C, have a dilution end point of 10^{-3} to 10^{-4}, and are infective for one to four days (21, 67, 106, 137). Morales (109) determined that BCMV has a 260/280 absorbance ratio of 1.27 and a molecular weight of 32.5 to 34.4 x 10^3 daltons for the capsid protein subunit.

Other physical properties have not yet been determined for this virus, since it is difficult to purify. BCMV particles tend to aggregate and precipitate at low centrifugal forces and are difficult to separate from major plant contaminants (21, 68, 101, 103, 110, 158). Recently, Morales (109) developed a purification method which permits the isolation of BCMV with a high degree of purity and in adequate amounts to produce a specific

Fig.9- Winged aphid adults such as these may act as virus vectors.

antiserum. This purification procedure utilizes clarification with chloroform and carbon tetrachloride, precipitation with polyethylene glycol and equilibrium centrifugation in cesium chloride.

Transmission and Epidemiology

BCMV particles may be transmitted mechanically, in pollen and seed from infected plants, and by insect vectors. BCMV-infected leaves, used as inoculum, can be homogenized in water or buffers such as potassium phosphate and then manually applied to leaves of healthy susceptible plants (109). Many workers also have added abrasives such as carborundum powder to inoculum to facilitate the introduction of virus particles into plant cells (33, 169).

An inoculation efficiency of nearly 100% can be achieved in the glasshouse, while in the field the efficiency is lower due to adverse environmental factors which may affect both the viruses and the plants.

Virus particles can be transmitted in pollen grains, ovules and flowers of infected plants (58, 59, 163, 169). Seed transmission likewise can occur in susceptible cultivars of *Phaseolus vulgaris, P. acutifolius, P. coccineus, P. polyanthus, P. mungo, Macroptilium lathyroides* and *Rhynchosia minima* (91, 103, 117, 122, 125, 126, 131, 137, 147). The percentage of seed transmission may vary from 3 to 95%. It is affected by the cultivar and the time of infection, especially before flowering (5, 28, 39, 40, 41, 42, 43, 44, 49, 54, 64, 65, 98, 106, 107, 118, 140, 169). BCMV particles are reported to survive in bean seed for at least 30 years (169).

Insect vectors such as aphids (Fig. 9) can transmit BCMV effectively from infected plants to healthy plants. Reported aphid vectors include *Macrosiphum solanifolii, M. pisi, M. ambrosiae, Myzus persicae, Aphis rumicis, A. gossypii, A. medicaginis, Hyalopterus atriplicis* and

Rhopalosiphum pseudobrassicae (169). Studies have determined that aphid populations often are lower than those of other insect species in bean fields, but that the aphids are responsible for transmission of BCMV particles. The efficiency of transmission depends upon the leaf (source of inoculum) on which aphids feed (170) and the period of pre- and post-feeding by aphids (172).

Infected seeds and plants of susceptible bean cultivars and weed hosts serve as sources of initial inoculum for BCMV in the tropics and other regions (131, 132, 133). Aphids are responsible for the secondary transmission of the virus. In Colombia, studies determined that relatively high apterous aphid populations were able to incite 100% plant infection from a seed source that was only 15-25% contaminated (39, 40).

Control by Cultural Practices

Various cultural practices, such as planting date and clean seed production, have been used to reduce the incidence of BCMV infection in susceptible cultivars. Burke (29) found a correlation between planting date and virus incidence which was associated with aphid population levels. Therefore, bean plantings should be adjusted to minimize the period during which susceptible cultivars may be exposed to infection by aphids migrating from other crops to beans during the growing season.

Production of seed free from BCMV can effectively reduce the initial inoculum. However, it also may be necessary to control the aphids with insecticides to reduce transmission of BCMV from other infected bean plants or weed hosts (40, 136). No chemicals or other treatments are available to remove or destroy BCMV particles present within infected seed (39, 169).

Control by Plant Resistance

Plant resistance to bean common mosaic virus has been available for nearly 60 years since the cultivar Robust was discovered to be resistant. The resistance of Robust was later determined to be conferred by a single recessive gene (11, 34, 72, 78, 120, 134, 169). Cultivars subsequently derived with Robust resistance include Great Northern U.I. No. 1, No. 59, No. 81, No. 123, Red Mexican U.I. No. 3 and No. 34, Royal Red, Pinto U.I. No. 72, No. 78 and 111 (32, 148, 149, 169). These cultivars have been resistant to the type strain of BCMV for more than 50 years (165, 168).

Nearly 50 years ago another source of resistance was identified in Corbett Refugee. This resistance was determined to be conferred by a dominant gene (hypersensitive gene affected by black root). The majority

of cultivars developed in the United States have derived their resistance from Corbett Refugee and include Wisconsin Refugee, Idaho Refugee, Refugee U.S. No. 5 (169). This resistance has been effective for nearly 50 years (165), and Burke and Silbernagel (30) have suggested that the Corbett Refugee type of resistance be widely incorporated into commercial cultivars.

These sources of resistance also have been used to develop resistant cultivars in Latin America, such as ICA-Tui and ICA-Pijao in Colombia, Titan and Arroz 3 in Chile, Peru 257 in Peru, Tacarigua in Venezuela, and Jamapa and Sataya 425 in Mexico (34, 40, 55, 106, 107, 119, 156, 173).

Hagel *et al.* (75) have reported that certain BCMV resistant cultivars, such as Black Turtle Soup, also express tolerance to insect vectors such as aphids. Additional studies are necessary to determine the effectiveness of this type of aphid resistance and its applicability to commercial production.

Plant resistance to BCMV is affected by the nature of the gene(s) conferring resistance, variability between virus strains and environmental conditions. Various workers have investigated the relationships between different virus strains and sources of resistance (6, 7, 14, 55, 56, 57, 144). Drijfhout and co-workers have assigned 22 cultivars to 11 resistance groups, and divided the 15 known viral strains in seven pathogenicity groups. Gálvez *et al.* (65) have proposed a similar system of nomenclature (BCMV-1 to BCMV-7) to distinguish these seven basic viral groups (Table 1). The International Working Group on Legume Viruses has presented another viral strain classification.

Cultivars in resistance groups one to six do not express systemic necrosis to any viral strains but do express systemic mosaic symptoms to one or more of the viral groups. These cultivars, therefore, possess recessive alleles for the necrosis gene "I". Likewise, line IVT 7214 (resistance group 7) does not exhibit systemic mosaic or necrosis upon inoculation with any known viral strain and possesses recessive alleles for the necrosis gene. Cultivars in resistance groups eight to 10 exhibit systemic necrosis to one or more viral strains, and no systemic mosaic symptoms to any viral strain. These cultivars, therefore, possess dominant alleles for the necrosis gene. The IVT 7233 line likewise possesses dominant alleles for the necrosis gene but exhibits only local necrotic lesions.

Results from these investigations should allow breeders and pathologists to incorporate resistance gene(s) effective against the known pathogenicity spectrum and provide growers with resistant commercial cultivars adapted to the tropics and other regions of the world.

Bean Yellow Mosaic Virus

Introduction

Bean yellow mosaic virus is widely distributed throughout the world on beans and many other hosts. The virus is reported to occur in North America, Europe, East Africa, Japan (20, 86, 159, 169), and Latin American countries such as Chile (27, 35), Argentina (121), Brazil (46, 95), Uruguay (Juan Izquierdo, personal communication), and possibly northern Mexico. The distribution of BYMV in Latin America is not completely known, since it often has been confused with bean golden mosaic virus.

BYMV can infect up to 100% of the plants grown in a field as observed in the United States (169). Hampton (77) reported that BYMV could cause serious yield losses with a 33% and 41% reduction in pod number and seed yield, respectively. Little research has been conducted in Latin America to measure yield losses induced by BYMV. However, the existence of virus complexes has made it difficult to measure accurately the effect of individual viruses.

Bean yellow mosaic virus has been called Phaseolus virus 2, Gladiolus mosaic virus, pea mosaic virus, and bean virus 2 by earlier workers (169). Common names frequently used for BYMV in Latin America include mosaico amarillo, mosaico amarelo and moteado amarillo.

Bean yellow mosaic virus has a wide host range which includes *Phaseolus vulgaris, P. aureus, P. lunatus, Cajanus indicus, Cicer arietinum, Lathyrus odoratus, Lens esculenta, Melilotus alba, Cucurbita sativum, Pisum sativum, Vicia faba, V. americana, V. monantha, V. villosa, V. sativa, V. atropurpurea, Vigna sesquipedalis, Vigna sinensis, Trifolium pratense, T. incarnatum, T. hybridum, Medicago sativa, M. lupulina, Glycine max, Gladiolus* spp., *Trigonella foenumgraecum, Crotalaria spectabilis, Lupinus deusiflorus, Proboscidea jussievi, Cladrastis lutea, Robinia pseudoacacia, Freesia* sp., *Babiana* sp., *Ixis* sp., *Sparaxis* sp., *Tritonia* sp., *Nicotiana tabacum, N. sylvestris* and *N. rustica* (20, 90, 127, 128, 169, 171).

Symptomatology

Initial symptoms of BYMV systemic infection appear as small chlorotic spots one to three mm in diameter, which are often surrounded by a halo. These spots gradually enlarge and coalesce to produce a general chlorosis

Fig. 10- Chlorotic leaf symptoms caused by BYMV infection.

Fig. 11- Leaf malformation induced by BYMV infection.

on affected leaves (Fig. 10). Young leaves become brittle, glossy, concave on the upper leaf surface, and may be malformed (Fig. 11). Yellow and green mottling becomes more intense on leaves as they age. Infection causes shortened internodes, proliferation of branches and plant stunting. It also may delay maturity (169).

Systemic necrosis symptoms can be induced by certain strains of BYMV. Symptoms appear as a purplish coloration at the base of the lower leaves, which may be accompanied by veinal, stem and petiole necrosis, top necrosis at the terminal growing point, or plant death. These symptoms may resemble those induced by necrotic strains of BCMV (Black Root). Other BYMV strains are able to incite local necrotic lesions on leaves. The typical chlorotic leaf symptoms also may be evident (35, 169). Reddish-brown spots may form on infected pods, which can be malformed, depending upon the specific virus strain (169).

Physical Properties and Purification

Particles of BYMV resemble those of BCMV since they are long, flexible (Fig. 12), and measure 750 nm in length and 15 nm in width (25, 26, 161). Cytoplasmic inclusions may be spiral, ring or lamellate pinwheels which

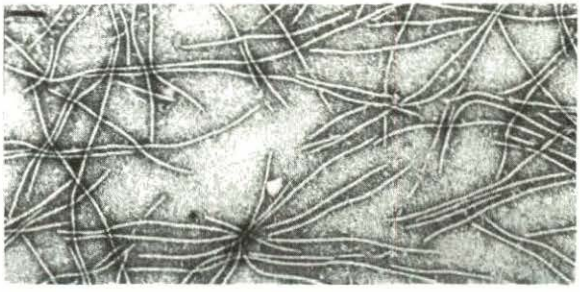

Fig. 12- Filamentous particles of BYMV.

are typical of the potyvirus group (19, 20, 27, 36, 87, 95, 153). These pinwheels are similar in morphology to those produced by bean common mosaic virus, see Fig. 8.

BYMV has a 260/280 absorbance ratio of 1.18 - 1.20 (89, 108). BYMV particles have a thermal end point between 50° to 60°C, and a dilution end point between 10^{-3} and 10^{-4}. Particles retain their infectivity for one to two days and occasionally up to seven days. These properties depend upon the virus source, host plant and experimental conditions (20, 116, 169).

Purification of BYMV was difficult in early work since particles aggregated easily and also agglutinated to plant chloroplasts. Various workers developed methods to partially purify BYMV (12, 83, 84, 162). Morales (108) developed a procedure which yields highly purified and nondenatured BYMV preparations. The purification procedure is similar to that described for BCMV. It utilizes clarification with chloroform and carbon tetrachloride, precipitation with polyethylene glycol and equilibrium centrifugation in cesium chloride. Sodium diethyldithiocarbamate (chelating agent) must be added to the extraction buffer to purify the necrotic strain of BYMV. Jones and Diachun (90) also have developed a reliable purification procedure.

BYMV has some serological similarities to BCMV but can be distinguished. BYMV also has various strains which now can be distinguished serologically (13, 14, 15, 20, 23, 24, 70, 90, 116, 169). Jones and Diachun (90) identified three BYMV subgroups within a collection of BYMV isolates obtained from infected red and white clover. These subgroups differ for serological and biological factors such as host range and symptoms. Additional work is required to establish an acceptable set of host differentials and strain classification.

Transmission and Epidemiology

BYMV particles may be easily transmitted mechanically and by insect vectors such as aphids. BYMV is not transmitted in seed of *Phaseolus vulgaris*. However, it can have a low transmission in seed of *Vicia faba* and some other legumes (20).

Aphid vectors include *Acyrthosiphon pisum, Macrosiphum euphorbiae, Myzus persicae* and *Aphis fabae* (20, 71, 150, 151, 152, 154). Aphid transmission from infected beans or other hosts is primarily responsible for natural epidemics of BYMV. Some strains of BYMV are not easily transmitted by aphids (63, 150, 154), and some BYMV strains may lose aphid transmissibility during storage or maintenance by mechanical inoculation (154).

Control

Alternate hosts of BYMV should be eliminated from bean fields and adjacent areas and as components of crop rotations. Chemical control may be utilized to reduce aphid populations present within bean fields or other host crops (74, 75, 76, 85, 132, 160, 169).

Plant resistance appears to be the most reliable control measure available (168). Resistance to specific strains is conditioned by specific plant genes such as By-2 (53, 142). Sources of resistance to the BYMV strain inducing pod malformation have been identified in various Great Northern lines such as G.N. U.I. No. 31, 59, 123 and 1140. This resistance is conferred by three recessive genes with modifiers (9, 10, 35, 73, 168). Resistance to BYMV strains and BCMV has been found in interspecific crosses between *Phaseolus vulgaris* and *P. coccineus* (8, 11, 169). Black Turtle Soup is resistant to BCMV and likewise is not a preferred host for aphids (75). Additional research is necessary to identify and incorporate sources of resistance effective against all strains of BYMV (129).

Cucumber Mosaic Virus

Introduction

Cucumber mosaic virus (CMV) is widely distributed throughout the world, including the United States, Puerto Rico, Spain, France and Brazil (16, 22, 102, 104, 105, 145, 169). The virus is not reported to be a serious or economically important disease (16, 104, 169).

Cucumber mosaic virus has been called cucumber virus 1, *Cucumis* virus 1, *Marmor cucumeris,* Spinach blight virus and tomato fein leaf virus. The common name frequently used for CMV in Latin America is virus del mosaico del pepino.

The host range of CMV includes *Phaseolus vulgaris, P. aborigeneus, P. aconitifolius, P. angularis, P. bracteatus, P. calcaratus, P. caracalla, P. coccineus, P. dumosus, P. erythroloma, P. lunatus, P. panduratus, P. phyllanthus, P. pilosus, P. polystachios, P. radiatus, Macroptilium atropurpureum, M. lathyroides, Capsicum annuum, Chenopodium album, Cucumis sativus, Nicotiana* spp., *Ocimum basilicum, Spinacia oleracea, Canavalia ensiformis, Lathyrus sativus, Pisum sativum, Vicia faba, Vigna unguiculata, Gomphrena globosa* and *Musa* spp. (22, 104, 124).

Symptomatology

Symptoms of CMV infection may consist of a mild mosaic, vein clearing, vein banding, leaf rolling, epinasty and/or apical necrosis. Symptoms may

resemble those induced by BCMV. The intensity of symptom expression may vary, depending upon the cultivar, strain and time of infection. Symptoms may become less noticeable in older tissue if infection occurred in very young plants. Pod distortion also may be evident (16, 17, 105, 124).

Physical Properties and Purification

CMV particles are isometric and may be 20-22 nm (105), 24-27 nm (104), or 30 nm (69) in diameter. The particles are present in clusters of 180 subunits which form pentameres or hexameres (69). CMV particles have a thermal end point of 70°C, a dilution end point between 10^{-4} and 10^{-5}, and are infective *in vitro* for three to six days at 23°C (105).

The virus particles have a sedimentation coefficient of 98 S, a molecular weight between 5.8 to 6.7 x 10^6 daltons, a diffusion coefficient of 1.23 at D20 x 10^{-7} cm ^{2}/sec, its isometric point at pH 4.7, and electrophoretic mobility of 8 x 10^{-5} cm^2/sec/volt in 0.1 M buffer at pH 7.0, a 260 nm absorbance of 5.0 and a 260/280 absorbance of 1.65. The virus particles contain RNA which has a molecular weight of 1 x 10^6d, protein subunits which have a molecular weight of 3.2 x 10^4d, and more than 280 amino acids (69).

Various purification procedures have been developed by workers (18, 22, 104, 115, 143). These procedures have enabled researchers to develop antisera to study CMV and its strains.

Transmission and Epidemiology

CMV particles are easily transmitted mechanically, in seed, and by insect vectors such as aphids. CMV may be transmitted mechanically from

Fig. 13- Leaf symptoms of cucumber mosaic virus in infected cucumber plants.

infected beans, tobacco, cucumbers (Fig. 13) and other hosts (16, 102, 104). Seed transmission may vary from less than 1% to 30%, depending upon the bean cultivar (16, 22, 102, 104, 124). Bos and Maat (22) reported that CMV retained its infectivity in stored bean seeds for 27 months.

More than 60 species of aphids may transmit CMV. They include *Aphis gossypii* and *Myzus persicae* (94, 104, 124). Meiners *et al.* (104) report that aphids retained infective particles of CMV for up to 40 minutes after a 10 minute accession feeding period.

Control

Control measures may include planting seed free of contamination by CMV and crop rotation to reduce the number of hosts for the virus and/or its insect vector. Chemical control may be used to reduce aphid populations in bean fields or other host crops. Cultivars may differ in their resistance. However, little research has been justified in this area since CMV is of such minor and/or currently unknown importance.

Table 1. Differentiation and grouping of BCMV strains and host resistance groups.

Host resistance group	Differential cultivar name	Pathogenicity group of the virus														
		I			II	III	IVa	IVb			Va	Vb	VIa	VI	VII	
		Westlandia NL1	Type US 1	Puerto Rico PR 1	NL 7	NL 8	Florida US 5	Western US 4	Idaho or B US 3	Colana NL 6	NY 15 US 2	Imuna NL 2	Michelite NL 3	Jolanda NL 5	Mexico US 6	Great North. NL 4
Cultivars with recessive alleles (I*I*) of the necrosis gene																
1	Dubbele Witte	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Str. Gr. Ref	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2	Redl. Gr. C	-	-	-	+	-	+	+	+	+	+t	+	+t	+	+	+
	Puregold Wax	-	-	-	+	-	+	+	+	+	+t	+	+t	+	+	+
	Imuna	-	-	-	+t	-	+	+	+	+	+t	+	+t	+	+	+
3	Redl. Gr. B	-	-	-	-	-	+	+	+	+	-	-	+	+	+	+
	Gr. North. 123	-	-	-	-	-	+	+	+	+	-	-	+t	+t	+	+
4	Sanilac	-	-	-	-	+	-	-	-	-	+	+	+	+	-	-
	Michelite 62	-	-	-	-	+	-	-	-	-	+	+	+	+	-	-
	Red Mex. 34	-	-	-	-	+	-	-	-	-	+	+	+	+	-	-
5	Pinto 114	-	-	-	-	-	-	-	-	-	+	+	+	+	-	-

6	Monroe	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
	Gr. North. 31	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
	Red. Mex. 35	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
7	IVT 7214	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cultivars with dominant alleles (II) of the necrosis gene																
8	Widusa	-	-	-	-	+n	-	±n	±n	±n	-	-	+n	+n	-	-
	Bl. Turtle S.	-	-	-	-	+n	-	±n	±n	±n	-	-	+n	+n	-	-
9a	Jubila	-	-	-	-	-	-	+n	+n	+n	-	±n	+n	+n	-	-
9b	Topcrop	-	-	-	-	-	-	±n	±n	±n	-	±n	+n	+n	-	-
	Imp. Tendergr.	-	-	-	-	-	-	±n	±n	±n	-	±n	+n	+n	-	-
10	Amanda	-	-	-	-	-	-	-	-	-	-	-	-	+n	-	-
11	IVT 7233	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

\+ Susceptible, sensitive, systemic mosaic.

+t Susceptible, tolerant, systemic symptoms questionable or very weak, virus recovered from uninoculated leaves by back-inoculation onto Dubbele Witte.

\- Resistant, no systemic symptoms, virus not recovered from uninoculated leaves by back-inoculation.

+n Susceptible, sensitive, usually all plants with systemic necrosis, not clearly dependent on temperature.

±n Susceptible or resistant, dependent on temperature, from none to all but mostly only a few plants with systemic necrosis, the number varying in repeated tests and increasing with temperature. Greenhouse mean temperature 22-26°C, day and night fluctuation at most 20-24°C in winter and 20-30°C in summer (55, 57).

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