Characteristics and Control of Viruses Infecting Peppers: A Literature Review

S. K. Green
Asian Vegetable Research and Development Center
P.O. Box 205, Taipei 10099

J. S. Kim
Agricultural Sciences Institute
Rural Development Administration
Suweon, Korea

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FOREWORD

Peppers are very important vegetables worldwide. They provide spice and color to foods while providing essential vitamins and minerals. In many poor households, peppers provide the variety needed to enhance intake of otherwise bland diets. Peppers likewise are good sources of income to small producers in many developing countries.

Results of a literature review and a survey conducted by AVRDC in 1987 revealed that pepper production in the tropics is constrained by a number of factors. Viruses were found to be the most serious disease problem in both hot and sweet peppers.

This report covers the literature on some 45 viruses, including their geographic distribution, disease syndrome, vectors, diagnoses and control.

It is the first major effort to compile information on viruses infecting peppers, and will hopefully prove to be a very useful reference material for students, extension workers and specialists working on the crop.

This volume is a collaborative effort between AVRDC and the Agricultural Sciences Institute of the Rural Development Administration in Korea.

Dong Soo Kim
Director General
Agricultural Sciences Institute
Rural Development Administration

Emil Q. Javier
Director General
AVRDC

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SUMMARY

Some 35 viruses have been reported to infect peppers (*Capsicum* spp.). Of these, more than half are transmitted by aphids. The other viruses are transmitted by nematodes, thrips, leafhoppers, whiteflies, beetles and fungi. Several are transmitted by contact and/or through the soil by mechanisms not yet understood. Most pepper viruses are distributed worldwide with the exception of chili veinal mottle virus, pepper severe mosaic virus, pepper veinal mottle virus, pepper mild mosaic virus and pepper mottle virus. These have been reported only in certain geographic areas. Virus-infected peppers generally exhibit a variety of symptoms, the most common of which are mosaic, mottle, necrosis and leaf distortion. Many of these viruses cause considerable yield losses. Various methods of control, aimed primarily at the vectors of the viruses, are reported here.

INTRODUCTION

Peppers (*Capsicum* spp.) originated in Mexico, southern Peru and Bolivia (Janick 1979; Greenleaf 1986; Pickersgill et al. 1979; Pyou et al. 1980). They are now grown worldwide under various environmental and climatic conditions, covering an area of nearly one million hectares (Pyou et al. 1980; Martelli and Quacquarelli 1983).

From an economic point of view, pepper yield is often low and variable. Virus diseases are an important factor contributing to low yields and reduced fruit quality (Alonso et al. 1989; Fujisawa et al. 1986; Gracia et al. 1968; Kang et al. 1973; Lockhart and Fischer 1974; Ong et al. 1980; Villalon 1975). One hundred percent losses of marketable fruit have been reported (Marte and Wetter 1986), and in some areas infection with viruses has rendered the growing of peppers uneconomical, causing whole fields to be abandoned prior to harvest (Greenleaf 1986; Lockhart and Fischer 1974).

Symptoms of virus infection vary greatly in expression and severity, and include mild mottle, mosaic, veinbanding, ringspots, various types of necroses, leaf discoloration, deformation and blistering and severe stunting of the whole plant. Leaves, stems and flowers, as well as fruits, may be affected (Appendix Fig. 1).

Virus identification should never be based on symptoms alone because symptoms vary with the strain of the virus, the host cultivar, the age of the host, environmental conditions and possible coinfection with other viruses (Sherwood et al. 1986). Furthermore, different viruses may cause similar symptoms, and insect damage, particularly by thrips and mites, may mimic virus symptoms. Certain herbicides, such as 2.4 D, and growth hormones may also cause reactions in the plant which resemble virus symptoms (Appendix Fig. 2). Exact identification of pepper viruses should be based on differential host plant tests, confirmed by serological tests (Marco and Cohen 1979) or vice versa, and if possible supplemented by electron microscopic characterization of the virus particle and virus-induced inclusions and by vector transmission tests.

Most pepper viruses are difficult to transmit from pepper to other hosts because of inhibitors in the pepper plant thought to be phenolic substances (Horvath and Nienhaus 1982; Fischer and Nienhaus

1973). This problem can be overcome by using additives such as sodium bisulfite or sodium diethyldithiocarbamate in the inoculum. The following buffer has been recommended by Pochard (1977) for routine inoculations of pepper viruses: 0.03 M disodium phosphate, pH 7.0, amended with 0.5% sodium bisulfite, 0.5% sodium diethyldithiocarbamate, 0.5% caffeine and 20 mg/ml activated charcoal. Passing the plant extract through a column of Sephadex G or of Controlled Pore Glass (CPG-10) (Horvath and Nienhaus 1982) has also been found useful in reducing the inhibitory effect of pepper plant extracts.

The most important and widespread virus diseases of peppers have been reviewed previously by Martelli and Quacquarelli (1983) and Conti and Marte (1983). The various diseases were discussed in terms of symptomatology, identification methods and ecology. Earlier reviews were also published by Ramakrishnan (1961) and Lovisolo and Conti (1976). Horvath (1986a,b,c) gave an overview of virus resistance in *Capsicum* species.

In this report, the literature on some 45 pepper viruses is reviewed, stressing their geographic distribution, the disease syndrome, vectors, diagnosis and control.

A general overview of pepper viruses — their morphological characteristics, vector transmission and geographic distribution — is given in Appendix Table 1. Viruses reported from Asian countries are presented in Appendix Table 2. The diagnostic host species of some common pepper viruses are listed in Appendix Table 3. Electron micrographs of the different virus groups are shown in Appendix Figures 3 and 4.

FILAMENTOUS VIRUSES

1. Potyviruses

Eight potyviruses have been reported to infect peppers: potato virus Y (PVY) (Laird et al. 1964; Gebré-Selassie et al. 1983), tobacco etch virus (TEV) (Laird et al. 1964), pepper mottle virus (PeMV) (Zitter 1972; Purcifull et al. 1975; Nelson and Zitter 1982), pepper mild mosaic virus (Ladera et al. 1982), pepper veinal mottle virus (PVMV) (Atiri and Dele 1985; Brunt and Kenten 1972; Ladipo and Roberts 1977), chili veinal mottle virus (CVMV) (Ong et al. 1979), pepper severe mosaic virus (PeSMV) (Feldman and Gracia 1977) and Peru tomato virus (PTV) (Fernandez-Northcote and Fulton 1980). Not all of these agents have been well characterized and their status as separate viruses seems to need further confirmation, e.g., pepper mild mosaic, pepper severe mosaic and Peru tomato virus.

Most of the pepper-infecting potyviruses also infect other solanaceous crops such as tomato and potato. They are transmitted in a nonpersistent (stylet-borne) manner by aphids. The green peach aphid (*Myzus persicae*) is considered to be the single most important vector, although several other aphid species such as *Aphis gossypii, Macrosiphum solanifolii, M. pisi* and *A. spiraecola* are also known to transmit these viruses (Laird and Dickson 1963; Raccah et al. 1985).

Potyviruses can be easily separated by host range and serology (Nelson and Wheeler 1978). They induce typical cylindrical (pinwheel) inclusions (Edwardson 1974) which can be recognized by electron and light microscopy (Christie and Edwardson 1977). Four distinctly different structural types of cylindrical inclusions which can be used in some cases to differentiate between individual potyviruses have been described (Edwardson 1974; Edwardson et al. 1984). The most typical types of inclusion bodies are shown in Figure 1.

The damage these viruses cause depends upon the strains involved, the host cultivars grown, and whether the viruses occur singly or in mixed infections. Insecticide application or roguing of infected plants is usually inadequate in reducing virus spread (Laird and Dickson 1963). The planting of virus-

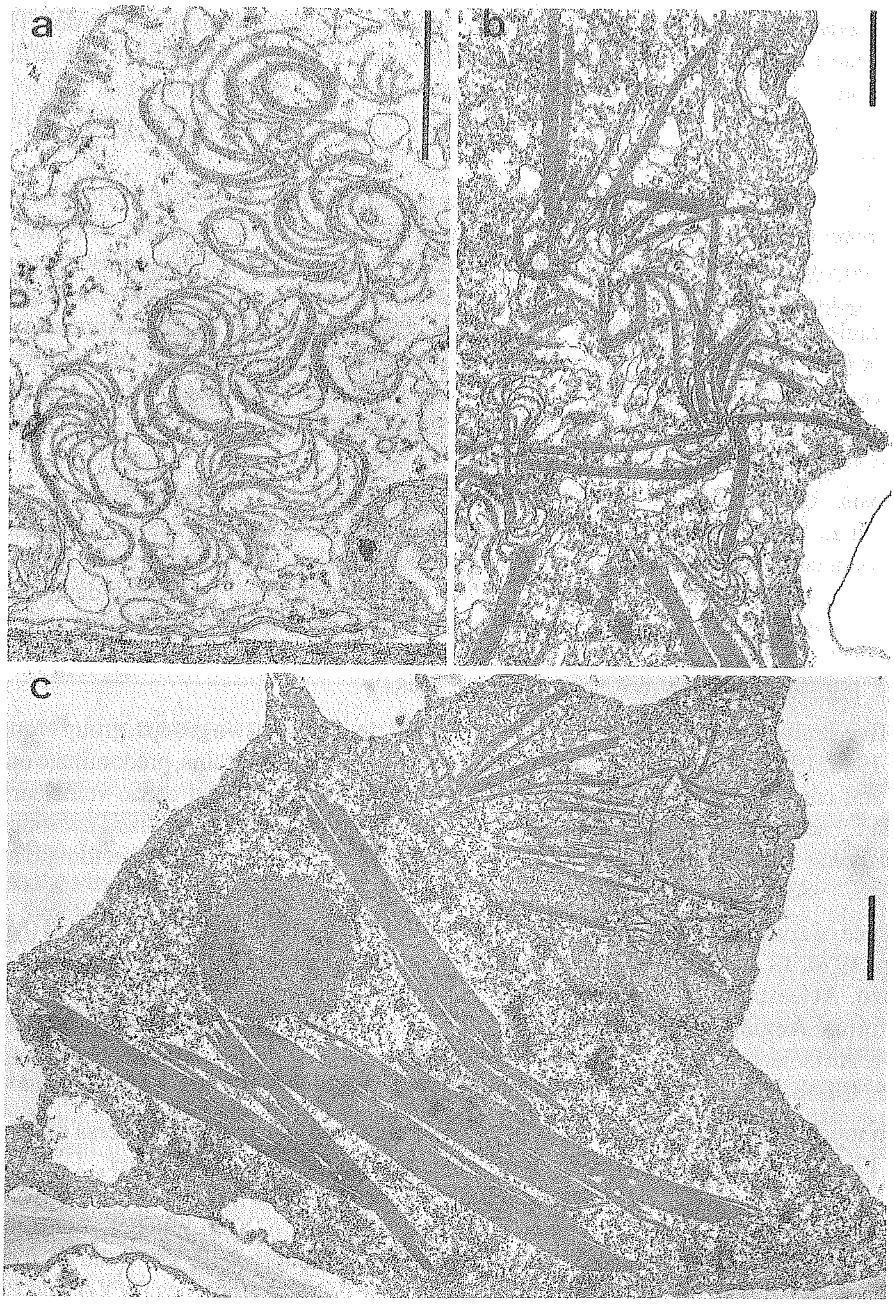


Fig. 1. Examples of characteristic cellular inclusion bodies induced by potyviruses infecting peppers, as seen in ultrathin sections of Epon-embedded tissues, (*D.E. Lesemann*)

a) Pinwheels and short curved laminated aggregates induced in the cytoplasm by potao virus Y (bar equals 500 nm)

b) Pinwheels and laminated aggregates induced in the cytoplasm by tobacco etch virus (bar equals 500 nm)

c) Nuclear inclusions induced by tobacco etch virus (bar equals 1 µm) resistant cultivars is the most promising method of control. Cultivars resistant to PeMV, TEV and certain strains of PVY have been reported (Nagai 1971, 1983; Cook 1966, 1982; Cook et al. 1976, 1977; Villalon 1981, 1983, 1986, 1987; Subramanya et al. 1983).

Potato virus Y

Potato virus Y (PVY) is the most common potyvirus infecting pepper. It occurs worldwide although it appears to be more important in warmer areas (Cook 1963; Milbrath and Cook 1971; Zitter 1972; Makkouk and Gumpf 1974, 1976; Villalon 1975, 1981; Arteaga and Gil-Ortega 1986; Nagai 1983; Mills and Abdul-Magid 1987). Disease incidence may be as high as 100% in some areas, resulting in considerable crop loss (Cook 1959; Sharma et al. 1989). Although mosaic (Appendix Fig. 1), mottle, dark green veinbanding, veinclearing and yellowing are typical symptoms of infection by PVY, other symptoms such as leaf crinkling, leaf distortion and stunted plant growth are also common, depending on the virulence of the strain and the host-pathogen interaction (Conti et al. 1982; Zitter et al. 1984; Horvath 1986; Sharma et al. 1989).

Vein necrosis, followed by top necrosis and death of the plant can also occur (Rana et al. 1971; Ragozzino et al. 1972; Pochard 1977). When plants are infected early, fruit set is reduced and fruits show pronounced mosaic patterns, making them unmarketable. The potato hybrid A6 (*Solanum demissum*) is a useful diagnostic host which reacts with necrotic local lesions on detached leaves (Bartels 1970). PVY does not normally infect *Datura stramonium* which distinguishes it from other potyviruses. The virus induces typical type IV inclusions (pinwheels and short curved laminated aggregates, Fig. 1a) according to Edwardson et al. (1984).

In Brazil, five strains are known to exist. These have been divided into two groups, group N and group W (Nagai 1968, 1983). The group W strains, also known as 'common' strains, predominate on pepper in Brazil and cause great economic losses. They also infect tomato and cause veinclearing and mottling in tobacco. Group N or necrotic strains are recognized by small localized necrotic lesions in *Nicandra physalodes* and necrotic lesions in tobacco. These strains do not infect tomato in nature (Nagai 1968, 1983). Incidence of group N infection in peppers in Brazil is rare.

The existence of common and necrotic strains of PVY is recognized throughout the world (Makkouk and Gumpf 1974, 1976; Pochard 1977), although relationships among individual strains are not well documented. At least five distinct strains (Makkouk and Gumpf 1976, 1974) were detected on pepper from California. Among these was the first naturally occurring necrotic strain on pepper to be reported in the USA. An isolate causing necrosis has also been reported to occur in southern Europe (Ragozzino et al. 1972; Gebré-Selassie, K. personal communication 1987).

It has been reported that the pepper strains of PVY do not infect potato and vice versa (de Bokx and Huttinga 1981). However, there is evidence that exceptions may exist (Zitter, T. A. personal communication 1990). Recently the pepper strains of PVY have been grouped into three pathotypes, PVY-0, PVY-1 and PVY-1-2, by reactions on *C. annuum* Bastidon, Yolo Wonder, Yolo Y, Florida VR-2 and Serrano VC (Gebré-Selassie et al. 1983) (Table 1). Pathotype PVY-0 is the most common (Gebré-Selassie et al. 1983, 1985; Arteaga and Gil-Ortega 1986). Pathotypes PVY-1 and PVY-1-2 appear predominantly in tropical and subtropical countries (Gebré-Selassie et al. 1985). PVY-resistant cultivars such as Delray Bell, Florida VR-2 and Florida VR-4 (resistant to pathotypes 0 and 1) are commercially available (Cook et al. 1976, 1977; Cook 1984; Villalon 1986, 1987). However, recently PVY isolates which could overcome the resistance in Delray Bell have been found (Abdalla and Desjardins 1985). Also, low temperatures may diminish the effectiveness of resistance in many cultivars (Shifriss and Cohen 1971). PVY is not known to be seed-transmitted in pepper (Cook 1959).

Tobacco etch virus

Tobacco etch virus (TEV) appears to be common on peppers in North and Central America (McLean 1962; Laird et al. 1964; Nagai and Smith 1968; Herold 1970; Zitter 1971, 1972, 1973; Villalon 1975, 1985; Weinbaum and Milbrath 1976; Benner et al. 1985). Recently TEV has also been reported in Sudan (Mills and Abdul-Magid 1987). The virus often occurs in mixed infections with PVY in peppers (Nelson and Wheeler 1978). Incidences of nearly 100% at harvest time have been reported (Padgett et al. 1987). Yield reductions due to TEV can be as high as 70% (Koenning and McClure 1981).

Table 1. Differentiation of PVY pathotypes of pepper PVY (*Gebré-Selassie et al. 1983*).

Host (*C. annuum*)	Potato Strains O,N	Tomato Strain	Pepper Strain Pathotype		
			0	1	1.2
Bastidon	R[1]	N	N	N or M	N
Yolo Wonder	R	M	M	M	M
Yolo Y	R	R	R	M	M
Florida VR 2	R	R	R	R	M
Serrano VC	R	R	R	R	R

[1]*R = resistant, M = mosaic or mottle, N = necrosis.*

The virus causes chlorotic mottle and necrosis of pepper (Purcifull and Hiebert 1982). Veinbanding along the whole length of the veins is another typical symptom (Appendix Fig. 1) (Zitter et al. 1984). Wilting, often followed by death, of *C. frutescens* Tabasco is a useful diagnostic symptom to distinguish the virus from other potyviruses, most of which generally cause only mottling on this host (Delgado-Sanchez and Grogan 1966; Makkouk and Gumpf 1974; Nagai and Smith 1968; Greenleaf 1953; Barrios et al. 1971; Nelson and Wheeler 1978; Shepherd and Purcifull 1971). *Capsicum frutescens* Greenleaf Tabasco is, however, immune to TEV (Purcifull et al. 1975).

The ability of TEV to infect *D. stramonium* systemically distinguishes it from PVY, to which *D. stramonium* is immune (Horvath 1967; Nelson and Wheeler 1978). According to Edwardson (1974), the virus induces pinwheel inclusions of type II (pinwheels and laminated aggregates) in the cytoplasm of infected cells (Fig. 1b). It also produces typical plate-like nuclear inclusions (Fig. 1c) which are absent in PVY-infected tissue (Laird et al. 1964). These inclusions can be used as a diagnostic tool for identifying TEV (Christie and Edwardson 1977). Seed transmission has not been reported yet. Commercial cultivars with resistance to TEV are already available (Cook et al. 1976, 1977; Greenleaf 1986; Villalon 1986, 1987). Resistance to TEV is apparently closely linked to that of PVY.

Pepper mottle virus

Pepper mottle virus (PeMV) occurs mainly in North and Central America and is often found in mixed infections with PVY and TEV (Zitter 1975; Purcifull et al. 1975; Nelson and Wheeler 1978; Nelson and Zitter 1982). The reported occurrence of PeMV in Thailand (Chandrasrikul and Patrakosol 1986) needs to be confirmed. The virus is limited to the Solanaceae family.

The most common symptom in pepper is mottle (Appendix Fig. 1), but other symptoms such as green veinbanding associated with TEV and PVY infections may also occur. Some isolates cause severe malformation of fruits. On *C. frutescens* Tabasco the virus causes characteristic necrotic local lesions, followed by a rapidly spreading systemic necrosis and premature death. The virus induces type IV and irregular cytoplasmic inclusions (Christie and Edwardson 1977). PeMV is serologically distinct from PVY and TEV (Nelson and Wheeler 1978). Commercial cultivars resistant to the virus are available (Cook et al. 1976, 1977; Greenleaf 1986; Villalon 1986, 1987).

Pepper veinal mottle virus

Pepper veinal mottle virus (PVMV) has been reported in several West African countries where disease incidences as high as 100% have frequently been observed (Brunt and Kenten 1971, 1972; de Wijs 1973; Lana et al. 1975a, b; Brunt et al. 1978; Ladipo and Roberts 1977; Givord 1982; Atiri and Dele 1985). Reports about its presence in India probably need to be confirmed (Prasada Rao and Yaraguntaiah 1979b; Nagaraju and Reddy 1980). The reported incidence of PVMV in Malaysia (Soh et al. 1977) could be chili veinal mottle virus and should also be confirmed.

Leaves of PVMV-infected plants commonly develop chlorosis of the veins followed by systemic interveinal chlorosis. Mottle, vein chlorosis and small distorted leaves also occur. Leaf abscission and fruit distortion have also been reported (Brunt and Kenten 1971). The virus is serologically unrelated to TEV, PVY, PeMV and other potyviruses (Brunt and Kenten 1972; Brunt et al. 1978). The existence of different strains is suspected (Brunt et al. 1978). The virus also causes severe disease in tomato and eggplant (Ladipo and Roberts 1977; Brunt et al. 1978). PVMV is not seedborne in pepper.

Chili veinal mottle virus

Chili veinal mottle virus (CVMV) is the most important virus of *C. annuum* and *C. frutescens* in Malaysia. Symptoms include dark green mottle (Appendix Fig. 1), reduced leaf size and distortion, and fewer and smaller fruits (Ong and Ting 1977; Ong et al. 1979; Abu Kassim 1986). The host range is confined to the Solanaceae (Ong et al. 1979; AVRDC 1990c). Yield reductions of more than 50% have been reported when the crop became infected at an early growth stage (Ong et al. 1980). Recently the virus has also been detected in pepper samples from Taiwan (AVRDC 1990a,b), Thailand (AVRDC 1990a), Korea (AVRDC 1990b), the Philippines (AVRDC 1990c), Indonesia (AVRDC 1990b) and Tanzania (Swai, I.S. and Green, S.K. unpublished results 1991).

In agar gel double diffusion tests and double antibody sandwich enzyme linked immunosorbent assay (DAS ELISA) tests, the virus does not react with antisera to PVY, TEV, PeMV and PVMV (AVRDC 1990c; Ong et al. 1979; Green, S.K. unpublished results 1990). Resistance in cultivated *Capsicum* spp. has not been reported so far, but was recently found in some wild *Capsicum* accessions at AVRDC and MARDI, Malaysia (AVRDC 1990b,c; Chew, B.H. personal communication 1989).

Pepper mild mosaic virus

This virus has been isolated in Venezuela (Debrot et al. 1981; Ladera et al. 1982). It is transmitted in a nonpersistent manner by *M. persicae* and infects pepper cultivars resistant to TEV and PVY, including *C. annuum* Florida VR-2. Infected pepper plants initially show veinclearing of new leaves followed by mild mosaic, green veinbanding and mild leaf deformation. In some cultivars slight stunting has also been observed (Debrot et al. 1981). Inoculated leaves of *C. frutescens* Tabasco react by developing necrotic flecks or small necrotic pinpoint lesions as well as clearly defined local lesions. Systemically infected leaves exhibit mosaic, deformation and occasionally necrotic flecks on leaves and stems. Other systemic hosts of PMMV include *Datura metel*, *Nicandra physalodes*, *Physalis floridana*, *Lycopersicon esculentum* and several *Nicotiana* spp. *Capsicum annuum* Delray Bell, *Datura stramonium*, *Chenopodium amaranticolor* and *C. quinoa* are not infected. The virus does not react with antisera to PVY, PeMV, PVMV and TEV in SDS agar gel immunodiffusion tests.

Pepper severe mosaic virus

The virus has been reported in peppers from Argentina (Feldman and Gracia 1977; 1985). PeSMV causes a severe disease in peppers with strong mottle, necrotic spots on the stems, necrotic streaks on the leaves and leaf abscission. Serious yield losses occur as a result of infection with this virus. The virus is related to, but serologically distinct from other potyviruses such as PVY, TEV, PeMV and PVMV.

Peru tomato virus

Peru tomato virus (PTV) has been reported in Peru as the causal agent of a pepper disease causing mottle, necrotic leaf spots, crinkling of the leaves and epinasty (Fernandez-Northcote and Fulton 1980). The host range is confined to the Solanaceae. The virus is not seed-transmitted in tomato and pepper, its major natural hosts. PTV can be differentiated from other potyviruses by circular chlorotic spots and chlorotic rings on *N. debneyi*. The virus produces local lesions on *C. amaranticolor* and *C. quinoa* and causes necrosis and death of *L. pimpinellifolium.*

2. Carlaviruses

Potato virus S and potato virus M

Both potato virus S (PVS) and potato virus M (PVM) have been reported to infect peppers in Bulgaria (Kratchanova and Ivanova 1979) and India (Misra et al. 1979). These viruses are transmitted by *Myzus persicae* in a nonpersistent manner (Wetter 1971, 1972) and are not considered economically important.

3. Potexviruses

Potato virus X

The only potexvirus infecting pepper in nature is potato virus X (PVX) (Steepy et al. 1967; Fribourg and Fernandez-Northcote 1972; Makkouk and Gumpf 1974; Conti and Marte 1983). The virus occurs worldwide mainly on solanaceous hosts such as tomato and potato, its major hosts. It occurs only rarely in peppers where apical necrosis is a typical symptom (Conti and Marte 1983). The virus is transmitted by contact (Koenig 1986).

Potato aucuba mosaic virus

Pepper is reported to be an experimental host for potato aucuba mosaic virus (PAMV) which produces local lesions, followed by systemic necrosis, severe mosaic and epinasty on *C. annuum* and *C. frutescens* (Horvath 1963; Kratchanova 1976). Infected plants usually die (Kassanis and Govier 1972).

ROD-SHAPED VIRUSES

1. Tobamoviruses

Five well characterized tobamoviruses are reported to infect peppers: tobacco mosaic virus (TMV), tomato mosaic virus (ToMV), tobacco mild green mosaic virus (TMGMV), pepper mild mottle virus (PMMV) and bell pepper mottle virus (BPeMV) (Alonso et al. 1989; Conti and Marte 1983; McKinney 1952; Miller and Thornberry 1958; Nagai et al. 1981; Rast 1980, 1988; Salamon et al. 1976; Tobias et al. 1982a,b; Wetter 1984a, 1986; Wetter et al. 1984, 1987; Wetter and Conti 1988). Recently another tobamovirus, dulcamara yellow fleck virus (DYFV), has been reported to infect peppers in Hungary (Salamon et al. 1987).

The tobamoviruses are transmitted by contact and also to a considerable degree by seed. Virus-carrying seeds and debris in the soil from a previous pepper crop often serve as primary sources of infection (Pares and Gunn 1989). Mixed infections of several tobamoviruses occur frequently (Wetter and Conti 1988). The viruses are present mainly as an external contamination of the seed, although they may very rarely infect seed internally (McKinney 1952; Tosic et al. 1980; Demski 1981; Rast and Stijger 1987; Wetter and Conti 1988). Symptoms caused by these viruses are usually mosaic and mottle (Appendix Fig. 1), but systemic necrosis and necrotic spots on leaves also occur. Reduction in flowering has also been noted (Tanzi et al. 1986a). A defoliating strain of TMV has been reported on peppers in Nigeria (Igwegbe and Ogungbade 1985). Crop losses may reach 100% because these viruses often induce changes to the fruits (Appendix Fig. 1), such as mosaic, blistering, necrotic flecks and deformations (Alonso et al. 1989; Anderson and Corbett 1957; Conti and Lovisolo 1983; Conti and Marte 1983; Marte and Wetter 1986; Murakishi 1960; Nagai et al. 1987; Pategas et al. 1989; Rast 1979).

Skimmed milk used as a dip for hands and tools while handling plants during pruning and harvesting has been shown to be effective in inhibiting TMV infection (Rast 1980). The use of attenuated strains has been attempted to reduce yield loss (Goto et al. 1984; Yamazaki et al. 1986; Nagai 1987). TMV can be eliminated from seed coats by soaking the seeds in 4.2% calcium hypochlorite or in 2.6% sodium hypochlorite for 15 minutes (Demski 1981) or in a 10% solution of trisodiumphosphate (Na_3PO_4) for two hours either immediately or during the first month after harvest (Rast and Stijger 1987; Demski 1981; Wetter and Conti 1988). Immersing seeds in 9% hydrochloric acid for 30 minutes has also resulted in elimination of TMV from seed (Demski 1981). Treatment with dry heat at 70°C for five days during the week after harvest, or at 76°C for three days at three months after harvest or later has also been shown to be efficient in eliminating TMV from seed coats and endosperm (Rast and Stijger 1987). However, in some cultivars the heat treatment may result in poor and delayed seed germination (Rast 1983, 1984; Rast and Stijger 1987). Apparently it is important to reduce the moisture content of the seed to 3-4% by preliminary drying at 30-50°C (Nagai 1981; Rast, A.Th. B. unpublished report 1988). Next to preventive seed treatments, genetic resistance offers the best chances of control. Resistance to some of the tobamoviruses is available in certain commercial cultivars (Greenleaf 1986).

Tobacco mosaic virus

Tobacco mosaic virus (TMV) was originally isolated from pungent peppers in the United States (Wetter 1984a; McKinney 1952; Greenleaf et al. 1964) but is known to occur on peppers worldwide. Symptoms on peppers are mosaic, mottle, necrotic lesions and leaf drop. The virus is generally not economically important in the pepper crop (Wetter, C. personal communication 1989), although in Hungary high incidences and considerable damage to crops have been observed (Horvath, J. personal communication 1989).

Tomato mosaic virus

Like TMV, tomato mosaic virus (ToMV) infects peppers worldwide. Symptoms vary with the genotype and include mosaic, systemic chlorosis, necrotic local lesions, leaf abscission, systemic leaf and stem necrosis and death (Pategas et al. 1989). The virus is of great economic importance in the United States (Murakishi 1960), France and Italy (Wetter, C. personal communication 1989).

Tobacco mild green mosaic virus

Tobacco mild green mosaic virus (TMGMV) has occasionally been found on peppers in the United States (Wetter 1984a,b) and Italy (Wetter 1984b, 1986; Wetter and Altschuh 1987). It has recently been isolated from peppers in Taiwan (Green 1991, Plant Disease, in press). The virus generally causes necrotic infections in pepper. However, certain cultivars are infected systemically, resulting in a high percentage of dead pepper plants. The virus is not of great economic importance to peppers (Wetter, C. personal communication 1989).

Pepper mild mottle virus

Pepper mild mottle virus (PMMV) causes no symptoms or only mild chlorosis on pepper leaves. Symptoms on fruits are very pronounced, however (Appendix Fig. 1). Small malformed and mottled fruits are common and necrotic depressed areas also occur (Wetter et al. 1984; Alonso et al. 1989). Severe stunting occurs when plants are infected at early growth stages (Wetter and Conti 1988). Disease incidence may be as high as 100% in farmers' fields, resulting in drastic yield losses (Conti and Marte 1983; Marte and Wetter 1986). The virus occurs worldwide and has been found in North America, Australia, Japan, Taiwan and Europe. Seed transmission as high as 29% has been reported (Wetter and Conti 1988; Nagai et al. 1987; Pares 1988). Pepper mild mottle virus is economically important because it infects most hot and sweet peppers systemically and reduces marketable fruit drastically (Wetter et al. 1984; Marte and Wetter 1986; Wetter and Conti 1988; Alonso et al. 1989).

Bell pepper mottle virus

Bell pepper mottle virus (BPeMV), originally considered an unusual strain of TMV, has so far only been reported from Argentina (Feldman and Oremianer 1972; Wetter et al. 1987) where it is gaining importance on pepper (Gracia, O. personal communication to Wetter 1990). An eggplant strain of the virus was isolated in the Netherlands (Rast 1985).

The above tobamoviruses can be distinguished serologically (Wetter 1984a, b; Wetter et al. 1984, 1987; Wetter and Conti 1988) and by the symptoms produced in diagnostic hosts (Table 2) (Mamula et al. 1974; Wetter et al. 1984, 1987). ToMV and TMV which can infect both pepper and tomato can be distinguished by their reactions on *Nicotiana tabacum* White Burley and *N. sylvestris*. TMV infects both plants systemically while ToMV produces local lesions only (Wetter et al. 1984). PMMV, TMGMV and BPeMV do not infect tomato.

Dulcamara yellow fleck virus

Dulcamara yellow fleck virus (DYFV), similar to ToMV, infects tomato systemically and produces local lesions on *N. sylvestris*. It can be differentiated from ToMV because it infects *Solanum dulcamara* systemically with mosaic (Table 2).

Table 2. Comparison of symptoms and host range reactions, induced by tobamoviruses: bell pepper mottle virus (BPeMV), tobacco mild green mosaic virus (TMGMV), pepper mild mottle virus (PMMV), tomato mosaic virus (ToMV), tobacco mosaic virus (TMV) and dulcamara yellow fleck virus (DYFV) (*Wetter et al. 1987; Wetter, C. personal communication 1990; Salamon et al. 1987; Salamon, P. personal communication 1989*).

Host	Viruses					
	BPeMV[1]	TMGMV[1]	PMMV[1]	ToMV[1]	TMV[1]	DYFV[2]
Capsicum frutescens	NLL[3]	NLL	M	NLL	NLL	NLL
Chenopodium quinoa	CLL	CLL	CLL	CLL/M	CLL	
Datura stramonium	NLL	NLL	NLL	NLL	NLL	NLL
Eryngium planum	SS	M	0	0	0	SL
Lycopersicon esculentum						
Hoffmann's Rendita, Rutgers	0	0	0	M	M	M
Nicotiana clevelandii	M	M	M	M	M	M
N. debneyi	CLL/M	CLL/SL	SS	M	M	M
N. glauca	SS	M	SL	M	M	SS
N. glutinosa	NLL	NLL	NLL	NLL	NLL	
N. sylvestris	NLL	NLL	NLL	NLL	M	NLL
N. tabacum						
Samsun	M	M	SL	M	M	M
White Burley	NLL	NLL	NLL	NLL	M	?
Xanthi-nc	NLL	NLL	NLL	NLL	NLL	NLL/M
Petunia hybrida	NLL/+	NLL	SS	NLL	M	NLL
Solanum dulcamara	0[2]	SL[2]	0[2]	SL[2]	SL[2]	M

[1]*Information on host range (except Solanum dulcamara) from: Wetter et al. 1987c and Wetter, C. personal communication 1989, 1990.*

[2]*Information on host range from Salamon et al. 1987 and Salamon, P. personal communication 1989.*

[3]*Abbreviations for symptoms: CLL = chlorotic local lesions; M = mosaic or mottle, systemic infection; NLL = necrotic local lesions; SL = symptomless local infection; SN = systemic necrotic infection; SS = symptomless systemic infection; + = lethal; O = no infection; ? = no information available.*

Previously, before Wetter et al. (1987) classified the pepper tobamoviruses into five distinct species, they were grouped for breeders' convenience and for practical purposes into TMV and ToMV, both of which can infect peppers as well as tomato, and into 'pepper strain of TMV' which only infects peppers (Table 3) (Greenleaf et al. 1964; Feldman and Oremianer 1972; Rast 1979; Wetter, C. personal communication 1989).

Table 3. Differentiation of pathotypes of the pepper strain of TMV (*Boukema et al. 1980; Boukema 1984; Rast 1988*).

Host	Proposed Genotype	TMV and ToMV	Pepper Strain of TMV Pathotype			
			P 0	P 1	P 1.2	P 1.2.3
L. esculentum Bonnie Best	+/+	M[1]	-	-	-	-
C. annuum Westlandia	L^+/L^+	SN	M	M	M	M
C. annuum Early Calwonder	L^+/L^+	M or SN	M	M	M	M
C. annuum Tisana	L^1/L^1	LL	LL	M	M	M
C. frutescens Tabasco	L^2/L^2	LL	LL	LL	M	M
C. baccatum PI 260549	L^2/L^2	LL	LL	LL	M	M
C. chinense PI 159236	L^3/L^3	LL	LL	LL	LL	M
C. chacoense PI 260429	L^4/L^4	LL	LL	LL	LL	LL

[1]M = mosaic, LL = local lesions, SN = systemic necrosis; - = no symptoms, no infection.

The 'pepper strain of TMV' is further subgrouped into 'pathotypes', according to their reactions on a set of differential *Capsicum* sp. hosts (Table 3) (Rast 1979, 1982, 1988; Boukema et al. 1980; Gebré-Selassie et al. 1981; Tobias et al. 1982a, b; Boukema 1984). The most commonly occurring pathotypes in nature are P0 and P1. Pathotype P1.2 has been isolated in France and Italy (Gebré-Selassie et al. 1981; Tanzi et al. 1986a) and pathotype 1.2.3 has also been reported from Italy (Betti et al. 1986; Tanzi et al. 1986b). Pathotype P0 corresponds to TMV and/or ToMV. Pathotypes P1.2 and P1.2.3 may belong to isolates of PMMV (Table 4) (Rast 1988; Wetter, C. personal communication 1989). As can be concluded from Table 4, grouping according to pathotype does not allow a proper identification of the pepper-infecting tobamoviruses.

Table 4. List of tobamoviruses and corresponding pepper pathotypes (*Rast 1988*).

Tobamovirus	Strain/isolate	Pathotype
Tobacco mosaic virus (TMV)	type or common strain, vulgare strain, U1	P 0
Tomato mosaic virus (ToMV)	dahlemense strain, Y-TAMV	P 0
Bell pepper mottle virus (BePMV)	unusual pepper strain F0, eggplant strain A1	P 0
Tobacco mild green mosaic virus (TMGMV)	para-tobacco mosaic virus, T2MV, U2, South Carolina mild mottling strain, G-TAMV	P 0 or P 1
Unnamed	P 11	P 1
Tomato mosaic virus (ToMV)	pepper strain 0b	P 1 or P 1.2
Pepper mild mottle virus (PMMV)	Samsun latent strain, SL-TMV, P 8, P 14, Capsicum mosaic virus	P 1.2 or P 1.2.3

2. Tobraviruses

Tobacco rattle virus

Tobacco rattle virus (TRV) causes a major disease of peppers in the United States, Brazil, Japan and Europe (Martelli and Quacquarelli 1983; Nagai 1983). It causes stunting of the plant, yellow-green mottle, bright white or yellowish ring and line patterns on the leaves, and sunken necrotic lesions often in the form of undulating lines and large rings on the fruits (Harrison 1970; Conti and Marte 1983). Considerable yield losses have been reported (Conti and Marte 1983). The virus is transmitted by *Trichodorus* sp., and, like its vector, is often patchily distributed in the field. In some hosts, including several weed species, the virus is also seed-transmitted (Bos 1977).

ISOMETRIC VIRUSES

1. Luteoviruses

Beet western yellows virus

Beet western yellows virus (BWYV) is transmitted by aphids in a persistent manner. The virus is not transmitted mechanically unless special techniques, such as pricking with fine needles, are used (Duffus 1972; Rochow and Duffus 1981). Seed transmission of the virus is not known to occur. The main symptom is yellowing, starting typically with the older and lower foliage, then progressing to the rest of the plant. The virus has been reported on peppers in Italy and the United States (Duffus 1972; Conti and Marte 1983).

2. Tobacco necrosis and satellite virus group

Tobacco necrosis virus

Tobacco necrosis virus (TNV) occurs on vegetable crops worldwide (Lovisolo 1980; Martelli and Quacquarelli 1983) but is not economically important. On peppers, TNV causes necrotic lesions on the roots and rarely infects systemically (Conti et al. 1972). It is generally found in the roots of naturally infected hosts. The virus is transmitted by the zoospores of the root-infecting fungus, *Olpidium brassicae* (Kassanis 1970). A strain distinct from the most prevalent strain D was recently isolated from peppers grown on nutrient film (Adam et al. 1990).

3. Tombusviruses

Tomato bushy stunt virus and Moroccan pepper virus

Tomato bushy stunt virus (TBSV) has been reported on peppers in Spain (Borges et al. 1979) and Tunisia (Cherif and Spire 1983). In Morocco a second tombusvirus, the Moroccan pepper virus (MPV), causes severe symptoms such as stunting, leaf deformation, strong mottle, flower abscission and lethal systemic necrosis. In Northern Italy, another not yet fully characterized tombusvirus which causes stunting, asteroid mosaic, deformation and necrosis on the leaves has been isolated from pepper (Martelli 1981).

Tombusviruses are highly infectious and readily transmitted by contact. The vectors of TBSV and MPV have not been identified, although transmission through the soil seems to occur (Roberts 1950; Kegler and Kegler 1981; Vetten and Koenig 1983). Seed transmission has also been demonstrated (Cherif 1981, cited in Martelli and Quacquarelli 1983).

4. Fabaviruses

Broad bean wilt virus

This aphid-transmitted virus has been reported on pepper in Argentina, Bulgaria, Hungary, Italy, Japan and Morocco (Boccardo and Conti 1973; Conti et al. 1972; Conti and Marte 1983; Gracia and Gutierrez 1982; Horvath, J. personal communication 1989; Imoto 1975; Lockhart and Fischer 1977; Yankulova and Kaitazova 1979). The virus causes mild leaf mottle and concentric rings on the fruits, symptoms similar to those caused by CMV but noticeably more severe (Lockhart and Fischer 1977).

Nasturtium ringspot virus (NRSV), a strain of BBWV, was isolated in Italy from pepper with mosaic and ringspot-like mosaic symptoms (Conti et al. 1972). NRSV produces ringspot-like mosaic on *Tropaeolum majus*. BBWV produces local lesions on *Vigna unguiculata* (Boccardo and Conti 1973; Lockhart and Fischer 1977) and systemically infects *Chenopodium quinoa*. The virus reacts with local lesions on the inoculated leaves of *C. quinoa*, followed by systemic chlorosis of the whole plant with epinasty and necrotic streaks (Taylor and Stubbs 1972). Nasturtium ringspot strain is not seed-transmitted in *Capsicum* spp. (Boccardo and Conti 1973).

Two groups of BBWV can be defined on the basis of serological interrelations. Serotype I occurs more in European countries whereas serotype II seems to prevail in the Asian region.

5. Nepoviruses

Tobacco ringspot virus, tomato ringspot virus and tomato black ring virus

These three viruses (TRSV, TomRSV and TBRV) are reported to infect *Capsicum* spp. in Europe, Canada, the United States and Japan (Villalon 1975; Conti and Masenga 1977; Martelli and Quacquarelli 1983). The viruses have a wide natural host range, which includes many economically important crops such as tobacco, soybean, grape and cherry, as well as other annual and perennial plants (Gergerich et al. 1983). In Texas, TRSV and TomRSV cause serious damage to bell pepper crops.

Tomato black ring virus causes a ringspot disease in pepper (Murant 1970). It is serologically unrelated to TRSV and TomRSV.

The three viruses are generally seed-transmitted in the hosts they infect (Murant 1970).

6. Tymoviruses

Belladonna mottle virus

Belladonna mottle virus (BMV) is transmitted by the flea beetle (*Epitrix atropae*) and has so far only been reported on peppers in Europe and the United States (Paul 1971; Lee et al. 1979). Yellow mottle is the typical symptom on peppers (Paul 1971). Three strains of BMV, namely BMV-T (type strain), BMV-K (Kansas strain) and BMV-I (Iowa strain), have been reported. These strains can be differentiated by their reactions on *L. esculentum*, *Nicotiana clevelandii*, *N. rustica*, *N. tabacum* Xanthi-nc and *Vinca rosea* (Lee et al. 1979).

7. Alfalfa mosaic virus group

Alfalfa mosaic virus

Alfalfa mosaic virus (AMV) has been recovered occasionally from pepper in North America (Berkeley 1947; Zitter et al. 1984), Italy (Conti et al. 1972), Malaysia (Abu Kassim 1986), Korea (Kang et al. 1973) and New Zealand (Fletcher 1983). AMV is a virus with unique multicomponent morphology. Purified virus extracts show the presence of five different components: one is isometric, the other four are bacilliform (see Appendix Table 1). The virus is transmitted by aphids in a nonpersistent manner (Jaspers and Bos 1980). Leaf symptoms are mottle, interveinal yellowing and bright yellow whitish mosaic, giving rise to typical 'calico' symptoms (Conti and Marte 1983). Veinal necrosis, chlorotic line patterns, chlorotic rings and spots are also common. Fruits are small, malformed and occasionally necrotic. Yield reductions as high as 44% have been recorded (Fletcher 1983). A low rate of seed transmission of 1-5% in chili pepper has been reported (Sutic 1959).

8. Cucumoviruses

Cucumber mosaic virus

Cucumber mosaic virus (CMV) is geographically one of the most widespread viruses, infecting more than 770 plant species belonging to 85 families (Francki 1979; Douine et al. 1979). Many more plant species can be infected experimentally (Horvath 1979, 1980). Twenty-six species of aphids are known to transmit the virus in a nonpersistent manner in nature. For peppers, *Myzus persicae* seems to be the most efficient vector in cold climates, whereas *Aphis gossypii* is the major vector in warmer regions (Conti et al. 1979; Francki 1979; Conti and Marte 1983).

Common symptoms caused by CMV are mottle, mosaic, yellow discoloration, veinclearing, leaf deformation (Appendix Fig. 1) and leaf narrowing (Conti and Marte 1983; Lockhart and Fischer 1976; Zitter et al. 1984). Necrotic symptoms, such as top necrosis, ringspots (Appendix Fig. 1) or oak leaf necrosis often appear on both foliage and fruits and are attributed to a shock reaction due to early virus infection (Sugiura et al. 1975; Francki 1979; Nagaraju and Reddy 1982; Conti and Marte 1983; Tobias 1983; Zitter et al. 1984; Fujisawa et al. 1986; Agrios et al. 1985). Yield losses of more than 60% from CMV have been reported in peppers (Joshi and Dubey 1973; Florini and Zitter 1987).

Several strains of the virus capable of infecting peppers are known to exist (Simons 1957b), and are frequently present in the same production area. CMV does not seem to be seed-transmitted in pepper (Sutic 1959) but it is in some weeds which are important sources of the virus (Conti et al. 1979). Recent evidence has shown that CMV infection can occur from infected soil debris via non-vectored soil transmission (Pares and Gunn 1989). Commercial lines with acceptable levels of CMV resistance or tolerance are not yet available. Several *C. annuum* lines with good field tolerance have been bred by Pochard at the Institut National de la Recherche Agronomique (INRA), Montfavet, France (Pochard, E. personal communication 1988; Pochard and Daubeze 1989).

Tomato aspermy virus

Tomato aspermy virus (TAV) has been reported on peppers in Japan, Hungary, New Zealand and the Netherlands (Horvath and Beczner 1983; Procter 1975; Tochihara 1970). The virus causes tip deformation, leaf distortion and necrosis, followed by yellow mosaic ('calico') similar to that caused by AMV on pepper. The virus is seed-transmitted in some hosts (Hollings and Stone 1971). It is not economically important in pepper.

9. Ilarviruses

Tobacco streak virus

Tobacco streak virus (TSV) has been reported to infect pepper in Argentina (Gracia and Feldman 1974). Symptoms of TSV infection in peppers are systemic necrosis, especially of the upper leaves, dark streaks on stems and petioles and leaf drop (Gracia and Feldman 1974). The virus is unstable in plant extracts unless chelating agents and/or antioxidants, such as Na-DIECA or sodium sulfite, are used (Fulton 1985). It has a wide host range, infecting over 30 hosts belonging to mono- and dicotyledonous families, and is readily transmitted by sap. Transmission by thrips has recently been implicated (Sdodee and Teakle 1987). Adults and nymphs of *T. tabaci*, when mixed with virus-carrying pollen from tomato infected with TSV and then placed on test plants of *Chenopodium* *amaranticolor*, regularly transmitted the virus. In some hosts the virus is seed-transmitted (Fulton 1985).

10. Cryptic viruses

Recently, red pepper cryptic virus 1 (RPCV 1) and red pepper cryptic virus 2 (RPCV 2) were found in red pepper in Japan (Natsuaki et al. 1987). The viruses have properties similar to those of other cryptic viruses, including particle size of about 30 nm, ds-RNA genome, a high rate of seed transmission, a low concentration within the plant, lack of symptoms in the host plant and lack of mechanical transmission (Boccardo et al. 1987).

GEMINIVIRUSES

Curly top virus

On pepper, the leafhopper-transmitted curly top virus (CTV) causes yellow discoloration and curling of the leaves, followed by decline and death of the plant. Symptoms vary with different strains. The virus is transmitted by sap, but with great difficulty, and pin pricking has to be used (Thomas and Mink 1979). A high incidence of CTV can cause considerable yield losses (Ungs et al. 1977).

Tobacco leaf curl virus

The whitefly-transmitted tobacco leaf curl virus (TLCV) causes curling, rolling, blistering and puckering of the leaves and swelling of the veins (Osaki and Inouye 1981). Infected plants are stunted and often bushy in appearance. The virus has been reported in India, Japan and Sri Lanka (Osaki and Inouye 1981; Singh and Singh 1976). Similar symptoms of whitefly-transmitted diseases have been reported on *Capsicum* spp. in India and Sri Lanka where the disease has been called leaf curl of chili or chili leaf curl (Mishra et al. 1963; Seth and Dhanraj 1972; Sugiura et al. 1975; Singh et al. 1979; Muniyappa and Veeresh 1984). Based on symptoms, host range and transmission, the causal agent is suspected to be tobacco leaf curl virus or a strain of it. However, because of the lack of electron microscopic evidence of the geminate particles, this has not yet been confirmed. Incidences of up to 100% in farmers' fields are not uncommon.

Pepper mild tigré virus

Pepper mild tigré virus (PMTV) is another whitefly-transmitted virus which has only recently been reported (Brown and Nelson 1989) to cause a severe disorder in commercial pepper plantings in Mexico. In whitefly-inoculated chili peppers, bright yellow interveinal chlorosis, mild stunting and fruit malformations have been observed. Yield losses of 50-85% due to PMTV infection have been reported in commercial plantings. Besides peppers, the host range of the virus includes *Datura stramonium*, *N. tabacum* Xanthi and *L. esculentum.*

Chino del tomate virus

The chino del tomate virus (CdTV), so far only reported in Mexico (Brown and Nelson 1988), occurs mainly on tomato where it may affect 100% of the plants in a field. The disease is characterized by curling and rolling of the leaves, thickening of the veins, yellow mosaic, stunting and a reduction in fruit set on tomato. On pepper (*C. annuum, C. frutescens*) the virus causes only mild symptoms, such as mottle, mosaic and veinclearing, and yield reduction is minimal.

Differences in host range and symptomatology suggest that the virus is distinct from the tobacco leaf curl in India, Japan and Sudan (Newton and Peiris 1953; Osaki and Inouye 1978; Rataul and Brar 1989), and tomato yellow dwarf virus in Ceylon and Japan (Newton and Peiris 1953; Osaki and Inouye 1978). CdTV appears to be similar to tomato yellow leaf curl virus (TYLCV) described in Africa (Cherif and Russo 1983; Yassin and Nour 1965) and the Middle East (Cohen and Nitzany 1966; Makkouk 1978), although the two viruses differ somewhat in geographical distribution, host range, symptomatology and virus-vector relationship (Cohen and Nitzany 1966; Brown et al. 1986) and the fact that TYLCV does not infect *Capsicum* species (Brown and Nelson 1988).

TOMATO SPOTTED WILT VIRUS GROUP

Tomato spotted wilt virus (TSWV) is common on solanaceous crops in tropical and subtropical regions throughout the world, although it may occasionally also occur in temperate regions (Ie 1970; Allen and Broadbent 1986). The virus is transmitted by six species of thrips: *Thrips tabaci, T. setosus, Frankliniella schultzei, F. occidentalis, F. fusca* and *Scirtothrips dorsalis* in a persistent manner. In Hawaii, *F. occidentalis* is the predominant vector (Cho et al. 1989) whereas in South America the most efficient vector is *F. schultzei* (Holmes 1958). Although only the larvae can acquire the virus, transmission is both by infectious larvae and adults after an incubation period of 4 to 10 days (Cho et al. 1989; Ie 1970).

The virus has a large host range which includes more than 400 species belonging to the Monocotyledonae and Dicotyledonae. In peppers, the virus causes chlorosis, bright, often sudden yellowing and browning, and chlorotic rings on the leaves. Necrotic leaf spots, necrosis of terminal shoots and general stunting may also be encountered. Fruits show chlorotic spots, green or red areas surrounded by yellow halos, large necrotic blotches and sometimes concentric rings (Appendix Fig. 1). Fruit distortions have also been reported (Bidari and Reddy 1984; Cho et al. 1989; Nagai 1984). Necrosis and abortion of developing flowers are common. Incidences of TSWV infection as high as 60% in pepper production areas (Greenough and Black 1984) and considerable yield loss due to this virus have been reported (Burgmans et al. 1986).

Weeds, other vegetables (tomato, potato, eggplant, celery and lettuce), fruits (papaya and pineapple), and ornamentals (marigold, zinnia, chrysanthemum, dahlia and gerbera) are important reservoirs of TSWV (Cho et al. 1986, 1987, 1989; Gracia and Feldman 1989). Besides vector control by insecticides or use of reflective mulches (Greenough 1985), the eradication of weeds is important to reduce virus incidence. Sequential plantings of susceptible crop species should also be avoided. Resistance of thrips to insecticides belonging to the same class is common under greenhouse conditions, and this necessitates alternation of selected compounds.

Frankliniella occidentalis, which at present occurs in the Netherlands and started small outbreaks of TSWV, probably after importation of chrysanthemum cuttings from Florida, is resistant to chemical control (Rast, A. Th. B. personal communication 1989).

Seed transmission has been reported in tomato and several weed species but apparently does not occur in air-dried seeds of peppers (Cho, J.J. personal communication 1989). A list of the host plants susceptible to TSWV has been compiled by Cho et al. (1987). Many strains of the virus are known to exist (Finlay 1952).

The virus is unstable in extracted plant sap (Ie 1970). Longevity in vitro is only two to five hours at room temperature. The addition of reducing agents, such as sodium sulfite or sodium thioglycollate stabilizes the virus in plant extracts (Ie 1970). The virus is characterized by a membranous envelope

(Ie 1970) and the presence of cytoplasmic inclusions. These appear as electron-dense striated (5 nm) bands surrounded by dark diffused material, or as 40 nm-wide hollow tubules interlaced with the endoplasmic reticulum, and are useful for diagnosis (Francki et al. 1985; Francki and Hatta 1981). Resistant pepper cultivars are not commercially available yet although some breeding programs are dealing with this virus (Reifschneider et al. 1986).

OTHER VIRUSES

A few other viruses have been reported to infect peppers but none of these have been precisely characterized.

Brinjal mosaic virus, transmitted by *Myzus persicae*, has been described from India. Symptoms are veinclearing, mosaic and stunting of *Capsicum* spp. (Naqvi and Mahmood 1975). The nematode-transmitted marigold mottle virus (Naqvi et al. 1978), the pepper veinbanding virus (Nagaraju and Reddy 1981; Prasada Rao and Yaraguntaiah 1979a) and launaea mosaic virus (Naqvi et al. 1976) have been reported to infect peppers in India.

A green veinbanding virus has been reported on pepper in Cuba (Lopez Cardet and Blanco 1972). The virus is transmitted by *M. persicae* and causes leaf deformation, chlorotic streaks and dark green veinbanding on the leaves, and small and deformed fruits on *Capsicum* spp. Incidence of the virus, which has not been further characterized, was reported to be as high as 50%.

A new disease, pepper yellow vein mosaic has been reported in Hungary (Salamon et al. 1982). The causal organism was found to be transmitted through the soil (Szurke and Salamon 1986). The virus is also transmitted mechanically (Salamon, P. personal communication 1989). The same disease was later described as pepper yellow vein disease in England (Fletcher et al. 1987) and in the Netherlands (Rast 1988). The natural vector of the causal agent is *Olpidium* spp. (Fletcher et al. 1987).

CONTROL MEASURES

For devising effective control measures and to initiate efficient breeding programs it is important that the viruses present in the particular geographic area are exactly identified and characterized and that their epidemiological behavior is understood.

For the prevention or reduction of virus infection, particularly for the viruses transmitted by aphids in a nonpersistent manner the following practices have been tried with varying degrees of success in growers' field: organic mulches; aluminum foil strips above the crop; insect traps; mulches of aluminum foil, silver vinyl, or white or translucent polyethylene; or aluminum painted polyethylene sheets; sticky yellow polyethylene sheets; mineral oil sprays; skimmed milk sprays; white washes and the cultivation of nonsusceptible barrier crops such as corn (Black and Rolston 1972; Cohen and Marco 1973; Francki et al. 1985; Gibbs and Harrison 1976; Greenough 1985; Kemp 1978; Marchoux et al. 1983; Marco 1985; Ong 1984; Sharma and Varma 1982; Simons 1957a; Simons et al. 1977; Simons and Zitter 1980; Smith et al. 1964; Su 1982; Zitter and Osaki 1978; Zitter and Simons 1980). Antiviral agents such as cytovirin have also been tested for the control of pepper viruses but were found to be phytotoxic at doses that were most effective (Simons 1960).

The planting of resistant pepper cultivars is the best way to control viruses. Many virus-resistant sweet and hot pepper lines are known and some have now been released (Greenleaf 1986).

Active programs for breeding for virus resistance exist in Argentina (La Consulta Experiment Station, La Consulta, Mendoza), Brazil (Instituto Agronomico, Campinas CNPH-EMBRAPA, Brasilia, D.F.); France (Institut National de la Recherche Agronomique [INRA], Montfavet); Hungary (Research Institute for Vegetable Crops, Budapest, and University of Agricultural Sciences, Keszthaly); other East European countries including Bulgaria and Yugoslavia; India (Indian Agriculture Research Institute [IARI], New Delhi); Israel (the Volcani Center, Bet Dagan); Korea (Horticultural Experiment Station [HES], Suweon); Malaysia (Malaysian Agriculture Research and Development Institute [MARDI], Serdang); Spain (Servicio de Investigacion Agraria, Deputacion General de Aragon [SIA-DGA], Zaragoza); and the United States (University of New Mexico, Las Cruces; University of Florida [Bells Glades and Gainesville] and University of Texas [Texas Agricultural Experiment Station, Weslaco]).

APPENDICES

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
Filamentous Viruses						
Potyviruses	Chili veinal mottle (CVMV)	750 × 12	A	Asia	*Capsicum* spp.	97,210,211,213, 214,289
	Pepper mild mosaic	714	A	Venezuela	Solanaceae	70,150
	Pepper mottle (PeMV)	737	A	El Salvador, USA Thailand	Solanaceae	8,43,235,207
	Pepper severe mosaic (PeSMV)	761 × 13	A	Argentina	Solanaceae	81,82
	Pepper veinal mottle (PVMV)	770 × 12 850 × 12	A	West Africa (Ghana, Ivory Coast, Nigeria)	Solanaceae	15,37,38,39,107, 151,154,155,323
	Peru tomato virus (PTV)	750 × 12	A	Peru	Solanaceae	84,96
	Potato virus Y (PVY)	730 × 11	A	Worldwide	Solanaceae	1,27,60,102,152, 153,156,166,167, 192,266,288,290
	Tobacco etch (TEV)	730 × 12-13	A	USA, Mexico, Sudan Nigeria, Venezuela	Dicotyledonae (mainly Solanaceae)	85,152,153,166, 179,234,265

(Continued)

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
Carlaviruses	Potato virus M (PVM)	650 × 12	A	USSR, India	Solanaceae	148,315
	Potato virus S (PVS)	650 × 12	A	USSR, India	Solanaceae	148,314
Potexviruses	Potato aucuba mosaic* (PAMV)	580 × 11-13	C	Worldwide	Solanaceae	142,147
	Potato virus X (PVX)	515 × 11-13	C,S	Worldwide	Solanaceae	5,20,69,95,131,284
Rod-Shaped Viruses						
Tobamoviruses	Pepper mild mottle (PMMV)	312 × 18	C	North America, Australia, Japan, Europe (Denmark, France, Greece, Italy, the Netherlands, Spain)	*Capsicum* spp.	7,16,101,173, 218,220,221, 320,321,322
	Tobacco mosaic (TMV)	300 × 18	C,S	Worldwide	Wide	2,83,108,115,131, 134,135,188,192, 196,198,245,246, 266,288,330
	Tomato mosaic (ToMV)	300 × 18	C	Worldwide	Wide	60,121,131, 195,223

(Continued)

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
	Bell pepper mottle virus (BPeMV)	300 × 18	C	Argentina	Solanaceae	322
	Tobacco mild green mosaic virus (TMGMV)	310 × 18	C	Worldwide (Germany, Hungary, Italy, USA, Brazil, North Africa, Spain, Canary Islands, Australia)	Solanaceae Umbelliferae Commelinaceae Gesneriaceae	59,178,316,317, 318,319 (C. Wetter and J. Horvath personal communication 1989)
	Dulcamara yellow fleck virus (DYFV)	300 × 19	C	Hungary	Solanaceae	257
Tobraviruses	Tobacco rattle (TRV)	2 components: 21-23 × 46-117 21-23 × 185-197	N	USA, Europe Brazil, Japan	Wide	58,60,118,172, 192,225
Isometric Viruses						
Luteoviruses	Beet western yellows (BWYV)	26	A	Europe, USA, Japan	Wide, mainly	59,77
Tobacco necrosis and satellite viruses	Tobacco necrosis (TNV)	26-28	F	Worldwide	Wide	141,175
Tombusviruses	Tomato bushy stunt (TBSV)	30	S	USA, Europe, North Africa	Wide	47,87,174, 176,306

(Continued)

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
	Moroccan pepper virus	30	S	Europe, North Africa	Solanaceae	87,306
Fabaviruses	Broad bean wilt (BBWV)	25	A	Argentina, Egypt, Europe, Japan, Morocco	Wide, mainly Dicotyledonae	25,57,60,112, 136,160,238, 295,305,328
Nepoviruses	Tobacco ringspot (TRSV)	28	N	North America	Wide, woody, herbaceous, ornamentals	283
	Tomato ringspot (TomRV)	28	N	USA	Wide Ornamentals, woody, Semi-woody plants	282
	Tomato black ring (TBRV)	30	N	Europe	Wide	42,189
Tymoviruses	Belladonna mottle (BMV)	27	B	Europe, USA	Solanaceae	156,224
Alfalfa mosaic virus group	Alfalfa mosaic (AMV)	5 components: 18×18 18×29 18×38 18×49 18×58	A	Worldwide	Wide (Dicotyledonae)	21,38,60,89,131, 136, 138,285

(Continued)

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
Cucumoviruses	Cucumber mosaic (CMV)	28	A	Worldwide	Wide	40,58,74,92,97,139, 159,175,192,201,209 271,275,288,297
	Tomato aspermy (TAV)	30	A	USA, Europe New Zealand	Wide	122,233
Ilarviruses	Tobacco streak (TSV)	27-35	T	USA, New Zealand, Argentina, Europe, Japan	Wide	98,109,260
Cryptic viruses	Red pepper cryptic virus (RPCV)	30	-	Japan	*Capsicum annuum*	205
Geminiviruses						
	Curly top (CTV)	18-20 × 32	L	North America, Turkey	Wide (Dicotyledonae)	296,301
	Tobacco leaf curl (TLCV)	15-20 × 25-30	W	Japan, India	Solanaceae Compositae Caprifoliae	183,216
	Pepper mild tigré (PMTV)	20 × 30	W	Mexico	*N. tabacum* *Datura stramonium*	34

(Continued)

Appendix Table 1. Viruses reported to infect peppers.

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
	Chino del tomate (CdTV)	18 × 20	W	Mexico	Leguminosae Solanaceae *Cynanchum acutum* *Malva* sp.	32,33,35
	Serrano golden mosaic	20 × 30	W	Mexico, USA	*L. esculentum* *D. stramonium* *Capsicum* spp.	36
Enveloped Viruses						
Tomato spotted wilt virus	Tomato spotted wilt (TSWV)	70-90	T	Possibly worldwide (temperate/subtropical regions)	Wide	2,6,23,40,48, 49,50,97,133 166,192,243
Other Not Well Characterized Viruses						
	Bell pepper dwarf mosaic	?	?	India	Solanaceae	51
	Brinjal mosaic	?	A	India	*Capsicum* spp.	203
	Chili leaf curl	?	W	Sri Lanka, India	Solanaceae	68,149,177,183 216,261,268
	Green veinbanding	?	A	Cuba	*Capsicum* spp.	161
	Launaea mosaic	?	A	India	*Capsicum* spp. *L. esculentum*	204

(Continued)

Appendix Table 1. Viruses reported to infect peppers. ***(Concluded)***

Taxonomic Group	Virus	Particle Size	Vector[1]	Geographical Distribution	Host Range	Reference
	Marigold mottle	?	N	India	*Capsicum* spp.	202
	Pepper veinbanding	17×679	A	India	*Capsicum* spp.	200,231
	Pepper yellow vein mosaic	?	F	England, Holland Hungary	*Capsicum* spp. *Lactuca sativa* *Solanum villosum*	90,292,259

[1]*A = aphid; B = beetle; C = contact; F = fungus; L = leafhopper; N = nematode; T = thrips; W = whitefly; S = soil, no insect vector found; - = no vector*

? = Particle size or vector not identified.

[*]Only infection by artificial inoculation has been reported.

Appendix Table 2. Viruses reported to infect peppers in South and East Asia.

Virus	China	India	Indonesia	Japan	Korea	Malaysia	Philippines	Sri Lanka	Taiwan	Thailand
	(120)[1,2]	(9,23,41, 51,74,149 177,199, 200,201, 202,203, 230,231, 232,241, 243,261, 263,275, 276,277, 278,279)	(78)	(136, 185, 186, 195, 197, 198)	(10, 13, 140, 222, 236)	(2,97, 210, 211, 212, 214 289 326)	(14, 303)	(109, 266, 268, 286, 288)[3]	(12, 13, 44, 45, 164)	(12, 43, 105, 324)[4]
Alfalfa mosaic	+[5]		+	+	+	+*	+**			+
Bell pepper dwarf mosaic		+								
Brinjal mosaic		+								
Broad bean wilt	+			+						
Chili leaf curl		+				+		+		
Chili veinal mottle			+*		+*	+	+*		+*	+
Cucumber mosaic	+	+	+	+	+	+	+*	+	+	+
Green veinbanding		+								
Launea mosaic		+								
Marigold mottle		+								
Pepper mild mottle virus									+	+*
Pepper mottle									+°	+°
Pepper veinal mottle		+°								
Pepper veinbanding		+								
Potato X	+	+	+	+	+				+	
Potato Y	+	+	+	+	+	+		+	+	+

(Continued)

Appendix Table 2. Viruses reported to infect peppers in South and East Asia. *(Concluded)*

Virus	China	India	Indonesia	Japan	Korea	Malaysia	Philippines	Sri Lanka	Taiwan	Thailand
	(120)[1,2]	(9,23,41, 51,74,149 177,199, 200,201, 202,203, 230,231, 232,241, 243,261, 263,275, 276,277, 278,279)	(78)	(136, 185, 186, 195, 197, 198)	(10, 13, 140, 222, 236)	(2,97, 210, 211, 212, 214 289 326)	(14, 303)	(109, 266, 268, 286, 288)[3]	(12, 13, 44, 45, 164)	(12, 43, 105, 324)[4]
Tobacco etch	+	+	+					+		+
Tobacco leafcurl		+								
Tobacco mild green mosaic virus									+	
Tobacco mosaic	+	+		+	+	+	+	+	+	+
Tobacco rattle virus	+	+								
Tomato mosaic	+	+			+		+	+		
Tomato ringspot virus	+									
Tomato spotted wilt		+	+**		+**	+	+**	+	+**	

[1]*numbers in parentheses refer to literature references.*

[2]*also Feng, Langxiang, Beijing, China, personal communication 1990.*

[3]*also L. Black, Louisiana State University, USA personal communication.*

[4]*K. Kittipakorn personal communication 1990.*

[5]*+ = virus has been reported in the literature; +* = not yet reported from the named country, but results of surveys by AVRDC gave positive reaction by ELISA; virus presence was further confirmed by isolation and host range tests; +** = not reported from respective country but ELISA positive in surveys by AVRDC; presence of virus was not confirmed by virus isolation and host range tests; +° = should be confirmed.*

Appendix Table 3. Symptoms of some common pepper viruses on diagnostic host species.[1]

Host	PVY	PeSMV	TEV	PeMV	PVMV	CVMV	TSWV	AMV	PVX	CMV
D. stramonium	-[2]	-	M,Dist.	-	-	M,N, VC	M,RS,N	syst. spots VC	M,RS	M, Def.
N. glutinosa	M	M	M	M	M	C.F. (syst)	LL,M,N, Def.	M, (calico)	RS,M	M,Def.
N. sylvestris	M	M	M	M	-	LL (syst.)	?	c.LL, spots, syst. VC	M	M
N. tabacum										
White Burley	M	M	VC,E,M CS, Dist.	M	LL	RS (syst.)	?	LL with necrotic edge	M	M
Xanthi	M	?	?	M	LL,RS	CS (syst.)	LL,N,NS	syst. NR	M	M
Samsun	M,RS,VC	M	M	M	LL,RS	LL (syst.)	LL,NS,N	?	M	M
L. esculentum	M	?	M, Dist.	1	M	M	Y.S. NS,def. N,RS	N,M	M,St	M,Def
C. frutescens Tabasco	M	?	N,M,W death	M,N	Dist.,M	M	M,N	oak leaf pattern	NB, NR	Def, M,N

(Continued)

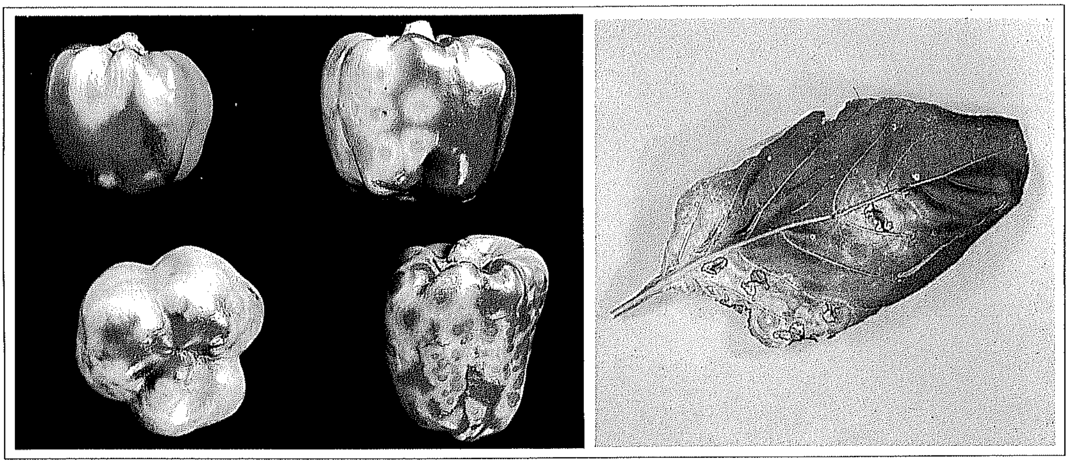
Appendix Table 3. Symptoms of some common pepper viruses on diagnostic host species.[1] *(Concluded)*

Host	PVY	PeSMV	TEV	PeMV	PVMV	CVMV	TSWV	AMV	PVX	CMV
C. frutescens Greenleaf Tabasco	-	?	M	-*	?	M	M,N	?	M?	M,N
C. annuum VR2	-[1]	?	- or M	M	VC,M	M	M,N	oak leaf pattern	LL?	M
Yolo Y	-[1]	?	M	M	VC,M	M	M,N	oak leaf pattern	LL?	M
Yolo Wonder	-[1]	?	M	M	VC,M	M	M,N	oak leaf pattern	M?	M
Chenopodium amaranticolor	LL	LL	LL	LL	LL	—	LL	LL, syst. flecks	RS,LL	LL

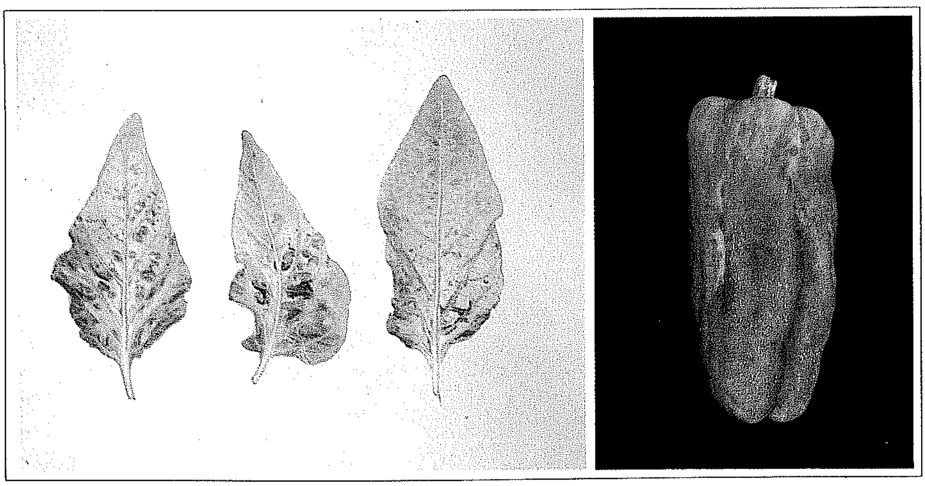
[1] *for PVY see also Table 4 and for tobamoviruses, Table 5.*

[2] *- = immune, C = chlorosis, CF = chlorotic flecks, CS = chlorotic spots, Dist. = distortion, E = etch, l = latent, LL = local lesions, M = mosaic, mottle, N = necrosis, NB = necrotic blight, NR = necrotic rings, NS = necrotic spots, RS = ringspot, St = stunt, syst. = systemic, VC = veinclearing, W = wilt, YS = yellow spot, ? = no information available; symptom symbol followed by ? = symptoms should be verified; * susceptible to the severe strain.*

Appendix Fig. 1. Symptoms of pepper viruses and viruslike symptoms.

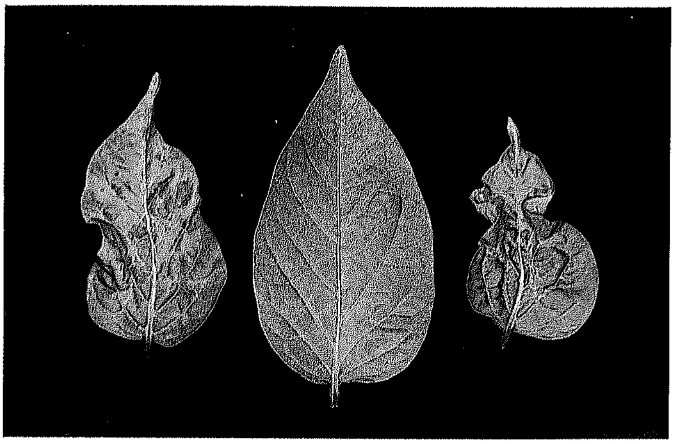


Tomato spotted wilt virus (*J.J. Cho & T.A. Zitter*)

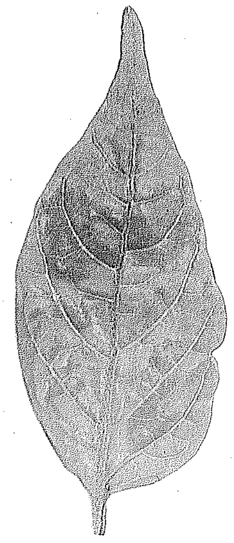


Pepper mild mottle virus *(C. Wetter)*

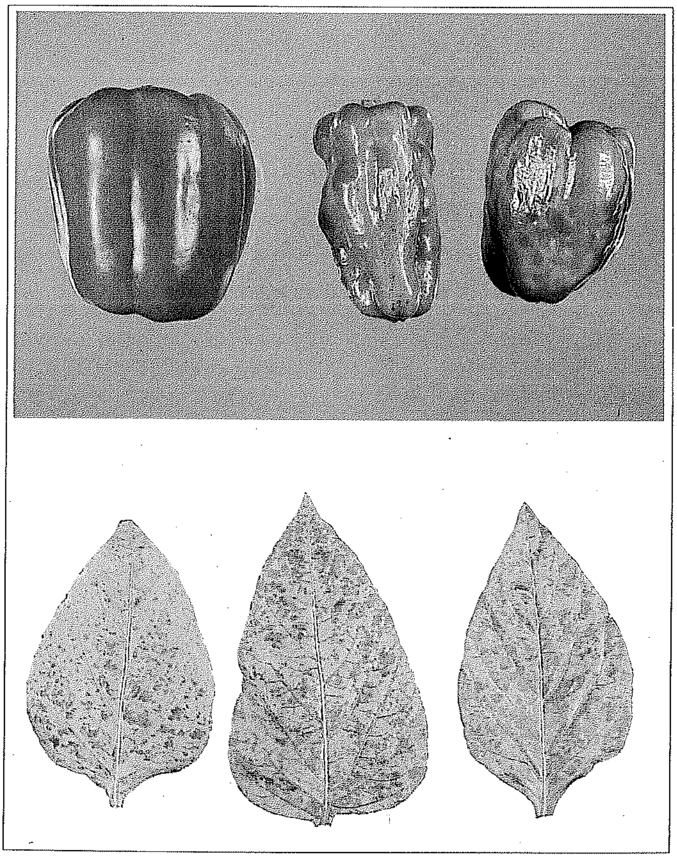
Tomato mosaic virus (*C. Wetter*)



Potato virus Y (*T.A. Zitter*)

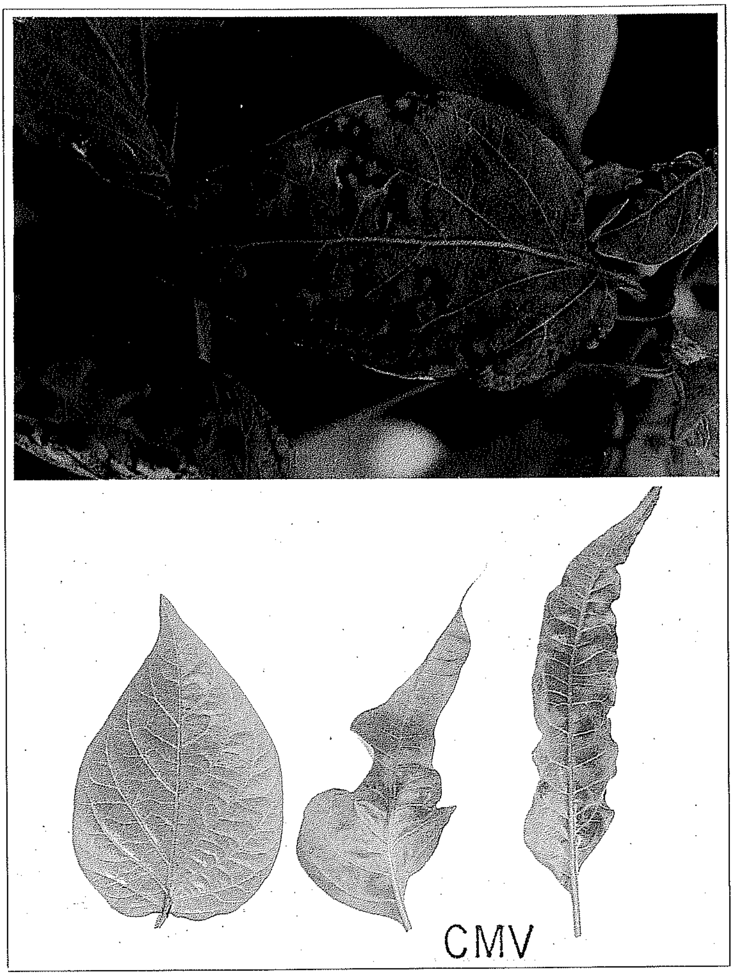


Chili veinal mottle virus
(*S.K. Green*)

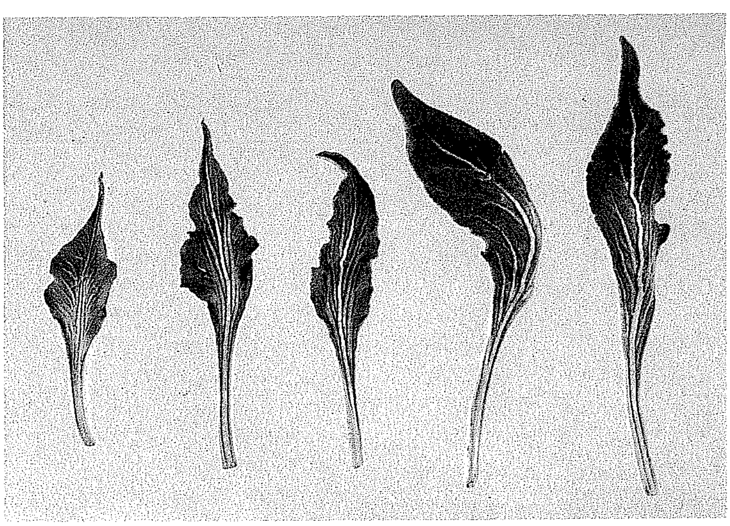


Pepper mottle virus (*T.A. Zitter*)

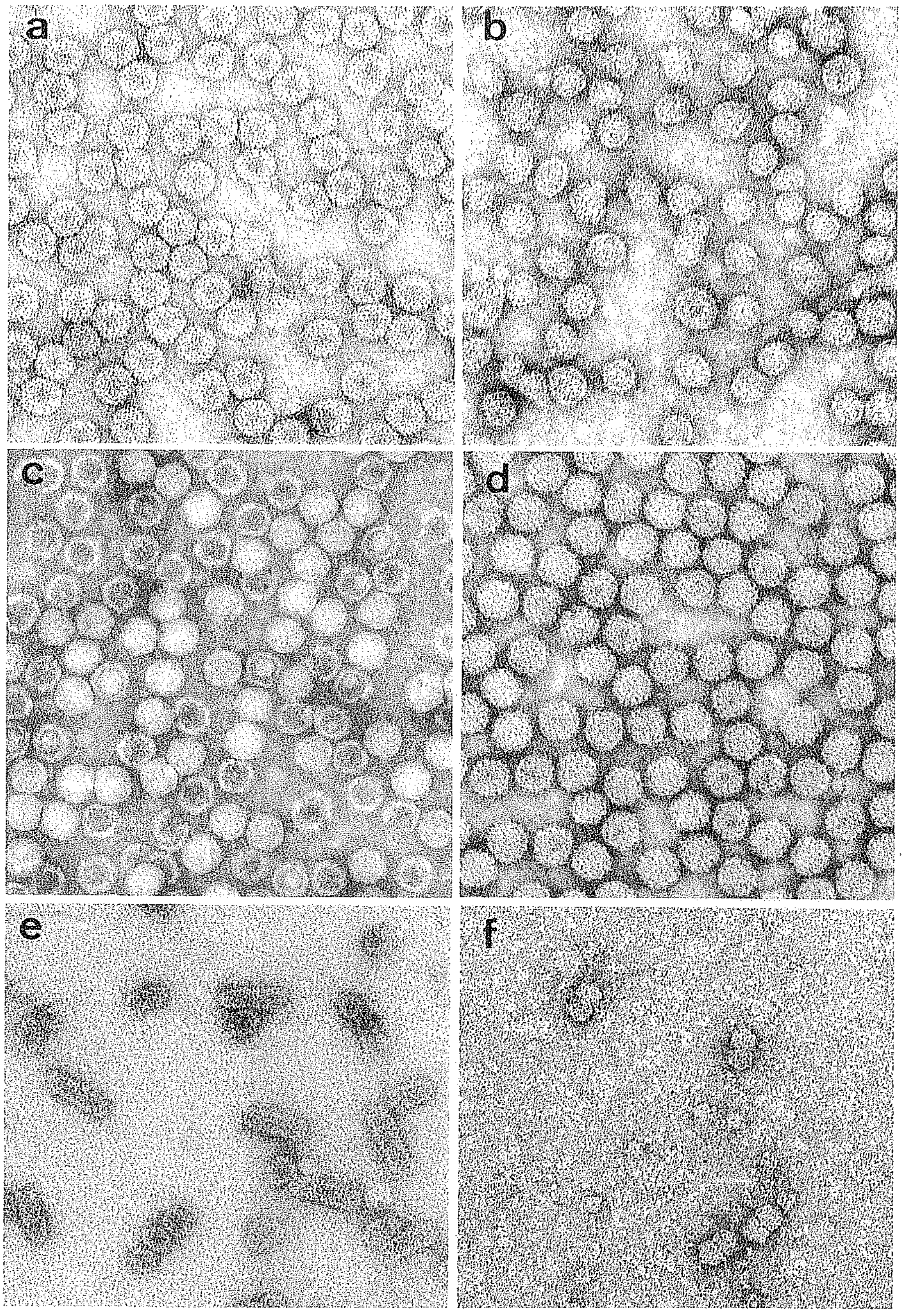
Tobacco etch virus (*T.A. Zitter*)



Cucumber mosaic virus
(*S.K. Green*)

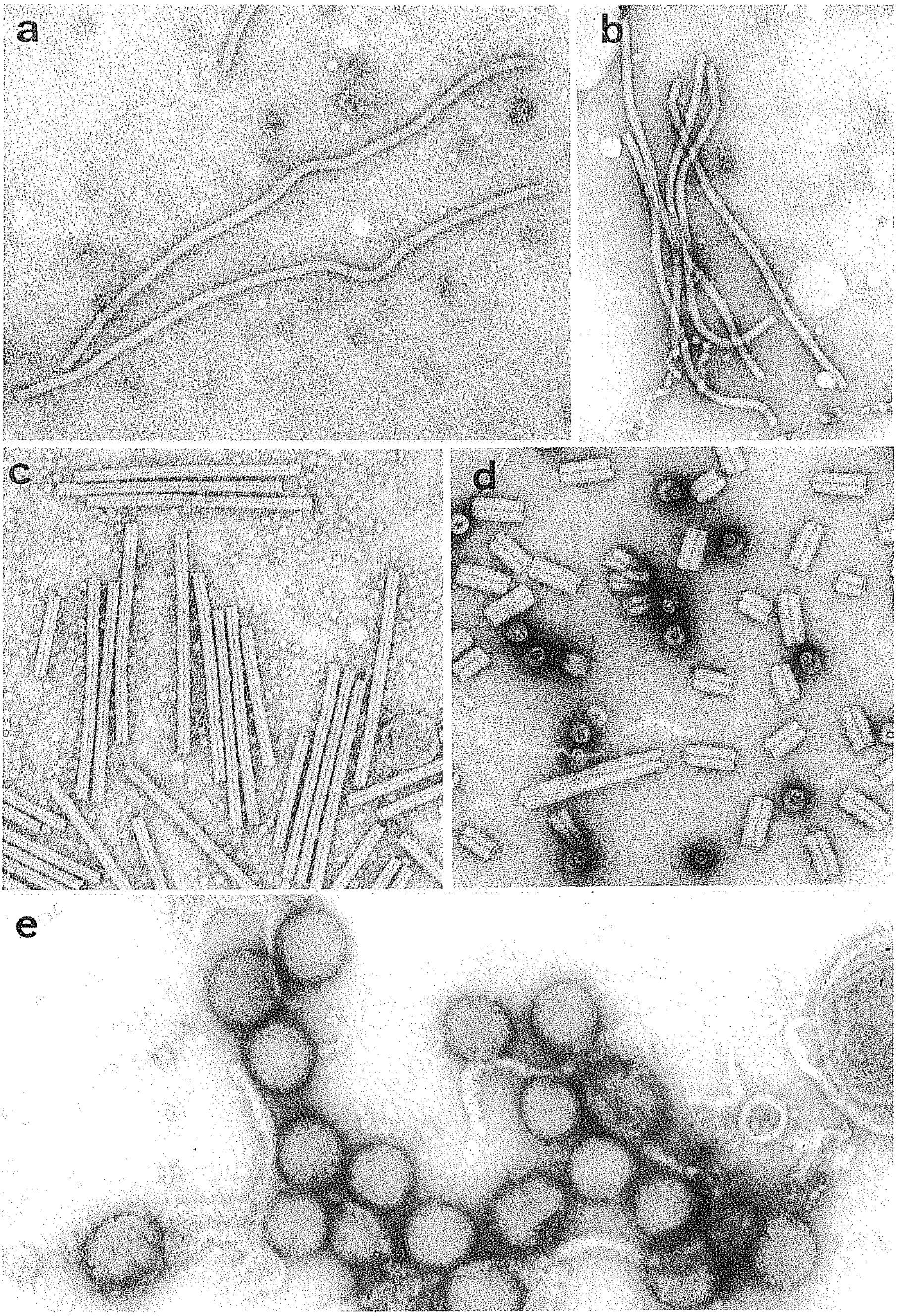


Appendix Fig. 2.
Herbicide (2.4D) damage
(*T.A. Zitter*)



Appendix Fig. 3. **Morphology of virus groups infecting peppers, with isometric bacilliform or geminate particles** (particles have been negatively stained with uranylacetate. Magnification 200,000×: bar equals 100 nm) (*D.E. Lesemann*)

a) Cucumovirus group
b) Ilarvirus group
c) Nepovirus group
d) Tombusvirus group
e) Alfalfa mosaic virus group
f) Geminivirus group



Appendix Fig. 4. Morphology of virus groups with elongated or membrane enveloped particles, which can infect pepper (particles have been negatively stained with uranylacetate; magnification 120,000×; bar equals 100nm) (*D.E. Lesemann*)

a) Potyvirus group
b) Potexvirus group
c) Tobamovirus group
d) Tobravirus group
e) Tomato spotted wilt virus group

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