Plant Pathology in the 21st Century

Maria Lodovica Gullino Ramon Albajes Philippe C. Nicot *Editors*

Integrated Pest and Disease Management in Greenhouse Crops

Second Edition





Plant Pathology in the 21st Century

Volume 9

More information about this series at http://www.springer.com/series/8169

Maria Lodovica Gullino • Ramon Albajes Philippe C. Nicot Editors

Integrated Pest and Disease Management in Greenhouse Crops

Second Edition



Editors Maria Lodovica Gullino Centro di Competenza per l'innovazione in campo agro-ambientale AGROINNOVA Università degli Studi di Torino Grugliasco, Torino, Italy

Philippe C. Nicot Plant Pathology Unit INRAE, Montfavet, France Ramon Albajes University of Lleida, Agrotecnio Center Lleida, Spain

Plant Pathology in the 21st Century ISBN 978-3-030-22303-8 ISBN 978-3-030-22304-5 (eBook) https://doi.org/10.1007/978-3-030-22304-5

© Springer Nature Switzerland AG 1999, 2020

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG. The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Introduction

Crops are grown in greenhouses to extend their growing season and protect them from adverse environmental conditions, diseases and pests. Greenhouse structures vary significantly in the different geographic areas and depending on the crops grown, consisting essentially of a light scaffolding covered by sheet glass, fibreglass, or plastic. Crops may be grown in ground beds, usually amended with different types of substrates; on benches; in pots containing soil, soil mixtures or soil substitutes; and in hydroponic systems, such as sand or rockwool cultures and flowing nutrient systems, without a matrix for the roots. Generally, value-added crops are grown under protected conditions, most of which are labour-intensive with high energy demands in cold weather. Quality is a high priority for greenhouse crops, requiring much care in pest and disease management, not only to secure yields but also to obtain a high aesthetic standard. Although technological changes are ultimately intended to reduce production costs and maximise profits, precise environmental and nutritional control has pushed plants to new limits of growth and productivity. These changes modify biotic and abiotic environments of crop plants and generate chronic stress conditions that are conducive to some pests and diseases, including Fusarium wilts. For example, short or no rotations of greenhouse crops can allow build-up of many soil-borne pathogens such as Fusarium oxysporum or Verticillium dahliae if the soil is not properly treated; they can also allow the increase of some insect or mite pest populations, free of natural enemies, if those are not released by augmentative biocontrol.

Growing crops in greenhouses presents both options and limitations with respect to disease and pest development and management. On the plus side, contamination with pathogens or colonisation by herbivore insects can be reduced in the greenhouse, in contrast to field environments. Moreover, it is easier to manipulate agricultural practices, for example fertilisation and irrigation, to favour crop growth over disease development or pest population enhancement. On the other hand, some cultural practices are conducive to more incidence of diseases and pests; for example, the high density of plants in greenhouse production favours disease development and spread, especially via the irrigation water, or high temperatures may limit the efficacy of some insect or mite predators. Once greenhouses are contaminated with pathogens or infested by pests, highly effective sanitation measures are needed. Increased yield and higher market prices justify the more intensive cropping and high investments in greenhouse production and the use of more expensive measures than those used in field cropping, for example soil disinfestation, but the economic risks are also high. This book is, at least partially, adjourning a previous one, edited 20 years ago by two of the authors. In 20 years many things changed, in terms of greenhouse structures, crops grown, and tools available for pest and disease management. The book, with its 23 chapters, tries to focus on the many advancements and improvements as well as the many constraints.

In the first part, more general chapters take into consideration the main pathogens and pests affecting greenhouse crops (Chaps. 1, 2, 3, 4 and 5). The situation described clearly indicates that in the case of dynamic systems such as greenhouse crops, new problems arise continuously, mostly due to the international exchange of seeds, planting material, and people that permit a very quick spread of new pests and diseases (Chaps. 6, 7 and 10). Fortunately, the diagnostic process, particularly in the case of pathogens, takes advantage of new effective and rapid tools, which permit early detection, with the adoption of effective management strategies (Chap. 8). Host resistance helps the management of many problems in various crops (Chap. 9), and cultural techniques often permit, particularly in the most sophisticated structures, to prevent many problems (Chap. 10). With the ability of many pathogens to be spread through infected seeds and propagative material, the use of healthy material is fundamental (Chap. 11), as well as the adoption of all possible methods to maintain soil (and substrate) health (Chap. 12). Biocontrol agents are much more intensively used now than in the past, responding to the increasing demand of markets for safer food that is mostly consumed fresh (Chaps. 13 and 14), while effective chemical pesticides are less numerous now than before and more and more replaced by biostimulants and natural products (Chap. 15). The second part of the book takes into consideration the implementation of IPM, from general concepts (Chap. 16) to practical cases on a number of crops (Chaps. 17, 18, 19, 20, 21 and 22) with a final Chap. 23 dealing with implementation of IPM in practice.

Hopefully this book will be helpful not only to students and researchers but also to the extension services, dealing daily with the not easy task to protect crops from pests and diseases.

Grugliasco, Italy Lleida, Spain Montfavet, France Maria Lodovica Gullino Ramon Albajes Philippe Nicot

Contents

Part I Major Diseases and Pests in Greenhouse Crops

1	Viral Diseases. Enrique Moriones and Eric Verdin	3
2	Bacterial Diseases	33
3	Fungal Diseases	55
4	Insect and Mite Pests	101
5	Nematodes Francisco Javier Sorribas, Caroline Djian-Caporalino, and Thierry Mateille	147
Par	t II Tools for IPDM in Greenhouses	
6	Integrated Pest Management Methods and Considerations Concerning Implementation in Greenhouses Joop C. van Lenteren and Philippe C. Nicot	177
7	Epidemiology and Population Dynamics: Modelisation, Monitoring and Management Geneviève Marchand, Philippe C. Nicot, Ramon Albajes,	195

and Odile Carisse

8	Diagnostics and Identification of Diseases, Insects and Mites	231
	Davide Spadaro, Nuria Agustí, Sara Franco Ortega,	
	and Monica A. Hurtado Ruiz	

9	Host Plant Resistance to Pests and Pathogens, the GeneticLeverage in Integrated Pest and Disease Management.Véronique Lefebvre, Nathalie Boissot, and Jean-Luc Gallois	259
10	Cultural Methods for Greenhouse Pest and Disease Management H. Marjolein Kruidhof and Wade H. Elmer	285
11	Seed and Propagative Material Gary P. Munkvold and Maria Lodovica Gullino	331
12	Soil and Substrate Health	355
13	Biocontrol Agents Against Diseases Marc Bardin and Massimo Pugliese	385
14	Biological Control Agents for Control of Pests in Greenhouses Joop C. van Lenteren, Oscar Alomar, Willem J. Ravensberg, and Alberto Urbaneja	409
15	Chemical and Natural Pesticides in IPM: Side-Effects and Application Maria Lodovica Gullino and Luciana Tavella	441
Par	t III Implementation of IPM in Major Greenhouse Crops	
16	Implementation of Integrated Pest and Disease Management in Greenhouses: From Research to the Consumer J. Riudavets, E. Moerman, and E. Vila	457
17	Tomatoes Cristina Castañé, Jan van der Blom, and Philippe C. Nicot	487
18	Sweet Peppers . Gerben J. Messelink, Roselyne Labbé, Geneviève Marchand, and Luciana Tavella	513
19	Cucurbits . Gerben J. Messelink, F. Javier Calvo, Francisco Marín, and Dirk Janssen	537
20	IPM for Protecting Leafy Vegetables Under Greenhouses Benjamin Gard and Giovanna Gilardi	567
21	Implementation of IPDM in Strawberries and Other Berries	597

22	Integrated Pest and Disease Management in Greenhouse Ornamentals Margery Daughtrey and Rose Buitenhuis	625
23	Implementation of IPDM in Greenhouses:	
	Customer Value as Guideline	681
	J. S. Buurma and N. J. A. van der Velden	

Part I Major Diseases and Pests in Greenhouse Crops

Chapter 1 Viral Diseases



Enrique Moriones and Eric Verdin

Abstract Viruses cause many important plant diseases and are responsible for yield and quality losses in crops in all parts of the world. No curative methods are available for infected plants and the main control strategies are cultural practices including prophylactic measures to prevent virus arrival, installation and spread into the crop or use genetic resistance to limit disease damage. Factors driving viral emergence include genetic variability of plant viruses, changes in agricultural practices, exchanges of plant material and new introduction or increase in the population of insect vectors in the environment of the crops. In this review, we briefly describe the most important viruses emerging in economically important vegetable greenhouse crops including pepper, tomato and cucurbit species.

Keywords Virus \cdot Emergence \cdot Vector \cdot Diversity \cdot Resistance \cdot Tomato \cdot Pepper \cdot Melon \cdot Zuchini \cdot Cucurbit

1.1 General Aspects

Viral diseases are a major limiting factor in many crop production systems. Plant viruses cause the largest fraction of emerging plant diseases (Anderson et al. 2004) mostly because of their ability to adapt to changing environmental conditions and to

E. Moriones

Instituto de Hortofruticultura Subtropical y Mediterránea "La Mayora", Universidad de Málaga-Consejo Superior de Investigaciones Científicas (IHSM-UMA-CSIC), Estación Experimental "La Mayora", Málaga, Spain e-mail: moriones@eelm.csic.es

© Springer Nature Switzerland AG 2020 M. L. Gullino et al. (eds.), *Integrated Pest and Disease Management in Greenhouse Crops*, Plant Pathology in the 21st Century 9, https://doi.org/10.1007/978-3-030-22304-5_1

E. Verdin (⊠) Pathologie Végétale, INRAE, Montfavet, France e-mail: eric.verdin@inra.fr

their easy dissemination frequently associated to vector transmission. Virus control is difficult because antiviral products are not available and control strategies are limited to a set of hygienic measures to prevent virus arrival, installation and spread into the crop or rely on genetic resistance to limit disease damage. Increasing international trade of plant materials and intensive production systems characterized by frequent cultural practices and rapid turnover of cultivars could enhance the risk of introducing new viruses and their vectors and foster the emergence of viral diseases. Thus, whitefly-transmitted viruses are an example of emergent viruses mostly resulting from global emergence of their whitefly (Hemiptera: Aleyrodidae) vectors. Bemisia tabaci whitefly populations have drastically increased worldwide since the early 1980s, especially in tropical and subtropical areas (De Barro et al. 2011). Even populations of the whitefly *Trialeurodes vaporariorum*, that have long been restricted to greenhouses, have been emerging in open-field vegetable production over the last 20 years, with large populations in summer crops and weed reservoirs (Wintermantel 2004). Virus emergence is a complex phenomenon that involves multiple ecological and genetic factors acting either during the first phase when the virus encounters the new host, the second phase that involves virus adaptation to the new host, or during the third phase in which the virus adapts to the new environment (Elena et al. 2014). Factors driving the emergence and establishment of viral diseases include the ability of viruses to evolve, changes in the vector populations, climate change, and human activities that promote emergence (Moreno-Pérez et al. 2014; Navas-Castillo et al. 2011).

In this review, we briefly describe the most important viruses emerging in economically important vegetable greenhouse crops including pepper, tomato and cucurbit species.

1.2 Emerging Viral Diseases in Pepper

Viral diseases are a major constraints on pepper (*Capsicum annuum*) production throughout the world (Florini and Zitter 1987; Green and Kim 1991). Among the 49 virus species described to infect pepper (Hanssen et al. 2010), 20 of them belonging to 15 different taxonomic groups have been reported to cause serious damage in pepper cultivation, especially in greenhouses. The most predominant are mechanically- and seed-transmitted viruses like tobamoviruses and insect-transmitted viruses like potyviruses, cucumoviruses, orthotospoviruses and begomoviruses. These threats are still relevant today but over the past 20–30 years, it has been noted that the incidence of viral diseases differed markedly between the Mediterranean basin, where only few emergences have been mentioned in pepper crops (Moury and Verdin 2012), and the tropical and subtropical areas with a significant increase of viral incidences (Kenyon et al. 2014a). In this chapter, we describe the biological characteristics of the most important viruses which affect pepper crops.

1.2.1 Potyviruses

Potyviruses are responsible for important diseases in a wide range of plant species all over the world. The *Potyvirus* genus of the family *Potyviridae* is among the largest group of plant virus species. Virions are 680–900 nm long and 11–13 nm wide flexuous particles possessing a helical symmetry with a pitch of about 3.4 nm. Particles encapsidate a monopartite single-stranded positive-sense RNA genome of about 9.7 kb in size with the VPg viral protein covalently-linked at the 5' end and a poly-adenylated tail at the 3' end. The genome encodes a single polyprotein which is cleaved into 10 proteins by viral proteinases and a frameshift during translation allows the synthesis of an additional 11th protein (Chung et al. 2008).

All potyviruses are transmitted in nature by aphid vectors in a non-persistent manner. Some of them are transmitted by seeds and occasionally by direct contact between leaves. The species that infect solanaceous plants belong to three clades. The largest clade includes the type member of the genus, *Potato virus Y* (PVY), which is subdivided in five major groups named C, N, O, Chile and Y^u. Only strains from groups C and Chile can infect pepper crops efficiently (Moury 2010; Janzac et al. 2015). PVY, which is the most prevalent potyvirus in pepper crops, was first reported in the 1930s in potato and is now distributed worldwide. Symptoms associated with PVY include generally systemic vein clearing, progressing into a mosaic (Fig. 1.1c). Vein necrosis of petioles and leaf blades can also occur, depending on the pepper cultivar and PVY strains, and can lead to plant death in some extreme cases (Dogimont et al. 1996). The most spectacular symptoms on fruits consist of mosaic patterns, necrotic spots and distortions; but these symptoms do not always occur. Economic losses depend on the earliness of infection and can reach 100% (Avilla et al. 1997a). Myzus persicae is one of the most efficient PVY aphid vector, that has a particular tropism toward warm climate conditions and proliferates at high densities in greenhouses or plastic tunnels.

Isolates of *Pepper veinal mottle virus* (PVMV) have been reported as causing epidemics in solanaceous crops, including pepper. They were mainly found in several West African countries (Thottappilly 1992), although the virus also affects pepper crops in Afghanistan (Lal and Singh 1988) and India (Nagaraju and Reddy 1980). PVMV-infected plants exhibit leaf chlorosis of the veins, followed by systemic interveinal chlorosis, mottle, and small distortion of leaves and sometimes leaf abscission and fruit distortion (Brunt et al. 1978). There have been various reports about the devastating effect of PVMV in Africa, contributing to low yield and reduced fruit quality and leading to great economic loss (54.5–64.3%) in chili and sweet pepper (Alegbejo and Abo 2002; Fajinmi 2011).

Chilli veinal mottle virus (ChiVMV) includes isolates that cause mottling, dark vein banding, narrowing and distorsion of leaves and stunted growth. ChiVMV is the most important pepper virus in Asia. Field surveys conducted in several Asian countries showed that the incidence of ChiVMV infection may reach 30–50% and may cause yield loss up to 95%, mainly in sweet chili pepper (Shah et al. 2009;



Fig. 1.1 Symptoms of cucumber mosaic virus, strain I17F (a), alfalfa mosaic virus (b), potato virus Y (c) and tomato spotted wilt virus (d) in pepper

Hidayat et al. 2012). ChiVMV can also infect other solanaceaous crops, including tomato, tobacco and weeds (*Physalis* and *Datura sp.*).

The *Tobacco etch virus* (TEV) species, which belong to a *Potyvirus* clade distinct from that of PVY, comprise isolates often associated with foliar vein banding and vein clearing, mosaic, mottle and distortion on leaves and fruits. The vein banding is distinct from that caused by PVY, consisting of pronounced dark-green mosaic and mottled areas which are usually associated with the larger veins. The growth of pepper plants is affected. If the plants are infected during the early growth stages, TEV can induce abortion of floral buds. Root necrosis and severe wilting symptoms followed by death of plants have also been described in some cultivars (Chu et al. 1997). TEV was found primarily in the North and Central America. In the Mediterranean basin, TEV was reported in pepper plants only in Turkey where yield reduction can reach 70% (Pernezny et al. 2003).

Prophylactic measures and genetic resistance of pepper cultivars are the main control methods to reduce potyvirus epidemics. Prophylactic methods targeting the aphid vectors are often unsuccessful because of the non-persistent transmission of potyviruses. As a matter of fact, insecticide treatment have a limited effect against aphid transmission, because the vectors can acquire and inoculate viruses during superficial and brief probes in the plant epidermal cells (Raccah 1986; Collar et al. 1997). The use of barrier crops, mineral oil sprays, polypropylene floating rowcovers

have been assessed more recently or are under investigation at a local/regional scale to reduce the aphid population size and partially decrease secondary infections and inoculum pressure (Avilla et al. 1997b; Fereres 2000; Anandam and Doraiswamy 2002; Hooks and Fereres 2006). Successful breeding programmes for resistant cultivars have been used for more than 50 years, relying on monogenic resistances. This is the case for two recessive resistance alleles at the *pvr2* locus (mapping on chromosome P4), $pvr2^1$ and $pvr2^2$, that confer efficient resistance against PVY. Allele $pvr2^2$ is also effective toward TEV (Ruffel et al. 2002). The dominant resistance gene Pvr4 (chromosome 10) related to hypersensitive reactions is also widely used in pepper cultivars because of its high durability. In addition, Pvr4 confers resistance not only to PVY but also to five additional potyvirus species that are present in the Americas (Janzac et al. 2009). The effect of polygenic resistance to PVY was assessed after the mapping of resistance OTLs (Caranta et al. 1997a). It was shown that quantitative trait loci (OTLs) have minor effects on resistance by themselves but increase the durability of the major $pvr2^3$ gene, which is rapidly overcome when present alone in pepper varieties (Palloix et al. 2009).

1.2.2 Cucumoviruses

Cucumber mosaic virus (CMV), the type species of the genus *Cucumovirus* of the family *Bromoviridae*, infects more than 1200 plant species in 100 families (Edwardson and Christie 1991) including dicots and monocots. Consequently, large numbers of weeds or wild plant species can act as reservoirs between growing periods making it one of the most economically important pepper viruses (Tomlinson 1987). Cucumoviruses are transmitted by aphid vectors in a non-persistent manner. Virions are 28–30 nm icosahedrical particles that have electron dense centers. The genomic RNAs are single-stranded positive-sense RNAs with 5' terminal cap, tRNA-like structures at 3' ends and containing at least five open reading frames. The viral genome consists of three genomic RNAs, RNA 1 (3.3 kb), RNA 2 (3.0 kb) and RNA 3 (2.2 kb) (Mochizuki and Ohki 2012). Virions encapsidate the three genomic RNAs separately and occasionally two subgenomic RNAs, RNA 4 (1.0 kb) and RNA 4A (0.7 kb) and satellite RNAs which are able to modulate the symptoms induced by CMV (Palukaitis et al. 1992).

CMV is distributed worldwide, predominantly in temperate regions but with increasing importance in tropical countries. Considering their nucleotide identity, CMV isolates are classified into two major subgroups named I and II (Palukaitis and Garcia-Arenal 2003). Subgroup I can be phylogenetically subdivided in two clades: IA and IB. (Roossinck et al. 1999). The geographical prevalence of the members of each subgroup depends on the climate conditions: isolates from subgroup I are more widely found under warm climate and isolates from subgroup II under cold climate (Marchoux et al. 1976; Quiot et al. 1979). The pepper crops that are more widely cultivated in regions with a hot climate are therefore probably more frequently affected by subgroup I isolates.

CMV is transmitted in nature by aphid vectors in a non-persistent manner and experimentally by mechanical inoculation. CMV is not considered a seed-borne virus in pepper since no sanitary problems linked to CMV transmission have been reported. Nevertheless some authors have reported a seed transmission rate ranging from 10% to 14% for CMV isolates from the subgroup IA (Ali and Kobayashi 2010). In pepper, CMV induces yield reduction, mainly due to stunting and sometimes plant sterility, and the production of non-marketable fruits because of reduced size, distortion and irregular maturation. CMV infections in pepper cause symptoms in leaves including mosaics (Fig. 1.1a). Some CMV isolates are associated with a filiform morphology of young leaves, and necrotic symptoms in older leaves. Stem necrosis and death of plants can occur after early infections. Yield losses greatly depend on the earliness of infection and can reach 80% (Avilla et al. 1997b).

Control of CMV is difficult because of its wide host range and its rapid natural transmission by aphids. Integrated control measures are recommended in protected crops to reduce CMV incidence: (i) elimination of infected plants, (ii) avoidance of aphid entrance in the greenhouse by covering entrances with aphid-proof nets, (iii) reduction of aphid populations and (iv) elimination of alternative spontaneous hosts present in and around the crop. Resistance to CMV has been largely exploited in pepper. However, in most cases resistance or tolerance is not absolute and is overcome by some CMV species (Caranta et al. 1997b; Palloix et al. 1997) although a major-effect resistance associated with the dominant resistance gene *CmrI* has been described in a Korean cultivar of pepper (Kang et al. 2010).

1.2.3 Alfamoviruses

Alfalfa mosaic virus (AMV), the type species of the genus *Alfamovirus* (family *Bromoviridae*), comprises isolates distributed worldwide (especially under temperate climate conditions). It infects over 250 plant species belonging to 48 families, mostly herbaceous plants. AMV is generally considered to be a minor threat to pepper. Infected peppers exhibit bright yellow to white mosaic that sometimes covers large areas of interveinal leaf tissue and bleaching on fruits. If infected at a young stage, the plants may be stunted, foliar necrosis appears (Fig. 1.1b) and the fruits will be deformed. AMV is transmitted by more than 20 aphid species (Marchoux et al. 2008). Seed transmission has been reported at a rate of 2% in pepper (Edwardson and Christie 1997) but there is no evidence for an impact of this mode of transmission on the natural spread of AMV in cultivated crops.

1.2.4 Fabaviruses

Broad bean wilt virus (BBWV), the type species of the genus *Fabavirus* (family *Comoviridae*), has a worldwide distribution. BBWV isolates are transmitted by aphids, mostly *Aphis gossypii* and *Myzus persicae*, in a non-persistent manner and

infect naturally more than 200 plant species in 41 families (Brunt et al. 1996; Marchoux et al. 2008). BBWV comprises two distinct viral clades recognizable by the divergence of their genome: BBWV-1 and BBWV-2 (van Regenmortel et al. 2000). BBWV is frequently found in pepper plants, especially in the Mediterranean area or in Asia (Moury and Verdin 2012; Kwak et al. 2013). Infected pepper plants display mosaic and concentric rings on leaves and fruits followed sometimes by necrotic spots on leaves and streaks on stems which may lead to the death of the plants. BBWV can also cause partial to general bleaching of pepper fruits reducing their commercial value. However, in pepper crops, BBWV shows a rather low prevalence and has a limited economic impact.

1.2.5 Poleroviruses

Unlike viruses mentioned above, viruses belonging to the genus *Polerovirus*, family Luteoviridae, are vectored by phloem-feeding insects in a persistent, circulative and non-propagative manner (Dietzgen et al. 2016). Virions are composed of a singlestranded positive-sense RNA, 5.3-5.7 kb in size, encapsidated in an icosahedral shell. Poleroviruses are often associated with interveinal yellowing, leaf discoloration, leafroll, and stunting symptoms. Discoloration and size reduction of fruits is also observed in symptomatic plants. Beet western yellows virus (BWYV) was the first described polerovirus species that infects pepper crops (Duffus 1960; Timmerman et al. 1985). Since then, other poleroviruses including Pepper vein yellows virus (PeVYV), Pepper vellow leaf curl virus (PYLCV) and Pepper vellows virus (PYV), were observed in several Asian countries, Africa, Europe, and North America (Dombrovsky et al. 2010; Knierim et al. 2013; Murakami et al. 2011; Buzkan et al. 2013; Villanueva et al. 2013; Alabi et al. 2015). A recent study highlights the existence of high genetic diversity within the poleroviruses, which could be associated with the emergence of new viral diseases in various crops worldwide, including pepper (Lotos et al. 2017).

1.2.6 Orthotospoviruses

Viruses belonging to the *Orthotospovirus* genus (family *Tospoviridae*), previoulsy named *Tospovirus*, cause serious diseases worldwide in economically important crops including pepper. Its main features (genome organisation, morphology, transmission) are mentioned in the Sect. 1.3.5 below.

Orthotospovirus includes numerous species that infect C. annuum, such as Capsicum chlorosis virus (CaCV), Chrysanthemum stem necrosis virus (CSNV), Groundnut bud necrosis virus (GBNV), Impatiens necrotic spot virus (INSV), Tomato necrotic ring virus (TNRV), Tomato spotted wilt virus (TSWV), Tomato yellow ring spot virus (TYRV), Watermelon bud necrosis virus (WBNV) and Watermelon silver mottle virus (WSMoV). Some of them are geographically

restricted to a continent, such as GBNV, TNRV, WBNV and WSMoV in Asia, or TCSV in South and North America. Others, on the contrary, are globally spread around the world (especially in temperate and subtropical areas), such as INSV and above all TSWV, the type member of *Orthotospovirus*. TSWV has one of the largest host ranges among plant viruses, equivalent to that of CMV (Parrella et al. 2003). In pepper, TSWV is more prevalent than INSV, which infects mainly ornamentals (Daughtrey et al. 1997). TSWV symptoms in *C. annuum* include stunting and yellowing of the whole plant, mosaic or necrotic spots and curling of the leaves. Infected fruits often show deformations, necrotic ring patterns and arabesque-like discolorations (Fig. 1.1d).

Control of TSWV is difficult because of the wide host ranges of both the virus and the vector, the efficient natural transmission by thrips combined with high fecundity and their capacity to develop resistance to insecticides. The application of sanitation measures must be intensified in glasshouses: eradication of infected plants and weeds and use of sticky cards to identify the presence of thrips. Biological control of thrips relies on the use of predatory mites or predatory bugs to decrease the virus inoculum pressure (Hatala Zseller and Kiss 1999; Maisonneuve and Marrec 1999). Genetic resistance to TSWV has been characterize and incorporated into commercial pepper cultivars. This is the case of the monogenic resistance conferred by the *Tsw* gene (Boiteux 1995; Moury et al. 1997). *Tsw* controls a hypersensitive reaction against most TSWV isolates and prevents virus movement from cell to cell (Soler et al. 1999), but is not efficient against other orthotospovirus species, like INSV. Breakdown of the resistance was described in *Tsw*-carrying cultivars rapidly after their deployment (Garcia-Arenal and McDonald 2003).

1.2.7 Begomoviruses

Begomoviruses (genus *Begomovirus*, family *Geminiviridae*) are transmitted by the whitefly *Bemisia tabaci* in a persistent and circulative manner. Seed transmission of begomoviruses in several hosts, including sweet pepper, has also been reported (Kil et al. 2017). Diseases caused by begomoviruses have emerged to be important constraints to the production of solanaceous crops, including peppers, in many tropical and subtropical regions of the world. The most studied so far is *Tomato yellow leaf curl virus* (TYLCV) which has spread from its likely origin in the Mediterranean basin region to the rest of the world. TYLCV was reported for the first time on *C. annuum* plants in Europe (Reina et al. 1999), later in North Africa (Gorsane et al. 2004), America (Quinones et al. 2002; Salati et al. 2002) and Asia (Tahir and Haider 2005). TYLCV-infected pepper plants are frequently symptomless, a fact that suggests that economic incidence of TYLCV on pepper production is probably low. It is presumed that pepper could be a dead-end host in the epidemiological cycle of TYLCV (Morilla et al. 2005). However, a potential role of pepper is also suggested in the epidemiology of TYLCV: pepper plants could act as reservoirs for TYLCV

dissemination, particularly among plants showing more severe symptoms as is the case for tomato, a crop often grown in close vicinity to pepper (Polston et al. 2006).

Other *Begomovirus* species infecting peppers can cause outbreaks in areas limited to a few countries. Beginning in the late 1980s, epidemics of begomovirus diseases of pepper occurred in Southwestern United States, Mexico, and Central America (Brown and Poulos 1990; Stenger et al. 1990). *Pepper golden mosaic virus* (initially named *Texas pepper virus*) isolates causing leaf distortion and mosaic symptoms were isolated from whitefly-infested greenhouses in Texas. Over the same period other begomoviruses, like *Pepper huasteco yellow vein virus*, were recovered from pepper during severe epidemics of « rizado amarillo » disease occurring in Mexico with yellow mosaics, interveinal chlorosis, wrinkling and stunting (Garzon-Tiznado et al. 1993). Since the late 1990s in Asia, epidemics of *Pepper yellow leaf curl Indonesia virus* have been noticed in many pepper producing regions especially from East Asia and cause major damage to pepper crop production (Rusli et al. 1999; Trisno et al. 2009). Although limited to a restricted geographical area, the dissemination of all these devastating begomoviruses at a larger scale on other countries or continents must be monitored.

1.2.8 Criniviruses

Phloem-restricted viruses belonging to the genus *Crinivirus* (family Closteroviridae) are transmitted by whiteflies including *B. tabaci*, *T. vaporariorum* and *T. abutilonea. Tomato chlorosis virus* (ToCV) is the only crinivirus described so far on pepper crops. ToCV is emerging as a problem worldwide on tomato plants since its first description in Florida in 1989 (Wisler et al. 1998). ToCV infected peppers have been reported in southeastern Spain in 1997 (Lozano et al. 2004). Since then, ToCV has also been found in greenhouses in Brazil and Costa Rica on sweet pepper (Barbosa et al. 2010; Vargas et al. 2011). Infected pepper plants exhibit stunting and symptoms of interveinal yellowing and mild upward leaf curling. ToCV causes significant yield losses that could severely limit pepper production in areas of high prevalence, favored mainly if whitefly vectors are present and tomato and pepper crops overlap (Fortes et al. 2012).

1.2.9 Tobamoviruses

The genus *Tobamovirus* (family *Virgaviridae*) includes particularly stable viruses distributed worldwide that cause devastating diseases in protected crops, mostly vegetables and ornamentals. Particles are elongated rigid and rod-shaped, about 18 nm in diameter and 300–310 nm long, that encapsidate a monopartite linear positive-sense single-stranded RNA, from 6.3 to 6.6 kb in size, with a methylated nucleotide cap structure at the 5' end and a tRNA-like structure at the 3' end. The

genome encodes at least four proteins that have been associated with replication, encapsidation, movement and symptom induction.

The most predominant tobamoviruses affecting *Capsicum* species are *Tobacco* mosaic virus (TMV), Tomato mosaic virus (ToMV), Tobacco mild green mosaic virus (TMGMV) and Pepper mild mottle virus (PMMoV). PMMoV is considered as the most destructive tobamovirus of protected pepper crops, with infections reaching up to 100% of the plants and drastic reduction in the yield of marketable fruit. ToMV can also cause severe losses on susceptible pepper cultivars (Brunt 1986). Symptom severity varies with virus strains and pepper genotypes and generally affect both quantity and quality of production. Tobamoviruses induce leaf chlorotic mosaic or mottling, leaf distortion and surface reduction, irregular shapes and colours associated with a reduction of size of fruits. Necroses can also be observed on leaves and fruits (Moury and Verdin 2012; Kenyon et al. 2014a). In nature, tobamoviruses are transmitted and easily spread between plants by contact, and during cultural operations, through contaminated instruments. Due to their high stability, the viruses can survive over months/years in plant debris and greenhouse structures. Most tobamoviruses are easily disseminated via infected seeds although tobamoviruses rarely reach the seed embryo or albumen. The virus is mostly carried in the external seed surface, allowing infection of seedlings during germination, and sometimes in maternal tissues such as seed coat or residual perisperm, which can remain infected for years (Johansen et al. 1994; Genda et al. 2011). No natural insect vectors are known for tobamoviruses.

To avoid primary infections, control methods involve prophylaxis, including seed sanitation by soaking in different solutions of active reagents (trisodium phosphate, hydrochloric acid, sodium hypochlorite) or by dry heat treatment (Rast and Stijger 1987), implementation of cautionary measures during handling of plants (since the viruses can be transmitted by physical contact between plants), removal of plant debris from previous susceptible crops and steam treatment of the soil and greenhouse structures. Cross protection was featured to control the tobamovirusassociated diseases in pepper (Goto et al. 1984; Hagiwara et al. 2002; Ichiki et al. 2009; Yoon et al. 1989). Its basis is that prior infection of a plant with one mild virus strain affords protection against secondary infection by severe strains that are closely genetically related (Pennazio et al. 2001; Zhou and Zhou 2012). This process has not been largely used in commercial conditions due to the widespread deployment of resistant cultivars. Different dominant alleles at the L locus have been identified in different Capsicum species. These alleles differ by their specificity towards tobamovirus pathotypes (called P₀, P₁, P_{1.2}, P_{1.2.3}, P_{1.2.3,4}) and by their efficiency under temperature stresses (Moury and Verdin 2012). Breakdown of resistance by PMMoV variants has been observed and mutations involved in these events identified (Tsuda et al. 1998; Hamada et al. 2002; Genda et al. 2007; Antignus et al. 2008).

1.2.10 Tombusviruses

Tombusviruses (genus *Tombusvirus*, family *Tombusviridae*) have a 30 nm icosahedral particles that encapsidate a monopartite, linear, positive-sense single-stranded RNA genome from 4 to 5.4 kb which lacks a cap structure and a poly-A tail. Particularly stable, tombusviruses are primarily soil-borne and are transmitted by contact and by seed. No invertebrate vector is known.

Moroccan pepper virus (MPV) and *Tomato bushy stunt virus* (TBSV) are the main tombusviruses described on *C. annuum*. Isolates of MPV cause leaf deformation, leaf and flower abscission, stunting and lethal systemic necrosis, while those of TBSV cause leaf mottling, leaf deformation and lack of fruit production. MPV was first described in Morocco in 1977 (Gallitelli and Russo 1987). Since then, no further observation in pepper crops has been reported. *Lettuce necrotic stunt virus*, a virus that takes increasing importance in lettuce crops in Asia and North America, was recently reclassified as MPV (Wintermantel and Hladky 2013). Thus, it should be appropriate to remain vigilant to ensure that MPV could not emerge into pepper crops. TBSV is not generally considered as an economically important plant pathogen in pepper production, with the possible exception of North Africa and Spain (Cherif and Spire 1983; Luis-Arteaga et al. 1996).

1.2.11 Ilarviruses

Ilarviruses (genus *llarvirus*, family *Bromoviridae*) have 28–30 nm icosahedrical particles that encapsidate a segmented, linear positive sense, single-stranded genome composed of 3 RNAs. Each genomic segment possesses a 5' cap and a 3' tRNA-like structure. Transmission of ilarviruses occurs primarily through pollen, often enhanced by vectors visiting flowers. Transmission by seed has also been described in several studies (Mink 1993).

Pepper plants infected with illarviruses may be symptomless or they may show leaf mosaic and necrosis, stem and fruit necrosis and sometimes apical necrosis. Among ilarviruses infecting pepper, *Tobacco streak virus* (TSV, type member) and *Potato yellowing virus* (PYV) have a worldwide distribution while *Parietaria mottle virus* (PMoV) appears to be located only in southern Europe. TSV has a wide host range but infected peppers were only mentioned in Argentina and in India (Gracia and Feldman 1974; Jain et al. 2005). PYV infects only *Solanum* species and was reported causing disease in pepper in Ecuador (Sivaprasad et al. 2015). PMoV infects several plant families including *Solanaceae* with a high prevalence in the Mediterranean countries of Europe. PMoV has been identified in bell pepper plants grown in greenhouses in Spain, France and Italy (Janssen et al. 2005; Moury and Verdin 2012; Parrella et al. 2016)

1.3 Emerging Viral Diseases in Tomato

Tomato (*Solanum lycopersicum*) plants with edible fruits have tremendous popularity in the world diet. Economically, tomato is by far the most important vegetable crop worldwide and has a large number of viral species reported able to infect it. There are at least 140 characterized viral species that have been described infecting tomato, some of them causing emergent viral diseases. Some good reviews are available compiling information about viruses causing damage to tomato (Hanssen and Lapidot 2012; Hanssen et al. 2010). Over recent years, several viral diseases, including those caused by isolates of *Tomato yellow leaf curl virus* (TYLCV), the two criniviruses *Tomato infectious chlorosis virus* (TICV) and ToCV, *Pepino mosaic virus* (PepMV), *Tomato torrado virus* (ToTV), or by orthotospoviruses and tobamoviruses have emerged in greenhouse tomato crops and are presently impacting fresh-market tomato production in diverse geographic areas worldwide. Characteristics of major viruses causing emergent damage in tomato are provided below.

1.3.1 Begomoviruses

Begomoviruses rank among the top of the most important plant viruses causing diseases of severe consequences in economically and socially relevant crops (Scholthof et al. 2011). Begomoviruses have a circular single-stranded DNA genome either bipartite (comprising two components named DNA-A and DNA-B) or monopartite (one component similar to DNA-A of bipartite begomoviruses). In nature they are transmitted in a persistent and circulative manner by members of the B. tabaci species complex (De Barro et al. 2011). Over the past 25 years, begomoviruses have emerged as serious constraints to cultivation of important crops in various part of the world, especially in warm regions. Emergence has also been observed in temperate regions seriously affecting greenhouse crop production. Emergence of these viruses is associated with the global spread of their insect vector, the whitefly B. tabaci (De Barro et al. 2011; Navas-Castillo et al. 2011). Factors driving this emergence have been reviewed (Navas-Castillo et al. 2011; Moriones et al. 2011). Also, the ability of these viruses to recombine (Lefeuvre and Moriones 2015) seems to be relevant for their emergence and adaptation to novel ecological conditions. About 90 different begomovirus species have been reported infecting tomato, most of them emerging locally such as in the Americas (Fernandes et al. 2008; Ribeiro et al. 2003; Geraud-Pouey et al. 2016) or in Asia (Kenyon et al. 2014b). However, the most significant emergence corresponds to the global spread of begomoviruses associated with the tomato yellow leaf curl disease (TYLCD) and among them of TYLCV. Because of this relevance, it is specifically revised here.

TYLCD-associated viruses cause one of the most devastating and emergent diseases of tomato crops in tropical and warm regions worldwide (Moriones et al. 2011). The first reports of TYLCD date back to 1929 in the Jordan Valley, but from the late

1980s on, a rapid emergence and geographic spread of TYLCD has occurred worldwide; this disease is now widespread in many agricultural production areas of warm climate zones worldwide, while in temperate regions it is mostly associated with glasshouse tomato cultivations (Moriones and Navas-Castillo 2000). At least ten different begomovirus species have been associated with TYLCD (Brown et al. 2015), TYLCV being the most widespread worldwide. Thanks to the availability of a significant number of sequences for TYLCV, molecular epidemiology studies helped to establish that epidemics of TYLCVs most probably arose in the Middle East between the 1930s and 1950s and that the global spread began in the 1980s (Lefeuvre et al. 2010). This virus was the first monopartite begomovirus introduced in the New World where it rapidly emerged in different countries (Duffy and Holmes 2007). The worldwide dissemination of TYLCD is one of the best examples of human impact on begomovirus emergence and spread (Moriones et al. 2011). TYLCD infections in tomato result into severe stunting of plants, with virtually no yield when infections occur during early growth stages. Symptoms consist of upward curling of leaflet margins and reduced size of young leaflets that can exhibit a yellow chlorosis (Fig. 1.2a). Also, flower sterility occurs in infected plants, and although no symptoms are observed in set fruits, as infected plants are less vigorous, they produce fruits with reduced market value.

Management of tomato-affecting begomoviruses, as for other begomoviruses, requires adoption of integrated management measures. Although a specific management section is available in this volume, nice reviews about management alternatives for begomoviruses have been published that might help to design control strategies in specific cases (Antignus 2007; Lapidot et al. 2014b). During the past decades several effective resistance sources to the virus and to the vector have been reported, some of them highly effective in commercial tomato cultivars (Lapidot et al. 2014a; Rodríguez-Lopez et al. 2011).

1.3.2 Criniviruses

During the mid 1990s, severe outbreaks of yellowing occurred in tomato, threatening tomato production in the United States. The disease was shown to be transmitted by several whitefly species and to be caused by isolates of two crinivirus species (genus *Crinivirus*, family *Closteroviridae*), TICV and ToCV (Tzanetakis et al. 2013; Wintermantel 2010). Criniviruses have large bipartite single-stranded positive-sense RNA genomes with long flexuous virions averaging between 650 and 900 nm in length. Both TICV and ToCV are transmitted in a semipersistent manner but whereas TICV is transmitted solely by the greenhouse whitefly *T. vaporariorum*, ToCV is transmitted by *B. tabaci*, *T. vaporariorum*, and *T. abutilonea*. Symptoms induced by isolates of TICV and ToCV on tomato are almost identical, consisting of a yellowing of leaves that is frequently attributed to nutritional disorders or pesticide phytotoxicity. Symptoms develop from basal to apical leaves and include interveinal yellowing and thickening of mature leaves (Fig. 1.2b). Production

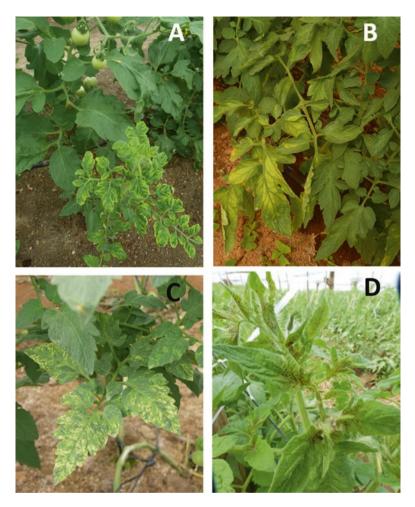


Fig. 1.2 Symptoms of tomato yellow leaf curl virus (healthy fruit on the left) (a), tomato chlorosis virus (b), pepino mosaic virus (c) and tomato torrado virus (d) in tomato

is reduced because of flower abortion, decreased fruit size and altered ripening that decrease commercial value of fruits. Early senescence also occurs. Both TICV and ToCV have a wide host range which complicates control because cultivars with resistance to these viruses are not yet commercially available. Control is mostly based on implementation of crop management measures to avoid whiteflies. These viruses are emerging over the last decades in association with the worldwide emergence of whiteflies. However, their pattern of distribution greatly differs. Whereas TICV exhibits a restricted geographic distribution, mainly in North America and in Europe, but with decreasing importance, ToCV shows a global distribution with increasing emergence worldwide (Navas-Castillo et al. 2011). Differences between ToCV and TICV incidence and geographical distribution are mostly associated with the differences in their whitefly vectors.

1.3.3 Potexviruses

Pepino mosaic virus (PepMV) (genus Potexvirus, family Flexiviridae) is a singlestranded positive-sense RNA virus with filamentous particles of around 510 nm in length that has been described recently as emerging in tomato. PepMV appears to affect mostly intensively-grown tomato crops, although the virus can infect other crop and weed species (Gómez et al. 2012b) that may act as reservoirs and/or virus sources. Initially identified in Peru affecting pepino (Solanum muricatum), it is thought that PepMV entered Europe from South America, resulting into multiple, geographically dispersed outbreaks between 2000 and 2002. The virus was first isolated from tomato in the Netherlands, in 1999 and then spread rapidly in tomato crops throughout the Northern hemisphere. Currently, it is present in many temperate regions in America, Africa, Asia, and Europe and is considered one of the most important epidemic viruses in agriculture (Gómez et al. 2012b; Hanssen et al. 2010). Ecological and genetic determinants seem to be involved in the emergence of this virus (Moreno-Perez et al. 2014). PepMV isolates seem to group in four main genetic types and mixtures of co-circulating genotypes might occur during epidemics (Gómez et al. 2012a). However, no strict correlation between the disease phenotype and genotype is observed. PepMV infections in tomato cause diverse symptoms in leaves, including more or less severe mosaics, chlorosis, blistering or bubbling and laminal distortions, and necrosis (Fig. 1.2c). Affected plants are often stunted. However, the major impact is on fruit quality and can result in great yield loss. Fruit marbling is the most typical and economically devastating symptom, but fruit discoloration and fruit splitting also occur. Importantly, fruit symptoms might arise without previous warning symptoms in the rest of the plant and they may even develop after harvest during ripening in commercialized fruit. Symptom expression is dependent on the cultivar, lighting and/or temperature within the greenhouse and on the PepMV isolate (Gomez et al. 2012a, b; Hanssen et al. 2009). Spread of PepMV is extremely effective during epidemics and mechanisms have been extensively reviewed (Gomez et al. 2012a, b; Hanssen et al. 2009). Initially, longrange PepMV dispersal probably occurs through contaminated seeds. Then, as mechanical transmission of PepMV is very efficient, the virus rapidly spreads and infects most plants if it is introduced into a tomato greenhouse. PepMV can also be transmitted by the soil fungus Olpidium virulentus in drainage water, a trait that may increase PepMV transmission by irrigation or the recirculation of contaminated water or solution in hydroponic crops. Moreover, PepMV can be vectored by bumble bees with enhanced risk of PepMV infection during pollination. The success of PepMV outbreaks may also reflect the stability of virion particles and persistence in soil and plant debris or contaminated tools and structures. Then, exhaustive hygiene measures to avoid transmission are essential, as there are currently no commercial tomato cultivars resistant to PepMV.

1.3.4 Torradoviruses

Torradoviruses (genus Torradovirus, family Secoviridae) belong to a group of emerging plant viruses that has been discovered recently in different parts of the world as a constraint to tomato production (van der Vlugt et al. 2015). ToTV, the type member of the genus, was first described in 2007 as the causal agent of a novel burn-like disease syndrome observed in tomato several years before. Symptoms of this disease initiate as necrotic spots surrounded by light green or yellow areas at the basal part of leaflets (Fig. 1.2d) that derive to leaf, stem, and fruit necrosis and plants exhibiting growth reduction. The virus exhibits isometric viral particles that contain a bipartite positive-sense ssRNA genome and is transmitted by whiteflies (either B. tabaci, T. vaporariorum, or T. abutilonea) in a stylet-borne semipersistent manner (Amari et al. 2008; Verbeek et al. 2014). Presence of this virus was reported in several countries of the world (e.g. Spain, France, Italy, Poland, Australia, Colombia, Hungary, Panama) and after the characterization of ToTV, other torradoviruses were reported causing similar symptoms to tomato in the Americas, such as isolates of Tomato marchitez virus, Tomato chocolate virus, Tomato chocolate spot virus, or of Tomato necrotic dwarf virus (van der Vlugt et al. 2015). The incidence of ToTV in commercial tomato crops can be significant (Gomez et al. 2010), and control is difficult through vector control. Efficient virus control depends heavily on the availability of healthy planting material as well as on timely recognition of infections. Deployment of plant genetic resistance might facilitate control and tomato cultivars that are not infected have been reported (Pospieszny et al. 2010).

1.3.5 Orthotospoviruses

Orthotospoviruses and tobamoviruses are the cause emergent and re-emergent viral diseases in tomato.

Orthotospoviruses are enveloped isometric viruses with a tripartite ssRNA ambisense genome that are emerging associated with increasing thrips populations, mostly related to the rapid expansion of the western flower thrips (*Frankliniella occidentalis*) (Prins and Goldbach 1998; Hanssen et al. 2010). They are transmitted by thrips in a persistent and propagative manner. Only larvae (and not adults) can acquire the virus but adults are epidemiologically the most important stage because they are more mobile and remain viruliferous for their entire life (German et al. 1992; Aramburu et al. 1997). No transovarial transmission has been reported. Viruses such as TSWV belonging to the orthotospovirus group are one of the most important plant viruses causing damage to a wide range of economically important crop plants all over the world. Orthotospoviruses have emerged in different parts of the world as a major constraint to production of important vegetable, legume and ornamental crops, among them tomato (Turina et al. 2016; Pappu et al. 2009; Mandal et al. 2011). Several new species have been reported causing increasing damage with at least 29 distinct orthotospoviruses identified as distinct or tentative

19

species (Turina et al. 2016; Webster et al. 2014). The high incidence of new orthotospoviruses in tropical Asian regions suggests a "hot spot" of viral genetic diversity in this region, where they can be transmitted to commercial crops through increasing vector populations (Mandal et al. 2011; Dong et al. 2008). Owing to the difficulty in combating thrips vectors with insecticides, the best way to limit orthotospovirus damage is through crop management strategies that includes virus resistance. TSWV is by far the most widely spread orthotospovirus species in tomato worldwide and has been targeted for genetic resistance approaches in tomato. Symptoms of the disease vary depending on the cultivar and the TSWV isolate and can include necrotic spots and necrotic/bronzed areas in leaves and necrotic ringspots or ring discolorations in fruits with stunted plants showing severe necrosis if heavily infected. The search for natural resistance sources and resistance genes has been intense, and within the past three decades several resistance sources have been reported and incorporated into commercial tomato cultivars. The gene Sw-5 originates from Solanum peruvianum (Stevens et al. 1995) and has been the most widely deployed resistance source because of its durability and the ability to provide stable resistance against several orthotospovirus species and isolates from different geographic locations. Nevertheless, resistance against orthotospoviruses is compromised by the continuous emergence of resistance-breaking strains and new species (Turina et al. 2016). In absence of resistance, control of orthotospoviruses is hampered by the rapid development of insecticide resistance within thrips populations. Therefore, alternatives to chemical thrips control are needed, primarily based on biological control in protected crops.

1.3.6 Tobamoviruses

Similar to orthotospoviruses, tobamoviruses (genus Tobamovirus, family Virgaviridae) cause emergent and re-emergent viral diseases in tomato. Tobamoviruses, mainly isolates of Tomato mosaic virus (ToMV), can cause significant yield losses to susceptible tomatoes (Broadbent 1976). The main features of tobamoviruses (genome organisation, morphology, transmission) are mentioned in the Sect. 1.2.9 above. Deformation, green mosaic, and/or necrotic symptoms are observed in leaves and fruits of infected plants. As described earlier in Sect. 1.2.9, tobamoviruses are transmitted by mechanical contact during crop operations and capable to preserve infectivity in seeds. Owing to these characteristics, control of infections is very difficult. However, the introgression in tomato of dominant resistance genes (Tm-1, Tm-2, and Tm-2²), proved to be very effective to manage infections, especially the $Tm-2^2$ gene that remained effective for more than 25 years (de Ronde et al. 2014; García-Arenal and McDonald 2003). However, concern for the future of the effectiveness of $Tm-2^2$ exists as new tobamoviruses infecting tomatoes are identified that might overcome the resistance. In this sense in Jordan, isolates of a new tobamovirus species named Tomato brown rugose fruit virus (ToBRFV) have been reported from infected tomatoes, and were shown to overcome $Tm-2^2$ resistance in Israel (Salem et al. 2016; Luria et al. 2017). The recent outbreaks of ToBRFV in Italy, Germany, Mexico, and United States of America (Menzel et al. 2019; European and Mediterranean Plant Protection Organization, EPPO, reports) suggests the dangerous spread of this virus to other tomato growing regions.

1.4 Emerging Viral Diseases in Cucurbits

Cucurbit crops (family Cucurbitaceae) are grown throughout the world for human consumption, with four major species being among the major vegetable crops cultivated worldwide: melon (Cucumis melo), cucumber (Cucumis sativus), watermelon (Citrullus lanatus) and squash/pumpkin (Cucurbita pepo, Cucurbita maxima, among others). Cucurbits are affected by a significant number of viruses belonging to several genera either possessing DNA or RNA genomes (Lecoq and Katis 2014). Some of these viruses cause significant economic damage and are typically emerging viruses that are becoming widely spread in relatively recent times. Virus infections in cucurbits result in major losses of marketable fruits. Flower abortion occurs and fruits develop abnormally exhibiting mosaic symptoms, necrosis, and/or growth alterations that depreciate them commercially (Fig. 1.3a, b). Severe yield loss might occur, especially when infections occur during early growth stages. Specific characteristics of the most prominent viruses emerging in cucurbit crops are summarized below. Control strategies to manage major cucurbit viruses have been comprehensively studied (Lecoq and Katis 2014). Characteristics of viral diseases/viruses emerging in cucurbit crops are provided below.

1.4.1 Criniviruses-Ipomoviruses-Poleroviruses-Carlavirus

There are a number of plant virus species with isolates causing emergent yellowing diseases in cucurbit crops worldwide. The most prominent among them are (i) the criniviruses (genus Crinivirus, family Closteroviridae) Cucumber yellow stunting disorder virus (CYSDV) and Beets pseudoyellows virus (BPYV), (ii) the ipomoviruses (genus Ipomovirus, family Potyviridae) Squash vein yellowing virus (SqVYV) and Cucumber vein yellowing virus (CVYV), and (iii) the polerovirus (genus Polerovirus, family Luteoviridae) Cucurbit aphid-borne yellows virus (CABYV). All these viruses have positive-sense single-stranded RNA and some of them are widely distributed in commercial crops (Kassem et al. 2007; Abrahamian and Abou-Jawdah 2014). The common aspect among most of these emergent viruses is that they are transmitted in nature by whiteflies in a semipersistent manner, either by T. vaporariorum (BPYV) or by B. tabaci (CYSDV, SqVYV and CVYV). In contrast, CABYV is transmitted by aphids in a persistent manner and it is more prevalent in open-field crops (Kassem et al. 2007). Emergence of CYSDV, SqVYV, and CVYV is a typical example of emergence associated with the global dissemination of the vector B. tabaci (De Barro et al. 2011). Characteristics of viruses transmitted

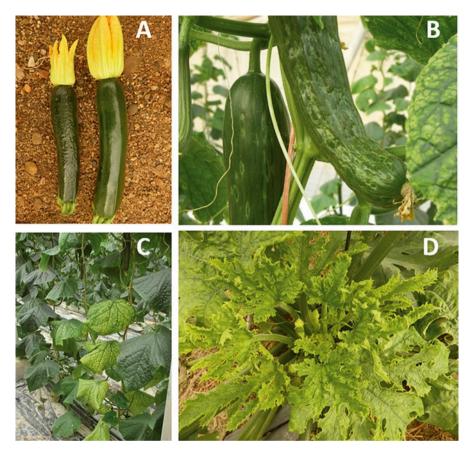


Fig. 1.3 Symptoms of tomato leaf curl New Delhi virus (healthy fruit on the right) (a) and cucumber green mottle mosaic virus (b) infections in zucchini squash and cucumber fruits (respectively), and of cucumber yellow stunting disorder virus (c) and tomato leaf curl New Delhi virus (d) in cucumber and zucchini squash plants (respectively)

by whiteflies have been reviewed by Navas-Castillo et al. (2011). Similar symptoms are induced in plants by CYSDV, BPYV, and CABYV, consisting on interveinal yellowing in older leaves that maintain green veins and are more brittle (Fig. 1.3c). These symptoms can be confused with nutritional or physiological disorders. In the case of CVYV, symptoms are more prominent in young leaves and consist of bright yellow veins and leaf deformation. Although the viruses considered previously are examples of viruses causing emerging yellowing diseases in cucurbits, in several production areas, more specific emergence cases occur that should also be taken into account. This can be the case of a novel flexivirus of the genus *Carlavirus* (family *Betaflexiviridae*) named melon yellowing-associated virus (MYaV) which is transmitted by the *B. tabaci* whitefly that has been reported as an emerging serious problem in Brazil causing a yellowing viral disease on melon plants (Costa et al. 2017; Nagata et al. 2005).