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► **To cite this version:**

Cecile Desbiez. The never-ending story of cucurbits and viruses. *Acta Horticulturae*, 2020, 1294, pp.173-192. 10.17660/ActaHortic.2020.1294.23 . hal-03019048

HAL Id: hal-03019048

<https://hal.inrae.fr/hal-03019048>

Submitted on 10 Feb 2022

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The never-ending story of cucurbits and viruses

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Abstract

Cucurbits are widely grown worldwide in diverse agroecosystems. Viruses represent one of the major threats for cucurbit production. More than 90 viruses have been described infecting cucurbits in natural conditions. Their prevalence and agronomic impact are highly contrasted, and the major problems at the worldwide level are related to circa 10 virus species, both « classic » - i.e known for decades- or recently emerged on a large scale. Among the « old » mosaic-inducing viruses, aphid-transmitted viruses (potyviruses, cucumber mosaic virus) remain agronomically important, particularly in temperate climates. Despite their long-term prevalence and apparent stability, introductions of new strains have been observed in several countries in the last years, probably *via* commercial exchanges of plant material. Some of these introduced strains have rapidly replaced pre-existing virus populations, sometimes resulting in an increased economic impact. In Mediterranean and tropical climates, as well as in heated greenhouses in temperate regions, whitefly-transmitted viruses (begomoviruses, ipomoviruses, criniviruses) now constitute major problems. Their rapid emergence can be explained by the combination of changes in climate and cultural practices that favour their natural vectors, and the increased exchanges of plant material that made possible their long-distance spread. Thrips-transmitted viruses are present in Asia and Latin America and can be locally very damaging. Viruses transmitted by seeds or by contact are also easily disseminated worldwide and represent important constraints for exchanges of plants or genetic material. Accurate and regular re-evaluation of the complex viral pathosystem infecting cucurbits in different countries, adaptation of cultural practices and development of resistant cultivars contribute to the continuous arm race against the introductions and local evolution of virus populations.

Keywords: epidemiology, viral disease, emergence, transmission, evolution, control, emergence

INTRODUCTION

Cucurbits are among the most important vegetable crops worldwide. Among the circa 800 species described, the major crops are melon (*Cucumis melo*), cucumber (*C. sativus*), watermelon (*Citrullus lanatus*) and different squashes (*Cucurbita pepo*, *C. moschata*, *C. maxima*). Other cucurbits (bitter gourd, chayote) are also grown in some parts of the world (<http://www.fao.org/faostat/>). Mature or immature cucurbit fruits are used for human or animal consumption. Seeds are used as snack or for oil production. Some cucurbits are grown for ornamental use (colocynths), as sponges (*Luffa acutangula*) or as containers or music instruments (Lecoq et al., 1998; Romay et al., 2014).

Whereas many wild cucurbits are perennial, cultivated ones are mostly annual. A great variety of types and cultivars are grown in relation to local conditions and consumer's tastes. Cucurbits are grown in very diverse agroecosystems, from traditional rain fed or irrigated gardens to sophisticated soilless glasshouses.

Cucurbits production is threatened by several pests and diseases. Insects or nematodes induce direct damages to the crops, and can also transmit viruses. Viruses represent challenging problems as they can impair both the yield and the quality of the crops, and no curative methods are available. Viruses rarely cause plant death, but they can induce different symptoms belonging mostly to three categories:

-mosaics, i.e. patterns of discoloration on the leaves or fruits, often associated with deformations and size reduction. Fruit quality can be altered with low sugar content, and sometimes marbling and hardening of the flesh

-necrosis affecting some organs (necrotic spots on leaves or fruits) or the whole plant, sometimes leading to general wilt and death

-yellowing of the older leaves that also become brittle. Fruit production can be reduced but the quality of the fruits is not obviously affected.

Mixed infection of several viruses in a single plant are common and can result in more severe symptoms.

Cucurbit-infecting viruses represent a highly dynamic system. Several novel virus species, and/or viruses that were present on other hosts but are now found to infect cucurbits, are described each year, as well as new locations or new hosts for known viruses. Many of these viruses have a potential or acknowledged agronomic impact. Until recently, descriptions of new viruses included a characterization of their symptomatology, host range, and transmission properties. With the development of high-throughput sequencing, some viruses are known only by their molecular properties without any information on their importance in plants. Completely asymptomatic viruses that could be commensal or even beneficial to plants are thus described, but the risks of their evolving to become deleterious are unknown.

1. APHID-TRANSMITTED VIRUSES: OLD VIRUSES, NEW STRAINS, PERSISTING PROBLEMS

Aphids constitute important agronomic problems in themselves. They induce direct damages to crops by their sap-sucking feeding: plant weakening, leaf crisping in response to saliva toxicity and photosynthesis reduction. Their feeding behaviour makes them particularly efficient virus vectors. For some virus genera, virus acquisition and transmission take place during short probing punctures of the aphid stylet in the epidermal cells of the plants (non-persistent transmission). In that case, the transmission is not very specific, many aphid species can transmit a given virus. The virus remains in the stylet of the aphid, its retention lasts only minutes to hours and the aphid remains viruliferous for less than one day. Other virus species are persistently transmitted: the aphid acquires the virus after several hours of feeding in the phloem of an infected plant. The virus transits through the insect gut and the haemolymph, then migrates to the salivary glands where it can be released to a new plant when the aphid feeds on the phloem of another healthy susceptible plant. In that case, the transmission is more specific, only one or a few aphid species can transmit a given virus. The aphid can remain viruliferous all its life (Ng and Perry, 2004).

In cucurbits, viruses from the genera *Cucumovirus* and *Potyvirus* are non-persistently aphid-transmitted, whereas viruses from the genus *Polerovirus* are persistently-transmitted.

Cucumber mosaic virus (CMV)

Cucumber mosaic virus (CMV, genus *Cucumovirus*) has small icosahedral particles of circa 29 nm in diameter. CMV is among the first plant viruses described, more than one century ago. Its genome consists of 3 positive-stranded RNAs, encapsidated separately. CMV has one of the broadest host ranges for a plant virus, it infects more than 1000 species, both dicots and monocots. The symptoms on cucurbits usually consist in mosaics and deformations on leaves and fruits. CMV is efficiently transmitted non-persistently by more than 60 aphid species. Interestingly, CMV-infected plants attract aphids by the emission of volatiles, but aphids perform poorly on infected plants and tend to emigrate quickly. This manipulation of aphid behaviour can increase virus spread (Mauck et al., 2010). CMV is seed-transmitted in some hosts, but seed transmission in cucurbits seems to be rare (Jacquemond, 2012; Lecoq et al., 1998).

Two major subgroups of CMV, namely groups I and II, have been defined based on biological, serological and molecular properties. Strains from group I were also called heat-resistant, contrary to the heat-sensitive group II (Jacquemond, 2012). Within group I, two major subgroups are acknowledged, namely IA and IB. Group IA is widespread throughout the world; group IB was mostly present in Asia until recently. Reassortants, i.e. virus isolates whose RNAs belong to different groups or subgroups, and recombinants –presenting genetic exchanges within one RNA– have been observed (Jacquemond, 2012; Ohshima et al., 2016). Reassortants can present fitness advantages in some hosts and become predominant in local populations (Ben Tamarzizt et al., 2013). Evolutionary analyses suggested that current CMV populations are the descendants of a

single ancestor existing 1600-2600 years ago but that the population mostly radiated 300-550 years ago, and that reassortant populations were locally confined and less than 250 years old (Ohshima et al., 2016).

Potviruses

At least 20 potviruses infect cucurbits (Table 1). Three of them, zucchini yellow mosaic virus, papaya ringspot virus and watermelon mosaic virus, are particularly important worldwide. Potviruses have a single-stranded monopartite genome of about 10 kb, encapsidated in filamentous flexuous particles about 700 nm long. Viruses in the family *Potviridae*, including potviruses, induce in their infected hosts typical pinwheel-like cytoplasmic inclusions. Potviruses are non-persistently transmitted by numerous aphid species. They can also be transmitted mechanically by pruning tools or by contact between plants.

Zucchini yellow mosaic virus (ZYMV)

Zucchini yellow mosaic virus still represents the challenging case of a very successful emerging virus. ZYMV was first observed in a garden in Italy in 1973, and the first severe epidemics took place in France in 1978 (Desbiez and Lecoq, 1997). Within a few years, ZYMV caused severe epidemics in almost all cucurbit-growing areas worldwide (Desbiez and Lecoq, 1997). ZYMV symptoms are usually very severe, and early infections can lead to complete crop losses. ZYMV presents a high biological variability in symptomatology, transmission and ability to overcome resistances. ZYMV has a narrow host range outside cucurbits. In areas where cucurbits are not grown year-round, ZYMV can be maintained in wild annual or perennial cucurbits. The few wild cucurbits present in Europe are not susceptible to ZYMV, and the sources of primary inoculum in epidemics remain a key question. Non-cucurbit hosts including weeds and ornamentals can constitute virus reservoirs (Lecoq et al., 2014) but their prevalence in the vicinity of the crops can be low. In temperate areas, ZYMV epidemics are often irregular, probably in relation to a low probability of primary infections (Lecoq et al., 2009; Lecoq et al., 2014). Studies on ZYMV molecular diversity have revealed three molecular groups, namely A, B, and C without host specificity. Groups B and C are restricted geographically whereas group A contains worldwide isolates including those of the first descriptions in France and Italy. Within group A, 4 to 6 subgroups were defined (Lecoq and Desbiez, 2012). Molecular analyses have allowed in some cases to track the origins of ZYMV strains emerging in new areas. Even in a single location, strain replacement or “switches” have been described (Lecoq et al., 2014), suggesting that distant sources of infection, besides local reservoirs, play an important role in ZYMV epidemics. Natural spread by aphids takes place mostly at a very local scale (Lecoq et al., 2014). Long-distance virus dissemination can happen through infected fruits or plants (Lecoq et al., 2003). Seed transmission of ZYMV has long remained controversial, with estimations ranging from 0 to 18%. Using a sensitive RT-PCR detection method, vertical transmission was observed in *Cucurbita pepo* subsp. *texana* at a 1.6% rate (Simmons et al., 2011). Positive plants were symptomless and had low virus titre, but they could be sources for further horizontal transmission, either by aphids or mechanically (Simmons et al., 2013). Seed transmission may thus have contributed to the rapid worldwide spread of ZYMV, and to the still ongoing frequent exchanges between viral populations.

Watermelon mosaic virus

Watermelon mosaic virus (WMV) is present worldwide in temperate and Mediterranean areas but is almost absent on cucurbits in tropical areas, without definitive explanation. WMV infects a wide range of cultivated and ornamental hosts as diverse as pea, orchids and ginseng, as well as numerous weeds that can constitute reservoirs. In cucurbits, WMV induces vein banding and mosaic symptoms milder than those of ZYMV, even if some strains cause severe leaf deformations. “Watermelon mosaic disease” has been observed for more than 50 years. Biological and serological studies revealed the presence of two viral entities named WMV-1 and WMV-2. WMV-1 was shown to be a strain of papaya ringspot virus (PRSV, see below) and WMV-2 was renamed WMV. WMV is closely related molecularly to soybean mosaic virus (SMV) but is an interspecific recombinant in the 5’ region of the genome between SMV and another legume-

infecting potyvirus, bean common mosaic virus (Desbiez and Lecoq, 2004). Despite its low biological variability, WMV molecular diversity is high. The first studies based on coat protein-coding regions revealed the presence of three molecular groups showing some correlation with the geographic origin of the isolates: In France and other European countries, Group1 strains present for more than 40 years have been replaced within a decade by Group3 ones probably introduced in the mid-1990s (Desbiez et al., 2009). During the few years of coexistence of the two types of strains, mixed infections were frequent and intraspecific recombinants were detected but they did not emerge in the populations (Desbiez et al., 2011a). The increase of the number of sequences available from worldwide isolates now shows a very complex situation with evidence for numerous long-distance exchanges. WMV has not been described as seed-borne in cucurbits. Long-distance virus spread could be the result of worldwide trade of vegetatively propagated hosts, including orchids or other ornamentals, and/or of cucurbit seedlings, plants or fruits.

Papaya ringspot virus (PRSV) and the « PRSV cluster »

Papaya ringspot virus (PRSV, formerly WMV-1) induces mosaics and deformations in cucurbit leaves and fruits. After it was considered as a distinct virus from WMV (formerly WMV-2) it was shown to belong to the same species as a virus previously described on papaya. P (papaya) strains of PRSV infect papaya but have a low infectivity on cucurbits, contrary to W (watermelon) strains that efficiently infect cucurbits but do not infect papaya. Phylogenetic analyses suggest that P isolates derive from W isolates, and that the switch took place frequently during the evolution of PRSV. Indeed, a single mutation in the major protease of the virus (N1a-Pro) is sufficient for the phenotypic change between the P and W phenotypes (Chen et al., 2008). Besides PRSV, several viruses closely related biologically, serologically and molecularly constitute a “cluster” of cucurbit-infecting viruses: Moroccan watermelon mosaic virus, Algerian watermelon mosaic virus, zucchini shoestring virus, zucchini tigre mosaic virus, Sudan watermelon mosaic virus, wild melon vein-banding virus, zucchini yellow fleck virus. They are geographically restricted to a few countries, mostly in Africa and Middle East, but MWMV is now emerging in the Mediterranean Basin (Desbiez et al., 2017)

Other potyviruses infect cucurbits. They are not particularly related serologically or molecularly between each other and with ZYMV, WMV or the PRSV cluster (Table 1). Clover yellow vein virus and turnip mosaic have a broad host range and are present worldwide but are only minor viruses on cucurbits. The other viruses are more cucurbit-restricted and have a limited geographic distribution even if they can be locally important (Lecoq et al., 1998; Perotto et al., 2017).

Poleroviruses

Poleroviruses are persistently transmitted by aphids. They are phloem-restricted and are not mechanically transmissible. In cucurbits, poleroviruses usually induce yellowing symptoms on the older leaves that become thickened and brittle. They affect the yield of infected plants but have usually no impact on fruit quality. Poleroviruses have single-stranded positive-stranded RNA genomes of 5.6 kb, encapsidated in icosahedral particles of circa 25 nm diameter. The first cucurbit polerovirus described in 1992 in France, cucurbit aphid-borne yellows virus (CABYV), was present there at least 10 years before but had long been unnoticed (Lecoq et al., 1992). Besides cucurbits, CABYV infects many weeds that are usually symptomless. CABYV is present worldwide except in some islands. Two main molecular groups have been observed, one containing Asian isolates, the other isolates from America, Africa and Europe (Kassem et al., 2013).

Besides CABYV, at least five poleroviruses inducing similar symptoms have later been described on cucurbits (Knierim et al., 2014) (Table 1). Recombinants between CABYV and melon aphid-borne yellows virus have been observed (Knierim et al., 2010). Except pepo aphid-borne yellows virus, all these viruses are present so far in Eastern Asia only (Table 1). No seed transmission was observed for cucurbit-infecting poleroviruses.

2. WHITEFLY-TRANSMITTED VIRUSES: EMERGING VECTORS, EMERGING VIRUSES

Whereas aphid-transmitted viruses remain important in temperate countries, whitefly-transmitted ones have emerged worldwide in the last decades. The greenhouse whitefly *Trialeurodes vaporariorum* and the tobacco whitefly *Bemisia tabaci* are the most important vectors. *B. tabaci* is now considered as a species complex including over 40 species (Elfekih et al., 2018). The MEAM1 and MED biotypes (formerly B and Q, respectively) have emerged throughout the world thanks to their high fitness and frequent resistance to insecticides. The most important viruses transmitted by whiteflies on cucurbits belong to the genera *Begomovirus*, *Ipomovirus* and *Crinivirus*.

Begomoviruses

Begomoviruses are single-stranded DNA viruses. Their genome consists of one or two circular DNAs (DNA-A and DNA-B) of 2.6 kb each, encapsidated in particles presenting a very typical double-icosahedral shape, giving its name to the *Geminiviridae* family (gemi = twin). Begomoviruses are persistently transmitted by whiteflies from the *Bemisia tabaci* complex. Virus acquisition takes place within several hours of insect feeding, then the insects remain viruliferous for their whole life. There is generally no replication in the vector nor transovarian transmission to the offspring. Some begomoviruses are also transmitted by other whiteflies including *T. vaporariorum* (Sangeetha et al., 2018).

Begomoviruses belong to two molecular clades, « Old World » (OW) and « New World » (NW). The OW clade is considered as basal in begomovirus evolution. It contains both monopartite and bipartite viruses, whereas NW viruses are bipartite (Nawaz-ul-Rehman and Fauquet, 2009). Cucurbit-infecting begomoviruses are found both in the OW and NW clades and are mostly bipartite (Romay et al., 2014) (Table 1). Begomoviruses can be associated with satellite molecules that are ssDNA molecules of circa 1.3 kb, dependent on their helper virus to complete their cycle. They do not encode any coat protein and are encapsidated in the capsid of their helper virus. Betasatellites usually increase the severity of viral infections and contribute to overcome resistance genes (Zhou, 2013). Alphasatellites, mostly associated with betasatellites, usually have no obvious effect on their helper virus (Zhou, 2013), but they can also contribute to reduce betasatellite accumulation and symptom severity (Idris et al., 2011). Satellites were thought to be associated with monopartite OW begomoviruses only, but atypical alphasatellites were found with some bipartite NW ones including melon chlorotic mosaic virus (MeCMV) (Romay et al., 2010). Beta- and alphasatellites are also associated with some OW bipartite begomoviruses, particularly tomato leaf curl New Delhi virus (ToLCNDV, see below)

Before 1998, only two begomoviruses were described on cucurbits: the OW watermelon chlorotic stunt virus (WmCSV) in the Red Sea region, and the NW squash leaf curl virus (SLCuV) in Central and Northern America (Lecoq and Desbiez, 2012). Since then, the emergence of *B. tabaci* MEAM1 and MED has prompted that of the viruses they transmit. Better knowledge of virus variability has also led to the characterization of new viruses and the distinction of members in species complexes, as for SLCuV and squash mild leaf curl virus that constitute different species. Asian squash-infecting begomoviruses are distinct from SLCuV and SqMLCV and constitute at least four species (Table 1) (<https://talk.ictvonline.org/taxonomy/>). Nowadays at least 18 begomovirus species are described on cucurbits, with contrasted geographic range and agronomic impact (Table 1). Limited long-distance exchanges have taken place: the NW virus SqLCV was introduced in the 2000s in Israel, Egypt and Jordan (Lecoq and Desbiez, 2012). The OW virus ToLCNDV was first described in India but is currently spreading in the Mediterranean Basin and Asia. ToLCNDV isolates from the Mediterranean Basin are very homogeneous molecularly, suggesting a unique dissemination event (Zaidi et al., 2017; Juarez et al., 2019). The host range of ToLCNDV includes tomato as a major host, but also 43 other species including cucurbits (Zaidi et al., 2017). The emerging Mediterranean Basin isolates are highly adapted to cucurbits but do not perform well on tomato even if whitefly transmission between tomato and cucurbits is possible (Fortes et al., 2016). In its country of origin, ToLCNDV is frequently associated with satellites with a low specificity (it can replicate several different satellites). DNA-A of ToLCNDV can also trans-replicate DNA-B of other begomoviruses, what may contribute to its

great adaptability and epidemiological success. No satellite was associated with the emerging Mediterranean Basin isolates so far. ToLCNDV has not yet emerged in America and Eastern Asia.

Ipomoviruses

Ipomoviruses, like potyviruses, are members of the family *Potyviridae*. Contrary to potyviruses they are not aphid-borne but are transmitted by whiteflies in a semi-persistent way: acquisition and transmission happen in a few hours. The viruses do not multiply in the whiteflies and are not transmitted to the offspring. Three ipomoviruses infect cucurbits: cucumber vein yellowing virus (CVYV), squash vein yellowing virus (SqVYV) and coccinia mottle virus (CocMoV). They share a similar genomic organization, differing from that of potyviruses in the 5' part of the genome (Dombrovsky et al., 2014). Ipomoviruses induce vein yellowing and mosaic symptoms on cucurbit leaves. Synergism in co-infection with other viruses can result in enhanced symptoms and important losses (Gil-Salas et al., 2012). CVYV was first described in Israel in 1960, and has since been observed throughout the Middle East and Mediterranean Basin. It is now emerging in southern Europe in relation to high populations of *B. tabaci* MEAM1 and MED. Phylogenetic analyses suggested that CVYV originated in the Middle East (Velasco et al., 2016), but highly divergent and variable CVYV isolates were also observed in Sudan, indicating long-term presence of the virus in Sub-Saharan Africa. The strains now emerging in the Mediterranean Basin are more closely related to the Middle East isolates than to the Sudanese ones (Desbiez et al., 2019). CocMoV, has been described in Sudan on the wild perennial cucurbit *Coccinia grandis*. Although it readily infects cultivated cucurbits in laboratory conditions, it has never been observed on crops. This may be related to a low transmissibility by the local vectors or absence of crops in the vicinity of the infected coccinia. It is an example of a minor virus that might emerge if it is introduced in a favourable environment (Desbiez et al., 2016). SqVYV was first described in Florida (Adkins et al., 2007) and later in Puerto Rico and California. Its host range is mostly limited to cucurbits, the most severe symptoms being observed in squash and in watermelon, where it induces vine decline and fruit rot. It was found in 2014 in Israel (Reingold et al., 2016) and in Iran (Abkhoo, direct GenBank submission). The high molecular divergence between isolates from America, Israel and Iran suggest that the presence of the virus in these areas is not related to direct and recent genetic exchanges.

Criniviruses

Criniviruses are single-stranded bipartite RNA viruses that have thin filamentous flexuous particles. Four criniviruses infect cucurbits: beet pseudo-yellows virus (BPYV), lettuce infectious yellows virus (LIYV), cucurbit yellow stunting disorder virus (CYSDV) and cucurbit chlorotic yellows virus (CCYV). The symptoms they induce on cucurbits are indistinguishable visually, and very similar to those of poleroviruses: interveinal yellowing of older leaves, sometimes spreading to almost all the plant for the most susceptible cultivars.

BPYV, the first whitefly-transmitted crinivirus described, has a wide host range including ornamentals, crops and weeds. Originally found in California, it is now present worldwide, probably in relation to frequent exchanges of susceptible hosts including vegetatively propagated ones. In temperate areas, BPYV is often found in greenhouses where the conditions are favourable for its vector *T. vaporariorum*.

LIYV was found in 1981 in the desert regions of California and Arizona (Wisler et al., 1998) where it caused important damages on cucurbits but also on lettuce and sugar beet. LIYV is well transmitted by the A biotype of *B. tabaci* but is very inefficiently transmitted by the MED and MEAM1 biotypes. When MEAM1 replaced the A biotype in the USA in the 1980s, LIYV completely disappeared but it was later replaced by viruses efficiently transmitted by MEAM1, particularly CYSDV (Wintermantel et al., 2017).

CYSDV and CCYV are transmitted by the same vector *B. tabaci* MEAM1 and MED and their dispersion patterns show some similarities. CYSDV was first described in the United Arab Emirates in 1982. It has spread to the whole Middle East and Mediterranean Basin in the 1980s-1990s, and is also present in Sub-Saharan Africa (Mohammed et al., 2014). Its host range among crops is mostly restricted to cucurbits, but it infects numerous weeds that can constitute

reservoirs (Orfanidou et al., 2019). It was detected in North America in 2000 and has now become an agronomic problem in that region, in relation to very high vector populations (Wintermantel et al., 2017). CCYV is also present in the Middle East and Sub-Saharan Africa and is now spreading in the Mediterranean Basin (Orfanidou et al., 2019) and North America (Wintermantel et al., 2019), but contrary to CYSDV it was first described in Japan (Okuda et al., 2010) and is present in China and Taiwan.

Molecular diversity within each crinivirus species is very limited, and makes it difficult to estimate genetic exchanges between distant areas (Orfanidou et al., 2019). For CYSDV, two clades have been described, “Eastern” (Arabia, Sudan, Iran) vs. “Western” (Mediterranean Basin). For CCYV, Asian and Mediterranean isolates were very similar, suggesting recent exchanges (Orfanidou et al., 2019).

3. THRIPS-TRANSMITTED VIRUSES: GEOGRAPHICALLY RESTRICTED BUT LOCALLY IMPORTANT

Six viruses in the genus *Tospovirus*, order *bunyavirales*, infect cucurbits. Tospoviruses are transmitted by thrips in a persistent multiplicative way. The viruses are acquired by larvae and transmitted by the adults, and they multiply in their vector. Indeed, many members of the *bunyavirales* are insect-infecting viruses and tospoviruses supposedly evolved from an insect-infecting ancestor (Marklewitz et al., 2015). Tospoviruses have a tripartite RNA genome, encapsidated in quasi-spherical enveloped particles 75 to 100 nm in diameter. Their symptoms on cucurbits are frequently very severe, including mosaics and dwarfing but also necrosis that can lead to plant death. The most common tospovirus worldwide is tomato spotted wilt virus (TSWV). It is a major pathogen on tomato and a wide range of crops and ornamentals, but on cucurbits it has only been observed occasionally in several regions of the world (Romay et al., 2014). The other cucurbit-infecting tospoviruses are geographically restricted and present a much narrower host range than TSWV but they can be locally important. Watermelon bud necrosis virus, watermelon silver mottle virus, and melon yellow spot virus (MYSV) are present in different countries from Asia (India, China, Thailand, Japan) whereas melon severe mosaic virus and zucchini lethal chlorosis virus were found in Latin and South America (Mexico, Brazil) (Table 1). No tospovirus has been observed inducing important epidemics so far in Europe, Africa and North America. However, the Asian MYSV was recently observed in Ecuador (Quito-Avila et al., 2014), indicating that the geographic structure of cucurbit tospoviruses is changing and long-distance spread can take place, probably through the trade of susceptible hosts or the accidental spread of viruliferous thrips. Since these viruses are very damaging and difficult to control, particular care should be taken to avoid their accidental long-distance dissemination.

4. CONTACT, -SEED-AND SOIL-TRANSMITTED VIRUSES

Tobamoviruses

Tobamoviruses were the first plant viruses studied. Their high stability in and outside plants contributes to their efficient dissemination and the difficulty to control them. Tobamoviruses have a ssRNA genome of ~6.5 kb, encapsidated in rigid rod-shaped particles 300 nm long. They do not have a specific biotic vector, but they are easily transmitted by contact and remain infectious for a long time on surfaces, in plant debris or in water. They are also seed-transmitted (Dombrovsky and Smith, 2017). Contrary to other plant viruses, tobamoviruses seem to have undergone long-term co-evolution with their hosts as they constitute three clusters associated with asteroid, rosid or caryophyllid angiosperms. The most important tobamovirus on cucurbits is cucumber green mottle mosaic virus (CGMMV). CGMMV induces more or less severe leaf and fruit mottling, particularly in cucumber and watermelon (Dombrovsky and Smith, 2017). Since its first description in 1935 in England; its distribution to additional countries increased slowly between 1935 and 1985, faster between 1986 and 2006, and rapidly between 2007 and 2016 (Dombrovsky et al., 2017). It is now present on all continents except in South America. Seed transmission must have contributed to its rapid spread, as well as its ability to rapidly colonize weeds close to infected crops, making eradication efforts useless (Dombrovsky and Smith, 2017). Phylogenetic analyses indicated the presence of distinct CGMMV clades correlated with

geographic origin of the isolates, showing a distinction between East Asia and European isolates (Dombrovsky and Smith, 2017), what does not appear consistent with a rapid worldwide dissemination through seed transmission. However phylogenetic signal is limited by the low genetic diversity of the virus.

At least five other tobamoviruses infect cucurbits (Table 1). They are mostly restricted to Eastern Asia so far (Table 1), even if their seed transmissibility makes them potential threats worldwide.

Other seed-borne viruses

Besides tobamoviruses, several viruses are transmitted through seed (Table 1), either via external contamination of the tegument or more rarely through infection of the embryo. Squash mosaic virus (genus *Comovirus*) is transmitted by several beetle species, mechanically by pruning operations, and by seeds, what is probably the means by which it has spread throughout the world (Lecoq et al., 1998). It can reach the embryo and multiply during germination, leading to rapid systemic infection of the plantlets (Lecoq and Katis, 2014). Melon rugose mosaic virus (genus *Tymovirus*) is seed transmitted in melon (Mahgoub et al., 1997); however it has not yet spread worldwide and is restricted so far to the Red Sea region.

Melon necrotic spot (MNSV, genus *Carmovirus*) is seed-transmitted in the presence of the soil fungus *Olpidium bornovanus*. The virus is carried in the seed, released in the soil during germination, and introduced in the plant by fungal zoospores. It is also transmitted directly from plant to plant by zoospores. *O. bornovanus* being a very resistant and ubiquitous fungus, vector-assisted seed transmission must have contributed to the worldwide spread of MNSV.

Traditional seed transmissibility tests include serological tests on seeds, what often greatly overestimate the real seed transmission, and observation of symptoms on plantlets after germination tests (Dombrovsky and Smith, 2017). However, in some cases plants infected from seed are asymptomatic and have very low virus titres that can be detected only by molecular methods (Simmons et al., 2013). Using molecular approaches, seed transmission was observed for viruses considered as non-seed-transmissible, including begomoviruses (Mabvakure et al., 2016; Sangeetha et al., 2018). The agronomic impact of cryptic infections after seed transmission is not well known, but since in some cases vector transmission to new plants has been demonstrated from asymptomatic plants infected from seeds, these plants can constitute primary inoculum to start epidemics. The importance of seed transmission for long-distance spread of plant viruses has probably long been underestimated, and particular care should be taken during seed trade.

Soil-borne viruses

Besides MNSV, some viruses are soil-transmitted, either by fungi or by nematodes. Several nepoviruses, transmitted by soil nematodes, infect cucurbits (Table 1). They generally have a broad host range outside cucurbits, including annual and perennial hosts. Each species is transmitted by a few specific nematode species, and some are also transmitted by seed. They are usually geographically restricted, but tobacco ringspot virus, endemic in cucurbits in America, has been reported on other crops in different areas where it probably spread through dissemination of infected plant material. Viruses transmitted by soil fungi include MNSV and other viruses in the same family *Tombusviridae*. They usually have a limited geographic distribution and their agronomic impact is low (Lecoq et al., 1998)

5. MINOR AND PARTIALLY CHARACTERIZED VIRUSES

Some viruses representing the unique cucurbit-infecting species in their genus have been known for long, but have never been observed outside the area where they were first described. It is the case for Ourmia melon virus, observed only in the North-West of Iran, the carlavirus melon yellowing-associated virus in Brazil, the torradovirus squash chlorotic leaf spot and the sobemovirus snake melon asteroid mosaic virus found only in Sudan (Table 1). Some of them may have a larger geographic range but may have been undetected because no accurate diagnostic was established. For highly damaging and/or widespread viruses, researches are usually undertaken

to characterize their biological and molecular properties and develop serological or molecular diagnostic tools, but it is not always the case for minor viruses. On the other hand, the development of untargeted molecular diagnostic by high-throughput sequencing (HTS) has revealed viruses that were widespread but latent, both in crops and in wild plants (Prendeville et al., 2012). Endornaviruses, for instance, are only transmitted vertically and do not induce symptoms in their hosts (Fukuhara et al., 2006; Sabanadzovic et al., 2016). They represent some of the lately discovered commensal or even symbiotic viruses that have long been unnoticed because only viruses causing damages on crops were studied (Prendeville et al., 2012; Roossinck, 2012). The use of HTS for diagnostic is a very powerful tool for virus characterization, but it should not be disconnected from biology. Indeed, many recent descriptions of new viruses rely only on their sequence properties, without information on their symptomatology, host range or transmission properties, what makes it difficult to estimate the risks of dissemination and potential agronomic impact of these viruses.

6. CONTROL OF VIRUSES

Despite the high diversity of plant viruses and of their modes of dissemination, control measures against these pathogens are to a large extent common to many of them (Lecoq and Katis, 2014). There is no curative chemical treatment against plant viruses. Virus control relies mostly on cultural practices and the use of host genetic resistance when it is available.

Prophylaxis and good cultural practices involve limitation of virus sources and virus vectors in the crops and their vicinity. Weeding and the removal of volunteers before planting contribute to reduce the primary inoculum in crops. Overlapping crops should also be avoided, to limit the sources of infection to the young crops. Seeds can be produced in regions where seed-borne viruses are not prevalent, or mother plants may be grown under protected conditions. Serological or molecular testing of seed lots, and destruction of the positive ones, are important components of virus containment. For stable seed-borne viruses like CGMMV, seed treatment with chemicals or heat can reduce or abolish seed transmission. Long-distance movements of plant material should be limited to reduce the risks of virus spread.

In crops, plastic or unwoven covers can protect young plants from viruliferous insects, but the covers have to be removed to allow pollination. Plastic mulches contribute to the limitation of weeds and also have a repellent effect on aphids and whiteflies, at least until plant growth covers most of their surface. Disinfection of grafting and pruning tools with trisodium phosphate or skimmed milk is recommended (Coutts et al., 2013; Lecoq and Katis, 2014). Control of vectors in crops can be more easily achieved in greenhouse conditions, with the use of insect-proof netting, than in the field. Insecticide treatment or biological control of the vectors may contribute to reducing virus spread, particularly for persistently-transmitted viruses, but their efficiency against non-persistently transmitted viruses is limited or null.

Cross-protection, i.e. the use of a mild strain to protect plants against a severe strain of the same virus, has been used successfully against ZYMV. Attenuated strains have been obtained for several other viruses but have not been broadly used (Lecoq and Katis, 2014). One limitation of cross-protection is its high specificity (Lecoq and Katis, 2014).

When they are available, resistant cultivars constitute the easiest and most environmentally-friendly way to control viruses. Resistance traits have been searched in the biodiversity of cultivated species and their wild relatives since the beginning of the 20th Century, both by private breeding companies and research institutes (Lecoq and Katis, 2014). Many commercial cultivars of cucurbits are resistant or tolerant to viruses. Most resistances used by breeders rely on one or a few major genes, as they were the most easily introgressed in agronomically interesting cultivars. Resistance factors can target any step of the virus cycle with very different mechanisms. Dominant resistance factors are involved in pathogen recognition of the virus, leading to a signalling pathway that results in induction of defence mechanisms. In the case of recessive resistance as well as non-host resistance, a plant factor required by the virus for its cycle is absent or modified so that the interaction with virus components cannot take place and the virus cannot complete its cycle (Lecoq and Katis, 2014). Pathogen-derived resistance has also

been used commercially against ZYMV, PRSV and CMV in squash in the USA (Lecoq and Katis, 2014).

One limitation of the use of resistance genes is the availability of resistance factors against each virus. Introducing these factors in high-standard cultivars is costly and time-consuming and it is difficult to keep pace with the increasing number of viruses. Resistance genes corresponding to factors important for viral infectivity can constitute good candidates for broad-spectrum virus resistance. For instance, melon and cucumber plants mutated or silenced in a translation initiation factor required for potyvirus infection presented broad virus resistance (Chandrasekaran et al., 2016; Rodriguez-Hernandez et al., 2012). However, plant viruses have developed counter-defence mechanisms and can in some cases evolve rapidly by mutation or recombination to overcome host resistance (Desbiez et al., 2011b; Harrison, 2002). The selection of putatively durable resistance early in the selection scheme, the optimized deployment of resistances in agricultural landscapes and the selection of multigenic, partial and broad-spectrum resistances or tolerances could contribute to preserve the long-term efficiency of genetic virus control (Acosta-Leal et al., 2011).

CONCLUSIONS

The number of virus species described as infecting cucurbits is still rapidly increasing: About 20 species were described in 1980 (Lovisolo, 1980), 35 in 1998 (Lecoq et al., 1998), 59 in 2012 (Lecoq and Desbiez, 2012) and more than 90 in 2019 (Table 1). Among the “new” viruses described, some are endemic whereas others are present worldwide. Aphid-borne viruses still constitute major problems in temperate climates, whereas whitefly-transmitted ones are emerging in Mediterranean/tropical areas wherever the invasive MED and MEAM1 *B. tabaci* are present. The high increase in host connectivity due to global trade, as well as climatic changes involving changes in hosts and vectors, play important roles in the rapidly changing situation of plant viruses (Elena et al., 2014). Why some viruses emerge while others remain unimportant is partially understood. Intrinsic properties like seed transmissibility and a large host range ought to favour virus emergence, but it is not always the case (Table 1). Local ecological conditions, as well as the chance of introduction of minor viruses in the international trade, can influence the dissemination and potential emergence of plant viruses. Particular care should be taken when exchanging genetic material, and good practices involving seed disinfection and insect control should always be applied to limit the impact of viral diseases on cucurbits.

ACKNOWLEDGEMENTS

We thank Dr H. Lecoq for critical review of the manuscript

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Table 1. Viruses infecting cucurbits and their biological properties. The most important or currently emerging viruses worldwide are indicated in bold. Viruses in italics are not yet acknowledged by the International Committee for the Taxonomy of Viruses (ICTV)

Genus and species	Means of spread	First description	Geographic distribution	Host range	
				Cucurbits	Outside cucurbits
• Begomovirus					
Melon chlorotic mosaic virus (MeCMV)	Whitefly	2004	Venezuela	narrow	narrow
Tomato leaf curl new Delhi virus (ToLCNDV)	Whitefly	1948	Indian Peninsula, Mediterranean Basin, Indonesia, Thailand	wide	wide
Squash leaf curl virus (SLCuV)	Whitefly	1981	USA, Israel, Jordan, Egypt	wide	narrow
Squash mild leaf curl virus (SMLCuV)	Whitefly	1978	USA, Jordan	narrow	narrow
Watermelon chlorotic stunt virus (WmCSV)	Whitefly	1994	Iran, Yemen, Sudan, Israel	intermediate	narrow
Cucurbit leaf crumple virus (CuLCrV)	Whitefly	2000	USA, Mexico	intermediate	narrow
Melon chlorotic leaf curl virus (WCLCuV)	Whitefly	2004	Nicaragua, Costa Rica, Guatemala	wide	wide
Telfairia golden mosaic virus (TelGMV)	Whitefly	2016	Cameroon	unknown	unknown
Coccinia mosaic Tamil Nadu virus (CMTNDV)	Whitefly	2016	India	unknown	unknown
Chayote yellow mosaic virus (ChaYMV)	Whitefly	2016	Nigeria, Benin, Togo	narrow	unknown
Tomato leaf curl Palampur virus (ToLCPaV)	Whitefly	2007	India, Pakistan, Iran	wide	wide
Tomato yellow leaf curl-Mild virus (TYLCV-Mld)	Whitefly	1964	Jordan, Latin America (on cucurbits)	narrow	intermediate
Luffa yellow mosaic virus (LYMV)	Whitefly	2003	Vietnam	unknown	unknown
Squash leaf curl China virus (SqLCCNV)	Whitefly	1998	Southern Asia, India	wide	unknown
Squash leaf curl Philippines virus (SLCuPhV)	Whitefly	2003	Philippines	unknown	unknown
Squash leaf curl Yunnan virus (SLCuYnV)	Whitefly	2003	China	unknown	unknown
Pumpkin yellow mosaic virus (PuYMV)	Whitefly	2001	Malaysia	unknown	unknown
• Curtovirus					
Beet curly top virus (BCTV)	Leafhopper	1909	Worldwide	wide	wide
• Clecrusatellite					
Melon chlorotic mosaic alphasatellite (MeCMA)	whitefly	2010	Venezuela	narrow	narrow
• Betasatellite					
Momordica yellow mosaic betasatellite (MomYMB)	whitefly	2016	Benin	(momordica, chayote)	unknown
• Alphacryptovirus					
Citrullus lanatus cryptic virus (CLCV)	Vertical	2013	Israel	unknown	unknown
• Alphaendornavirus					
Cucumis melo alphaendornavirus (CmEV)	Vertical t	2016	Worldwide	intermediate	unknown
Lagenaria siceraria alphaendornavirus (LsEV)	Vertical	2014	China		

• Nucleorhabdovirus						
Eggplant mottled dwarf virus (EMDV)	leafhopper	1982	Mediterranean Basin	intermediate	wide	
• Tospovirus						
Tomato spotted wilt virus (TSWV)	Thrips	1930	worldwide	wide	wide	
Zucchini lethal chlorosis virus (ZLCV)	Thrips	1999	Brazil	wide	narrow	
Melon severe mosaic virus (MeCSV)	Thrips	2009	Mexico	intermediate	narrow	
Watermelon silver mottle virus (WSMoV)	Thrips	1982	China, Taiwan, Thailand	wide	wide	
Melon yellow spot virus (MYSV)	Thrips	1999	China, Japan, Thailand, India, Ecuador	wide	intermediate	
Watermelon bud necrosis virus (WBNV)	Thrips	1993	India	wide	wide	
• Tenuivirus						
Melon chlorotic spot virus (MeCSV)	unknown (planthopper?)	2019	France	narrow	wide	
• Comovirus						
Squash mosaic virus (SqMV)	Beetle, seed	1941	Worldwide	wide	narrow	
• Fabavirus						
Cucurbit mild mosaic virus (CuMMV)	Aphid	2012	China	unknown	unknown	
• Nepovirus						
Tobacco ringspot virus (TRSV)	Nematode, seed	1927	Worldwide	wide	wide	
Tomato ringspot virus (ToRSV)	nematode	1936	Worldwide	wide	wide	
Tobacco black ring virus (TBRV)	nematode	1946	Worldwide	wide	wide	
Artichoke yellow ringspot virus (AYRSV)	nematode(?)	1973	Greece, Italy, Turkey	wide	wide	
Melon mild mottle virus (MMMoV)	nematode(?)	2011	Japan	narrow	narrow	
• Torradovirus						
Squash chlorotic leaf spot virus (SqCLSV)	Whitefly	2016	Sudan	wide	narrow	
• Tymovirus						
Melon rugose mosaic virus (MEMV)	Mechanical	1983	Yemen, Sudan	intermediate	narrow	
Chayote mosaic virus (ChMV)	Mechanical	1997	Costa Rica	intermediate	narrow	
Wild cucumber mosaic virus (WCMV)	Mechanical, beetle	1952	USA	wide	narrow	
• Potexvirus						
Lagenaria mild mosaic virus (LaMMoV)	Mechanical, seed	2011	Myanmar, India	wide	narrow	
• Carlavirus						
Melon yellowing associated virus (MYaV)	Whitefly	2005	Brazil	unknown	unknown	
Cucumber vein clearing virus (CuVCV)	whitefly	2011	Tanzania	(cucumber)	unknown	
• Potyvirus						
Zucchini yellow mosaic virus (ZYMV)	Aphid	1981	Worldwide	wide	intermediate	
Papaya ringspot virus (PRSV)	Aphid	1949	Worldwide	wide	narrow	

Watermelon mosaic virus (WMV)	Aphid	1954	Worldwide	wide	wide
Moroccan watermelon mosaic virus (MWMV)	Aphid	1974	Africa, Mediterranean Basin	wide	narrow
Algerian watermelon mosaic virus (AWMV)	Aphid	1990	Algeria, Nigeria	wide	narrow
Zucchini yellow fleck virus (ZYFV)	Aphid	1981	France, Italy, Israel	wide	narrow
Clover yellow vein virus (CIYVV)	Aphid	1965	Worldwide, occasional	narrow	wide
Turnip mosaic virus (TuMV)	Aphid	1921	Worldwide, occasional	wide	wide
Melon vein-banding mosaic virus (MVBMV)	Aphid	1993	China, Taiwan	wide	intermediate
Telfairia mosaic virus (TelMV)	Aphid	1975	Nigeria	wide	wide
Watermelon leaf mottle virus (WLMV)	Aphid	2000	Florida	wide	unknown
Zucchini tigré mosaic virus (ZTMV)	Aphid	1986	America, Reunion, Myanmar, France, India, Pakistan, China	wide	narrow
Zucchini shoestring virus (ZSTV)	Aphid	2016	South Africa	unknown	unknown
Sudan watermelon mosaic virus (SuWMV)	Aphid	2016	Sudan	wide	narrow
Wild melon vein banding virus (WMVBV)	Aphid	2016	Sudan	wide	narrow
Cucurbit vein banding virus (CVBV)	Aphid	2018	Argentina	unknown	unknown
• Ipomovirus					
Cucumber vein yellowing virus (CVYV)	Whiteflies	1960	Mediterranean Basin, Sudan	wide	narrow
Squash vein yellowing virus (SqVYV)	Whiteflies	2007	USA, Israel	wide	narrow
Coccinia mottle virus (CocMoV)	Whiteflies	2016	Sudan	wide	narrow
• Polerovirus					
Cucurbit aphid borne yellows virus (CABYV)	Aphid	1992	Worldwide	wide	intermediate
Melon aphid borne yellows virus (MABYV)	Aphid	2008	Taiwan, China	wide	unknown
Suakwa aphid borne yellows virus (SABYV)	Aphid	2009	Taiwan	wide	unknown
<i>Luffa aphid borne yellows virus (LABYV)</i>	Aphid	2014	Thailand	wide	unknown
Pepo aphid borne yellows virus (PABYV)	Aphid	2014	Africa, Greece	wide	unknown
<i>Cucumber aphid borne yellows Henan virus (CuABYV-Hn)</i>	Aphid	2014	China	unknown	unknown
• Tombusvirus					
Cucumber necrosis virus (CNV)	Fungus,	1959	Canada, USA	wide	wide
Cucumber Bulgarian latent virus (CBLV)	Fungus	2003	Bulgaria	narrow	narrow
• Aureusvirus					
Cucumber leaf spot virus (CLSV)	fungus, mechanical	1982	Bulgaria, Greece, Spain France, Israel	wide	wide
• Carmovirus					
Melon necrotic spot virus (MNSV)	fungus, seed	1966	Worldwide	wide	narrow
Cucumber soil-borne virus (CuSBV)	fungus	1983	Lebanon	wide	wide
• Necrovirus					
Tobacco necrosis virus (TNV)	Fungus	1935	France, Italy	wide	wide

<ul style="list-style-type: none"> Cucumovirus 						
Cucumber mosaic virus (CMV)	Aphid	1916	Worldwide	wide	wide	
<ul style="list-style-type: none"> Illarvirus 						
Tobacco streak virus (TSV)	Pollen, seed	1936	Worldwide	narrow	wide	
<ul style="list-style-type: none"> Crinivirus 						
Cucurbit yellow stunting disorder virus (CYSDV)	Whitefly	1996	Mediterranean Basin, Texas, Mexico	intermediate	narrow	
Beet pseudo-yellows virus (BPYV)	Whitefly	1965	Europe, Mediterranean Basin, California	wide	wide	
Lettuce infectious yellows virus (LIYV)	Whitefly	1982	California	wide	wide	
Cucurbit chlorotic yellows virus (CCYV)	Whitefly	2010	China, Taiwan, Japan, Sudan, Iran, Greece, USA	wide	narrow	
<ul style="list-style-type: none"> Tobamovirus 						
Cucumber green mottle mosaic virus (CGMMV)	Mechanical, seed	1935	Worldwide	wide	narrow	
Cucumber fruit mottle mosaic virus (CFMMV)	Mechanical, seed	2001	Israel, Korea	wide	narrow	
Kyuri green mottle mosaic virus (KGMMV)	Mechanical, seed	2000	Japan, Korea, Indonesia	wide	narrow	
Zucchini green mottle mosaic virus (ZGMMV)	Mechanical, seed	2000	Korea	wide	unknown	
<i>Watermelon green mottle mosaic virus (WGMMV)</i>	Mechanical, seed	2019	<i>Taiwan</i>	wide	narrow	
Cucumber mottle virus (CuMoV)	Mechanical, seed	2007	Japan	wide	narrow	
<ul style="list-style-type: none"> Sobemovirus 						
Snake melon asteroid mosaic virus (SMAMV)	Beetle	2011	Sudan	narrow	narrow	
<ul style="list-style-type: none"> Ourmiavirus 						
Ourmia melon virus (OuMV)	Mechanical	1988	Iran	intermediate	wide	
<ul style="list-style-type: none"> Warnavirus 						
Watermelon virus A (WVA)	unknown	2017	China	unknown	unknown	
<ul style="list-style-type: none"> Unknown 						
<i>Watermelon crinkle-leaf associated virus 1 (WCLaV-1)</i>	unknown	2017	China	unknown	unknown	
<i>Watermelon crinkle-leaf associated virus 2 (WLCaV-2)</i>	unknown	2017	China	unknown	unknown	