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Review

# Viruses of cucurbit crops: current status in the Mediterranean Region

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**Summary.** Cucurbits are among the most cultivated crops, and the most economically important species are melon (*Cucumis melo* L.), cucumber (*Cucumis sativus* L.), watermelon (*Citrullus lanatus* Thumb.), squash (*Cucurbita pepo* L.), and pumpkin (*Cucurbita* spp.). These crops have become important income sources providing export and local consumption commodities in many Mediterranean countries. Increased area of cucurbits has led to the emergence of several viral diseases, which can have impacts on crop production and threaten agricultural sustainability. An overview of the most damaging cucurbit viruses in the Mediterranean area is provided to improve understanding of the diseases they cause and to emphasize effective disease management strategies. An updating of the geographical distribution of these viruses, the symptoms they cause and their means of transmission is also provided. Disease management methods and measures by farmers and phytosanitary authorities to address the virus outbreaks are outlined, including diagnostics, use of tolerant cultivars, and chemical and biological vector control. Mediterranean region farmers have learned many lessons from the damaging pandemics caused by cucurbit viruses, through the extensive published research, and this review provides a basis for managing future outbreaks of newly emerging virus infections.

**Keywords.** Alternative disease management strategies, whitefly-borne viruses, aphid-borne viruses, emerging diseases.

## INTRODUCTION

The *Cucurbitaceae* family includes more than 800 plant species in 120 genera (Welbaum, 2015), which are herbaceous plants, annuals or perennials, found in temperate and tropical regions. The most cultivated cucurbit crops in

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the Mediterranean region are cucumber (*Cucumis sativus* L.), melon (*Cucumis melo* L.), watermelon (*Citrullus lanatus* Thunb.), pumpkin (*Cucurbita maxima* Duch. and *Cucurbita moschata* Duch.), and zucchini (*Cucurbita pepo* L.) (Robinson *et al*., 1997). Due to the economic importance of these crops, cucurbit-producing countries need to improve the quality and quantity of their production.

Cucurbits are threatened by a large number of pests and pathogens, including viruses. About 28 plant viruses are currently threatening cucurbit crop production in the Mediterranean region (Lecoq and Desbiez, 2012). The emergence of new virus diseases is now common the pathogens evolve and their genetic diversity increases. This is mainly due to the favourable Mediterranean conditions for virus vectors (mainly insects) to settle and reproduce. Ecosystem simplification, expanding trade, and movement are also important factors of virus dispersion, and vectors play important roles in virus evolution through pathogen dispersion in a variety of plants and zones. This leads recombination and genetic variation in the pathogens, and this continuous and evolutionary process has allowed viruses to adapt to their hosts, by integrating their most complex properties (Navas-Castillo *et al*., 2014; Pozzi *et al*., 2020).

Virus diseases have been emerging for decades among cucurbit species, causing economic and food security threats. These diseases are widely described and studied. The appearance of new viral species over time in several families is frequent (Juárez *et al*., 2019). The incidence and geographical distribution of these viruses increase and expand over time. It is worth noting that viral disease symptoms are variable and diverse and the majority of the viruses induce similar symptoms which makes their identification, based only on symptoms, a difficult task.

Cucurbit-producing countries annually report detection of new viruses or virus isolates. Common symptoms caused by cucurbit viruses include leaf mosaic and curling, and plant size reduction, severe wilting, deformation, discolouration, mottling, embossing, yellowing, and necrosis, symptoms which affect the aesthetic value and yields of produced cucurbit fruit (Blancard *et al*., 1994). The main symptoms observed on cucurbit crops grown in Morocco are illustrated in Figure 1.

Understanding the factors leading to virus disease emergence is the first step in their management, and innovative control strategies are now required. The best disease prevention and management strategies rely on knowledge of the viruses and their vectors (including biological properties and epidemiology), the application of prophylactic measures, and recourse to biological and chemical control methods when required.

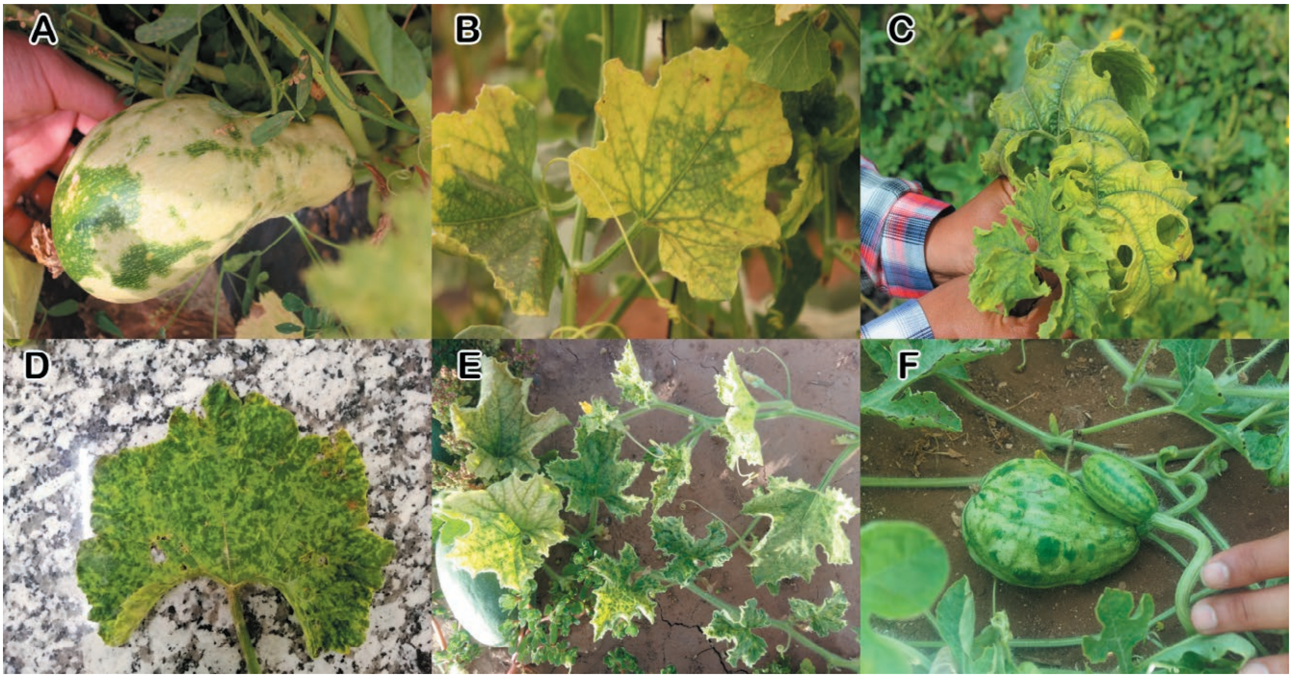

**Figure 1.** Symptoms of virus infections on several cucurbit crops. A. ToLCNDV affecting zucchini fruit, B. ToLCNDV affecting melon leaves C. ToLCNDV affecting zucchini leaf, D. ToLCNDV affecting squash leaf, E. Viral infection symptoms on melon leaves, and F. Viral infection symptoms on watermelon fruits.

This review emphasizes the current situation of the main virus diseases of cucurbits in the Mediterranean region. The viruses included are the most important since they cause significant losses in this area. Research is reviewed on virus genetic diversity, host ranges, transmission, biological properties, and the symptoms they cause. Genetic diversity and mutation and recombination of these pathogens are perceived as major driving forces in the evolution of viruses. Different detection and diagnostic methods are also summarized, which assist understanding of the virus genetic variability and taxonomy. Common strategies for management of cucurbit viruses are also reviewed, including prophylactic measures, pesticides, tolerant host varieties, and biological control.

Cucurbit crops are infected by a variety of viruses that belong to different families. *Geminiviridae* (especially *Begomovirus*) includes the greatest number of viruses reported to cause significant economic losses to cucurbit production (Lecoq and Desbiez, 2012). Other economically important viruses are in *Potyviridae, Bromoviridae,* and *Luteoviridae*. These include *cucurbit aphid-borne yellow virus* (CABYV), *watermelon mosaic virus* (WMV), *cucumber mosaic virus* (CMV), and *zucchini yellow mosaic virus* (ZYMV), which are reported in most Mediterranean countries and are associated with important economic production losses (Adams *et al*., 2011; Lecoq and Desbiez, 2012). Different types of insects act as vectors for cucurbit viruses, including aphids, leafhoppers, and whiteflies which have been the most reported, and these vectors transmit the majority of virus species that affect cucurbits. Several factors are involved in virus emergence through transmission by insects, including virus genetic variation and long-distance transport for trade of vegetables. These can spread viruses to new geographical regions with potential to infect new hosts (Navas-Castillo *et al*., 2011).

## MAJOR VIRUSES THAT AFFECT CUCURBIT CROPS IN THE MEDITERRANEAN REGION

### *Begomoviruses*

#### *Tomato leaf curl New Delhi virus* (ToLCNDV)

ToLCNDV (*Geminiviridae*, *Begomovirus*) is a bipartite begomovirus. The DNA strand of this virus encodes AV1 and AV2 genes in sense orientation of DNA-A, and AC1, AC2, AC3 and AC4 in the complementary sense orientation (Zaidi *et al*., 2017). ToLCNDV DNA-B encodes a nuclear shuttle protein NSR (Open reading frame BV1) and a movement protein MP (Open reading frame BC1). For both ToLCNDV components, virus genes are separated with an intergenic region that comprises a conserved sequence between DNA-A and DNA-B. This region is termed the common region (CR) (Zaidi *et al*., 2017).

ToLCNDV is the only bipartite *Begomovirus* with an extensive host range (Briddon *et al*., 2014). After the first report of this virus on tomato crops (*Solanum lycopersicum* L.) in India (Padidam *et al*., 1995), ToLCNDV was found to be associated with several cultivated plants, including cucurbit crops (watermelon, cucumber, melon, and squash) (Ruiz *et al*., 2016; Moriones *et al*., 2017).

When first described, ToLCNDV was limited to Asian countries including Pakistan, Thailand, Indonesia, Bangladesh, and the Indian subcontinent. Recently, the virus has spread to new geographical regions and has extended its host range. ToLCNDV is present in several countries, from the Middle East (Iran) to the Mediterranean Basin (Morocco, Algeria, Tunisia, Italy, and Spain) (Moriones *et al*., 2017; Kheireddine *et al*., 2019) (Figure 2).

ToLCNDV was spreading in the Mediterranean region during the period 2012 to 2017. It was first identified in Spain in 2012 in Murcia and Almeria provinces, causing leaf curl on cucurbit plants. In 2013, similar symptoms were observed on zucchini crops grown in Almeria (López *et al*., 2015). Severe damage was observed in 2015 in Tunisia on zucchini, melon, and cucumber crops. Symptoms consisted of severe yellowing and mosaic and curling of young leaves (Mnari-Hattab *et al*., 2015). These symptoms were observed on zucchini squash in Italy in 2015 (Panno *et al*., 2016). In Morocco, similar symptoms were observed in 2017, on zucchini crops grown in Agadir and Taroudant regions (Radouane *et al*., 2018). The virus was also reported in southern France in September 2020 on zucchini (EPPO, 2020; Desbiez *et al*., 2021). These reports suggest recent ToLCNDV introductions into North Africa and Southern Europe. This could be the result of several factors (e.g international trade, vector migration) which could be enhanced by climatic changes.

ToLCNDV is transmitted by the whitefly *Bemisia tabaci* Gennadius in a circulative and persistent manner (Sáez *et al*., 2016). Several genetically distinct but morphologically indistinguishable *B. tabaci* morphocryptic species were identified as vectors of ToLCNDV. The Middle East-Asia Minor 1 and Asia II 1/5/7 strains were reported to transmit the virus in different South Asian regions. However, different *B. tabaci* morphocryptic species were reported to spread the virus in the Mediterranean area. In Spain, ToLCNDV is transmitted by the Q1 cryptic species in tomato, melon, and zucchini crops (Moriones *et al*., 2017). Many ToLCNDV isolates can be

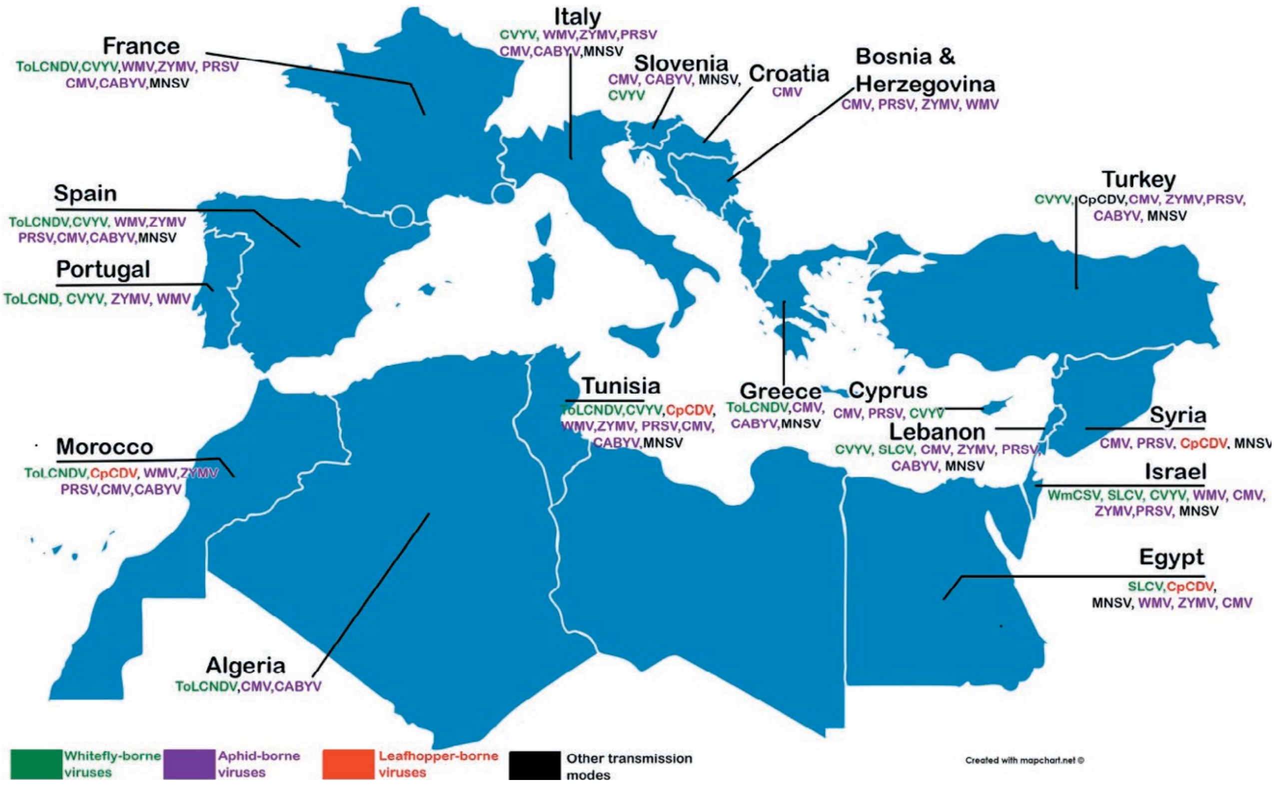

**Figure 2.** Geographic distribution of viruses affecting cucurbit crops in the Mediterranean region.

mechanically transmitted to several hosts. In Taiwan, ToLCNDV causes leaf curl and mosaic, and was reported to be sap transmitted to *Nicotiana benthamniana* Domin and some cucurbit crops including zucchini and cucumber (López *et al.*, 2015).

### *Squash leaf curl virus* (SLCV)

SLCV (*Geminiviridae*, *Begomovirus*) is a bipartite begomovirus. It has geminate particles of 22 x 38 nm (Cohen *et al.*, 1983). The SLCV genome encodes genes in the virion (AV1, BV1) and complementary (AC1, AC2, AC3, AC4, BC1) senses (Abrahamian and Abou-Jawdah, 2013). SLCV was first reported in the United States of America (USA), in Texas (Isakeit, 1994). In the Mediterranean area (CABI/EPPO, 2014), SLCV has been recorded Lebanon (Sobh *et al.*, 2012), Egypt (Mazyad, 2014), and Israel (Antignus *et al.*, 2003). Its geographical distribution was extended to Asia (Jordan and Saudi Arabia), North America (Mexico, Arizona, and California), Central America, and the Caribbean (Guatemala) (CABI/EPPO, 2014) (Figure 2).

SLCV is restricted to cucurbit hosts, including *C. melo*, *C. sativus*, *C. lanatus, C. pepo, C. maxima,* and *C. moschata*. Cucurbit plants infected by SLCV show severe symptoms, including systemic stunting and leaf curling, and chlorosis and mosaic symptoms are observed on watermelon and squash (CABI, 2019). SLCV is naturally transmitted by *B. tabaci*, in a persistent manner (Cohen *et al.*, 1983).

### *Watermelon chlorotic stunt virus* (WmCSV)

WmCSV (*Geminiviridae*, *Begomovirus*) is a bipartite begomovirus. The structure and organization of the WmCSV genome are similar to those of the SLCV (Loebenstein and Lecoq, 2012). Symptoms caused by WmCSV have been observed on almost all cultivated cucurbits, and the virus causes severe damage to watermelon and melon (Abudy *et al.*, 2010). WmCSV was first reported in Yemen, in 1986, on watermelon crops (Walkey *et al.*, 1990), and was subsequently reported in Uganda, Sudan, Iran, Jordan, Oman, and Palestine (Bedford *et al.*, 1994; Kheyr-Pour *et al.*, 2000; Abudy *et al.*, 2010; Al-Musa *et al.*, 2011; Khan *et al.*, 2012; Ali-Shtayeh *et al.*, 2014). In 2002, the virus was isolated from watermelon fields, in Eilat, on the Red Sea coast. Despite eradication of entire crops where WmCSV was reported, the virus quickly spread to many other regions. The first report of WmCSV in the Mediterranean basin was in Israel and Lebanon in 2010 (Samsatly *et al.*, 2012). WmCSV has not been reported in other Mediterranean countries, although WmCSV outbreaks could occur in the Mediterranean region (Abudy *et al.*, 2010; Lecoq and Desbiez, 2012) (Figure 2).

WmCSV infects watermelon and melon crops, and has also been recorded on snake cucumber (*C. melo 'flexuosus'*), *C. moschata,* and wild cucurbits including *Citrullus colocynthis*, and *C. melo 'agrestis'*. Symptoms include chlorotic mottling, vein yellowing, growth delay of young leaves, and reductions in fruit yield. Typical yellowing of shoot apices occurs on watermelon (Kheyr-Pour *et al.*, 2000). WmCSV is transmitted by *B. tabaci* in circulative and persistent mode (Lecoq and Desbiez, 2012).

### *Potyviruses*

#### *Cucumber vein yellowing virus* (CVYV)

CVYV (*Potyviridae*, *Ipomovirus*) has a single 9.7 kb filament (Janssen et al., 2005; Lecoq et al., 2000). CVYV was first reported in Israel by Cohen and Nitzany (1960). It has since been reported in the Mediterranean area (Spain, Portugal, Cyprus, and Tunisia) (Louro *et al.*, 2004; Cuadrado *et al.*, 2007; Yakoubi *et al.*, 2007), in the Middle East (Lebanon, Iran, Jordan, and Turkey) (Mansour and Al-Musa, 1993; Bananej *et al.*, 2007; Abrahamian *et al.*, 2013), in France (Lecoq *et al.*, 2007), and in Sudan (Martelli and Gallitelli, 2008).

CVYV infects several cucurbit hosts including *C. melo*, *C. sativus*, *C. pepo,* and C. *lanatus*. The virus was also identified in several weed species including *Sonchus oleraceus*, *S. asper, S. tenerrimus* (*Compositae*), *Convolvulus arvensis* (*Convolvulaceae*), *Ecballium elaterium* (*Cucurbitaceae*), and *Malva parviflora* (*Malvaceae*) (Janssen *et al.*, 2002) (Figure 2). CVYV induces severe vein yellowing symptoms. Plant growth is also reduced following CVYV infection, causing crop yield losses (Cohen and Nitzany, 1960). Fruit from CVYV-infected cucumber plants expressed pale green mosaic symptoms. Watermelon plants infected with CVYV develop clearly visible leaf cracks. Infected melon plants have symptoms of thinning, necrosis, and retarded growth, with associated yield reductions. CVYV is a yield-limiting factor for cucurbit production in Spain, in single infections or infections with other viruses (Gil-Salas *et al.*, 2012).

CVYV is transmitted by *B. tabaci* (Mansour and Al-Musa, 1993) in a semi-persistent manner, and this vector retains the virus for less than 6 h. Therefore, individuals moving to non-host plants may not remain viruliferous long enough to transmit the virus. *Aphis gossypii* Glover. and *Myzus persicae* Sulzer have not been reported as vectors of CVYV (Martelli and Gallitelli, 2008), and the virus was also reported to be mechanically transmitted.

#### *Watermelon mosaic virus* (WMV)

WMV (*Potyviridae*, *Potyvirus*) has flexuous and filiform morphology and particle length 730–780 mp. It is considered as one of the main viruses infecting cucurbit crops in temperate and Mediterranean regions. The virus causes serious diseases in legumes, orchids, and weeds (Desbiez *et al.*, 2009; Lecoq and Desbiez, 2012).WMV was first reported in Israel in 1963 (Cohen and Nitzany, 1963). The virus was then reported in the USA (in 1965) (Rajbanshi and Ali, 2016), Yugoslavia (1967), Egypt (1969), Spain, Italy (1973), Tunisia (1975), France (1976), Bosnia and Herzegovina, China (2015), and Morocco (2016) (Radouane *et al.*, 2020). WMV is currently considered one of the most widespread and severe cucurbit viruses in the Mediterranean region (Loebenstein and Lecoq, 2012). Foliar symptoms induced by WMV include mosaic, vein banding, deformation, blisters, and size reduction. Fruit from affected plants of some cultivars have severe discolouration and slight deformation. Necrosis of grafted watermelon fruits was caused by newly identified isolates reported from Italy (Crescenzi *et al.*, 2001) (Figure 2). WMV can infect 170 plant species under experimental conditions, including watermelon, melon, zucchini, and squash (Wang and Li, 2017)**.**

WMV transmission is has been demonstrated for at least 35 aphid species (in 19 genera), and transmission is in a non-persistent manner. *Aphis craccivora* Kock*, A. gossypii*, and *M. persicae* are considered as the most efficient vectors of WMV (Lecoq and Desbiez, 2008).

#### *Zucchini yellow mosaic virus* (ZYMV)

ZYMV (*Potyviridae*, *Potyvirus*) infects cucurbits plants, mainly squash, melon, and cucumber. High variability has been observed within ZYMV field isolates, which influences the expressed symptoms. Some isolates induced severe symptoms including mosaic, necrosis, and wilting, whereas others caused mild symptoms, while some ZYMV-infected plants remain asymptomatic. Trials to assess the resistance of some melon and squash cultivars to ZYMV have been conducted in the Mediterranean region, and these have indicated that 81 squash varieties show resistance to different ZYMV isolates (Pitrat and Lecoq, 1984; Desbiez *et al.*, 2003).

ZYMV was first reported in Italy, in 1973 (Desbiez and Lecoq, 1997). In 1979, several melon crops were destroyed by this virus in southwestern France (Desbiez and Lecoq, 1997). Subsequently, ZYMV spread rapidly to other countries, including Lebanon (in 1979), Israel and Spain (1982), Egypt and Turkey (1983) (Desbiez and Lecoq, 1997), India (Verma *et al*., 2007), Argentina (Gracia, 2007), Ivory Coast (Koné *et al*., 2010), Pakistan (Ashfaq *et al*., 2015), Korea (Cho *et al*., 2019), China (Niu *et al*., 2015), and Morocco (Radouane *et al*., 2020) (Figure 2).

ZYMV mainly infects cucurbits (Lecoq and Desbiez, 2008), causing vein thinning, yellow mosaic, plant stunting, leaf deformation, and fruit mottling in melon plants following their infection by ZYMV (Pitrat and Lecoq, 1984; Desbiez and Lecoq, 1997). Squash plants manifest severe symptoms on the leaves. Fruit deformation is also observed, with external mosaic, necrotic cracks, and flesh hardening. Symptoms on cucumber and watermelon include severe mosaic on leaves and fruit deformations.

*M. persicae* and *A. gossypii* are the most efficient ZYMV vectors. They transmit the virus in a non-persistent mode. Recorded transmission rates for these aphids have been 41% for *M. persicae* and 35% for *A. gossypii* (Simmons *et al*., 2013). ZYMV seed-borne transmission has been demonstrated for: *C. pepo* '*styriaca*' (clamshell pumpkin), *C. pepo* subsp. *Texana* (Simmons *et al*., 2013), and squash (Coutts *et al*., 2011). Plants from infected seeds remain asymptomatic, and this makes diagnosis difficult, especially when standard serological tests are applied, and only Reverse Transcription-Polymerase Chain Reaction (RT-PCR) techniques can detect the virus in these plants (Simmons *et al*., 2013). In some tropical and subtropical regions, where cucurbits are planted throughout each year, ZYMV can easily switch from previous to new crops.

### *Papaya ring spot virus* (PRSV)

The PRSV (*Potyviridae*, *Potyvirus*) genome is 9000 to 10,326 nts, and the virus particles are flexuous filamentous rod, and measuring 760-800 × 12 nm. The particles are encapsidated by a CP of 30 – 36 kD (Gogoi *et al*., 2019). PRSV isolates are classified into two main types; type P and type W. PRSV-P can infect papaya and cucurbit crop species, but PRSV-W infects only cucurbits (Cabrera Mederos *et al*., 2019).

PRSV occurs in many Mediterranean countries, including Cyprus, Lebanon, France, Spain, Syria, Tunisia, Bulgaria, Turkey, Italy, Israel (Papayiannis *et al*., 2005; Köklü and Yilmaz, 2006), and Morocco (Radouane *et al*., 2020). The virus was also reported in India, Brazil, Iran, Sudan, and Bangladesh (Pourrahim *et al*., 2003; Jain *et al*., 2004; Verma *et al*., 2006; Jadão *et al*., 2010) (Figure 2). The PRSV host range is isolate-dependent, and the virus infects many cucurbits, including melon, cucumber, zucchini, bottle gourd, bitter gourd, watermelon, and squash (CABI, 2020).

Aphids transmit PRSV, in non-persistent modes (dos Santos Martins *et al*., 2016), and approx. 21 aphid species have been reported to transmit the virus (Allan, 1980). These include *Acyrthosiphon malvae* (Mosley), *A. craccivora*, *A. fabae* Scopoli, *A. coreopsidis* Thomas, *A. gossypii*, *A. medicaginis* Koch, *A. nerii* Boyer de Fonscolombe, *A. rumicis* Linnaeus, *A. spiraecola* Patch, *Uroleucon sonchi* Linnaeus, *M. persicae*, *Pentalonia nigronervosa* Coquerel, *Rhopalosiphum maidis* (Fitch), *Toxoptera aurantii* (Boyer de Fonscolombe), and *T. citricidus* (Kirkaldy) (Allan, 1980).

## *Other virus genera*

### *Cucumber mosaic virus* (CMV)

CMV (*Bromoviridae*, *Cucumovirus*) was associated with the mosaic diseases of cucurbit crops in the early 20th century (Doolittle, 1916) in the USA. The CMV genome comprises three +ssRNA, with isometric particles containing 180 subunits, and diameter of 29 nm. Symptoms caused by the virus are variable, which makes diagnosis difficult. Use of Double Antibody Sandwich-Enzyme Linked ImmunoSorbent Assay (DAS-ELISA) was reported to ensure easy and quick diagnosis of the virus (Adams *et al*., 2011).

CMV was first reported 1916 in the USA, and the virus has since spread to several countries including those of the Mediterranean region, and is very common on cucurbit crops grown in temperate and Mediterranean areas (Lecoq and Desbiez, 2012) (Figure 2). CMV infects melon and squash, and can also infect weed species which play key roles in inoculum conservation after cucurbit crops have been harvested.

In melon and cucumber, CMV induced typical mosaic leaf symptom accompanied by plant stunting and yield reductions. Mottling and mosaic symptoms may also occur on fruit, and rapid and complete wilting can occur on adult cucumber plants. Symptoms of CMV in squash are more severe, including leaf mosaic, yellow spots, and deformations with plant stunting and decreased fruit yields. Watermelon infection by CMV is rare, but is manifested by appearance of dark necrotic lesions on fruit (Lecoq and Desbiez, 2012).

More than 60 aphid species, including *A. gossypii* and *M. persicae*, can transmit CMV (Kennedy *et al*., 1962). Acquisition of the virus by vectors takes at least one minute, with the absence of a latency phase, and the vectors retain the virus for 4 h. CMV is not transmitted to vector progeny. CMV is seed transmitted in seed-producing squash varieties, and natural root grafting spread of CMV has been demonstrated in pepper crops (Mauck *et al*., 2015).

### *Cucumber aphid-borne yellows virus* (CABYV)

CABYV (*Luteoviridae, Polerovirus*) is a phloem-restricted virus, of approx. 5.7 kb, with virions of approx. 25 nm in diam. (Kassem *et al*., 2007). CABYV was first reported in France, in 1992 (Lecoq, 1992). DAS-ELISA has been the most commonly used test for CABYV diagnoses in the Mediterranean region (Lecoq *et al*., 1992). This virus has been reported in 15 Mediterranean countries, including Algeria, Turkey, Greece (Lecoq and Desbiez, 2012), Lebanon (Abou-Jawdah *et al*., 1997), Spain (Juarez *et al*., 2004), Italy (Tomassoli and Meneghini, 2007), Tunisia (Mnari-Hattab *et al*., 2009), Morocco (Aarabe *et al*., 2018), and Slovenia (Mehle *et al*., 2019). In Spain, CABYV incidence was determined in 924 melon and squash samples collected during 2003 to 2004. The virus was detected in 83% of melon crops and 66% of squash crops. In Tunisia, CABYV incidence was approx. 70% in 330 cucurbit samples collected between 2000 and 2004 (Mnari-Hattab *et al*., 2009). The virus was has also been reported outside the Mediterranean region, especially in Iran, China, Saudi Arabia, Pakistan, Tanzania, the USA, Czech Republic, Serbia, Korea, and India (Lemaire, 1993; Bananej *et al*., 2006; Xiang *et al*., 2008; Svoboda *et al*., 2011; Vučurović *et al*., 2011; Al-Saleh *et al*., 2015; Choi and Choi, 2016; Desbiez *et al*., 2016; Suveditha *et al*., 2017; Ahsan *et al*., 2020) (Figure 2).

CABYV has a wide, mostly cucurbit, host range, but can also infect fodder beet and lettuce (Lecoq *et al*., 1992). The main cucurbit species infected with this virus are cucumber, melon, squash, watermelon, and pumpkin. Symptoms include yellowing of old leaves that progressively thicken and become brittle, and severity of symptoms depends on host cultivar, varying from limited yellowing of a few old leaves to complete discolouration of whole plants (Lecoq *et al*., 1992).

CABYV incidence depends on the host growing conditions, and crop yields can be reduced by 50% from cucumber and 15% from melon (Lecoq, 1999).

Fruit quality is not affected by CABYV infections. However, the virus can cause flower abortion, resulting in reductions of numbers of fruit per plant (Lecoq *et al*., 1992). CABYV is transmitted by *A. gossypii, M. persicae* and *M. euphorbiae* Thomas, with persistent modes (Lecoq *et al*., 1992; Dogimont *et al*., 1996).

### *Chickpea chlorotic dwarf virus* (CpCDV)

CpCDV (*Geminiviridae*, *Mastrevirus*) is a circular monopartite virus with a ssDNA genome of approx. 2.5–2.7 kb (Khalid *et al*., 2017). All mastreviruses infecting chickpea, isolated from Africa, Australia, and Asia with at least 78% nucleotide sequence similarity were considered as one species, CpCDV (Muhire *et al*., 2013; Marwal *et al*., 2014).

Symptoms induced by CpCDV are similar to those caused by other mastreviruses. These include host stunting, yellowing, necrosis, and leaf curling (Marwal *et al*., 2014). CpCDV was first reported in chickpea plants in India (Horn *et al*., 1993), and has since spread widely. The virus has been reported in Asia (Pakistan, Iran), Africa (Morocco, Tunisia, Egypt, Burkina Faso, Sudan, South Africa, Nigeria, Eritiria), the Middle East (Yemen, Turkey, Syria, Oman), and Australia (Kraberger *et al*., 2013, 2015; Zaagueri *et al*., 2017; Kanakala and Kuria, 2019; Radouane *et al*., 2019) (Figure 2). In addition to chickpea, the virus was reported to infect other hosts, including watermelon, zucchini, and tomato (Kumari *et al*., 2006). A high rate of infection with CpCDV (100%) has been demonstrated when the virus infects before host flowering.

Studies to identify CpCDV vector(s) have been conducted in different countries. In Pakistan, two aphids (*A. craccivora* and *M. persicae*) and two leafhoppers (*Empoasca devastans* Distant. and *Orosius albicinctus* Distant.) were assessed. Transmission tests showed that only the leafhopper *O. albicinctus* transmitted CpCDV. The presence of CpCDV in the inoculated plants and *O. albicinctus* was confirmed by DAS-ELISA using specific polyclonal antibodies (Horn *et al*., 1993). Studies in Iran showed that *O. orientalis* efficiently transmitted CpCDV to numerous plant species belonging to *Chenopodiaceae*, *Fabaceae*, and *Solanaceae*. Symptoms reported on plants tested for CpCDV transmission by *O. albicinctus* were similar in tested plants for CpCDV transmission by *O. orientalis* (Farzadfar *et al*., 2009). A minimum period of 5 min has been reported for CpCDV acquisition by *O. orientalis*, and the latency phase lasts 3 h. The vector can retain CpCDV for 17 d until the vector dies, and efficiency of CpCDV transmission is positively correlated with the number of insect vectors feeding on an infected plant (Hamed, 2007). CpCDV is not mechanically transmitted, but can be transmitted by *Agrobacterium* spp. to the plants in the laboratory (Adams *et al*., 2011).

### *Melon necrotic spot virus* (MNSV)

MNSV (*Tombusviridae, Carmovirus)* is an isometric phytovirus of 30 nm with a single-stranded RNA genome. MNSV causes heavy damage in open fields and in cucumber and melon crops under shelter. The virus has spherical morphology, with a positive sense single RNA molecule. Its genome is approximately 4,266 nts (Mackie *et al.*, 2020).

MNSV was first reported Japan in 1966 (Kishi, 1966). It has since been reported in Asia, America, Europe (Yakoubi *et al.*, 2008), and Mediterranean countries, including Lebanon, Syria, Israel, Turkey, Greece, France, Italy, Spain, and Tunisia (CABI and EPPO, 2010). The virus was also been reported in the Netherlands, USA, Brazil, Panama, Guatemala, and China (Choi *et al.*, 2003; Jordá *et al.*, 2005; Herrera *et al.*, 2006; Yu *et al.*, 2016; Moura *et al.*, 2018) (Figure 2). MNSV has a narrow host range. It does not infect all *Cucurbitaceae* species, and melon, cucumber, and watermelon are the main MNSV hosts (Gonzalez-Garza *et al.*, 1979).

In watermelon, cucumber, and melon, MNSV causes leaf necroses, and streaks on the stems, and also kills infected plants. The virus can cause significant economic losses in melon. Infected fruits have decreased sugar contents and also develop necrotic spots (Kido *et al.*, 2008). MNSV is very common in hydroponic crops because the virus is mainly transmitted by the fungus *Olpidium bornovanus* (Sahtiy.) Karling (Riviere *et al.*, 1989).

MNSV is generally introduced into new areas by transport of infected plant debris or as virions carried by surface water in irrigation or precipitation. The virus is very stable and can remain viable in the soil for up to several years (Gosalvez *et al.*, 2003). This virus is also seed- and soil-transmitted, and can be mechanically transmitted under artificial conditions (Ohshima *et al.*, 2000). Seed transmission poses a serious risk for MNSV dissemination (Kubo *et al.*, 2005).

## FACTORS AFFECTING EMERGENCE OF CUCURBIT VIRUSES

Several definitions of emerging viruses exist. A virus is considered to be emerging when it occupies a new zone or a new niche. Several cucurbit viruses were reported to from cucurbit crops during the last decade, but a majority did not constitute real danger to cucurbit production due to the presence of resistant cultivars. This is the case for ZYMV and WMV (Rojas and Gilbertson, 2008; Lecoq and Katis, 2014). However, recently introduced ToLCNDV, or CpCDV, that have evolved to affect cucurbits crops in the Mediterranean region, are affecting cucurbit production in the region. Lecoq & Katis (2014) showed that the number of viruses that infect cucurbits crops has increased since 2003 from 55 to 70 in 2014, and some of these viruses can cause severe symptoms and major cucurbit yield losses. However, not all the viruses were widespread in the region. Some virus species were limited to some geographical zones, while others were having minor economic importance, or were limited to specific cropping systems. Among the long-established viruses that still cause important agronomic impacts is the aphid transmitted virus CMV; while the whitefly transmitted viruses also becoming major problems in the region (Desbiez, 2020).

Several factors have contributed to emergence of new virus species in the Mediterranean region. These include the rapid expansion of international seeds and plant trades, movement of crop plants away from their domestication centres to be cultivated elsewhere as monocultures, issues from seed production by multinational seed companies, and from free trade. These factors have increased the risks of seed crop infections with seed-borne viruses that can emerge into the local crops and vegetation. Difficulties in management of virus diseases due to climate instability and global warming are also important (Jones, 2021).

Climatic changes have also affected viruses and vectors leading to the emergence of new virus species or new strains of regionally established viruses. Changes in the hormonal and physiological defense systems in plants and changes in virus virulence from DNA/RNA mutations were also affected by the environment. Temperature increases have not affected some viruses. However, observation of CVYV infection was suggested to have increased with high temperatures in cucumber crops, but for vectors, high temperatures increase insect activity, which probably increased virus transmission in open fields (Velasco *et al.*, 2020). Movement of pests and pathogens has possibly increased with increasing temperatures, due to “global warming driven pest movement” (Bebber *et al.*, 2013).

Table 1 provides an overview of the most known viruses associated with cucurbit crops.

## VIRUS EVOLUTION IN CUCURBIT CROPS

Much research indicates that virus multiplication generates new variants (Hull, 2014), with variability resulting from errors during copying processes of virus genomes. These mutations can then be redistributed by recombination (Roossinck, 1997). Since the generation time of viruses is short compared to that for hosts and/or vectors, and because large numbers of virus descendants are produced in each generation, evolution is discernible

**Table 1.** Taxonomy, virion shape, host range, and origin of detection of viruses inducing diseases on cucurbit crops.

| Family | Genus | Virus species | Virion shape | Vector | Cucurbit host species | Geographical origin | First description | First report |
|---|---|---|---|---|---|---|---|---|
| *Geminiviridae* | *Begomovirus* | *Tomato leaf curl New Delhi virus* (ToLCNDV) | Twinned (Geminate) | *Bemisia tabaci* | *Citrullus lanatus*<br>*Cucumis sativus*<br>*Cucumis melo*<br>*Cucurbita pepo* | India | 1995 | Padidam *et al.*, 1995 |
| | | *Watermelon chlorotic stunt virus* (WmCSV) | Twinned (Geminate) | *Bemisia tabaci* | *Citrullus lanatus*<br>*Cucumis melo*<br>*Cucurbita moschata*<br>*Citrullus colocynthis* | Yemen | 1990 | Walkey *et al.*, 1990 |
| | | *Squash leaf curl virus* (SLCV) | Twinned (Geminate) | *Bemisia tabaci* | *Cucumis melo*<br>*Cucumis sativus*<br>*Citrullus lanatus*<br>*Cucurbita pepo*<br>*C. maxima*<br>*C. moschata* | Texas | 1994 | Isakeit, 1994 |
| | *Mastrevirus* | *Chickpea chlorotic dwarf virus* (CpCDV) | Twinned (Geminate) | *Aphis craccivora*<br>*Myzus persicae*<br>*Empoasca devastans*<br>*Orosius albicinctus* | *Citrullus lanatus*<br>*Cucurbita pepo*<br>*Cucumis sativus* | India | 1993 | Horn *et al.*, 1993 |
| *Potyviridae* | *Ipomovirus* | *Cucumber vein yellowing virus* (CVYV) | Flexuous filaments with no envelope | *Bemisia tabaci* | *Cucumis sativus*<br>*Cucumis melo*<br>*Citrullus lanatus*<br>*Cucurbita pepo* | Israel | 1960 | Cohen and Nitzany, 1960 |
| | *Potyvirus* | *Watermelon mosaic virus* (WMV) | Flexuous filaments with no envelope | *Aphis craccivora*<br>*Aphis gossypii*<br>*Myzus persicae* | *Citrullus lanatus*<br>*Cucurbita pepo*<br>*Cucumis melo*<br>*Cucurbita moschata* | Israel | 1963 | Cohen and Nitzany, 1963 |
| | | *Zucchini yellow mosaic virus* (ZYMV) | Flexuous filaments with no envelope | *Aphis gossypii* | *Cucurbita pepo*<br>*Citrullus lanatus*<br>*Cucumis sativus* | Italy | 1973 | Lisa *et al.*, 1981 |
| | | *Papaya ring spot virus* (PRSV) | Flexuous filaments with no envelope | Aphid species | *Cucumis sativus*<br>*Cucumis melo*<br>*Cucurbita pepo*<br>*Citrullus lanatus*<br>*Cucurbita moschata* | India | 1948 | Yeh, 1984 |
| *Bromoviridae* | *Cucumovirus* | *Cucumber mosaic virus* (CMV) | Spherical/ Quasi-spherical | Aphid species | *Cucumis sativus*<br>*Cucumis melo*<br>*Cucurbita pepo*<br>*Citrullus lanatus* | United States | 1916 | Doolittle, 1916 |
| *Luteoviridae* | *Polerovirus* | *Cucumber aphid-borne yellows virus* (CABYV) | Hexagonal in outline with no envelope | *Aphis gossypii*<br>*Myzus persicae*<br>*Macrosiphum euphorbia* | *Cucumis sativus*<br>*Cucumis melo*<br>*Cucurbita pepo*<br>*Citrullus lanatus* | France | 1992 | Lecoq, 1992 |
| *Tombusviridae* | *Carmovirus* | *Melon necrotic spot virus* (MNSV) | Icosahedral | *Olpidium bornovanus* | *Cucumis melo*<br>*Citrullus lanatus*<br>*Cucumis sativus*<br>*Citrullus vulgaris* | Japan | 1966 | Kishi, 1966 |

process (Astier *et al.*, 2001). Mutations are generated by polymerase errors when synthesizing new nucleic acid molecules (García-Arenal *et al.*, 2001; Pita and Roossinck, 2007). These errors result in imperfect copies of genetic material from parents to progeny (Acosta-Leal *et al.*, 2011). These alterations correspond to punctual errors which generally appear in three forms: substitution, insertion, or deletion of nucleotide bases (Smith and Inglis, 1987). Unlike mutations, the molecular changes caused by recombination are induced by incorporation of one or more nucleotides from another genome or from another genomic region. Recombination is a molecular process by which nucleotide sequences are exchanged. New combinations of genetic material can thus be generated within a genome when the parents are genetically different (Nagy and Simon, 1997; Vuillaume *et al*., 2011). Recombination probably makes important contributions to evolution and epidemiology of viruses infecting plants and animals (Burke, 1997; Padidam *et al*., 1999; Froissart *et al*., 2005; He *et al*., 2009). Pseudorecombination ("reassortment"), is different from recombination. It is a process whereby entire components of multipartite viruses (with genome divided into at least two segments) are exchanged between variants, strains, or species (Martin *et al*., 2011). By extrapolation, pseudo-recombination can also include virus/satellite associations (Briddon *et al*., 2001). Satellites are small circular ssDNAs with sizes of approx. 1.3 kb. These are associated with some (but not all) Eastern Hemisphere monopartite begomoviruses. Satellites are divided into two types; beta- and alpha-satellites (Briddon *et al*., 2001). The points discussed above show that mutation, recombination, and pseudo-recombination together generate significant genomic diversity, which can potentially lead to the emergence of viruses with new phenotypic characters.

The mutation frequency analysis by Juárez *et al*., (2019) for ToLCNDV virus strains from different geographical locations in Spain showed average mutation frequency rates (mutations/nucleotide) of $6.5 \times 10^{-3}$ to $5.7 \times 10^{-3}$ for both DNA components. This could explain the genetic diversity of ToLCNDV populations and indicate that wild plants could be the key driving ToLCNDV evolution.

Changes in vector transmission of some cucurbit viruses has been reported through recombination. This was the case for CABYV, an RNA virus, for which (Costa *et al*., 2020) reported that the recombinant CABYV isolate was transmitted by the whitefly *B. tabaci* MEAM1, rather than *A. gossipii*. Furthermore, a DNA mastrevirus infecting dicotyledonous plants was able to recombine. The first report of mixed infection by a mastrevirus and a begomovirus was in 2012 in *Xanthium strumarium* L. A recombination event was also reported between CpCDV and *Cotton leaf curl Burewala virus* (CLCuBuV) under experimental conditions the exchange of the CP of CpCDV by that of CLCuBuV resulted in the CpCDV-CLCUBuV recombinant which was whitefly transmitted, whereas CpCDV was transmissible by leafhopper species (Khalid *et al*., 2017).

For DNA viruses in mixed infections, DNA-A and DNA-B components of ToLCNDV interact with a variety of virus and betasatellite diseases (Shah Nawaz-Ul-Rehman and Fauquet, 2009; Zaidi *et al*., 2017). ToLCNDV can interact with betasatellites associated with other begomoviruses, thus expanding its host range. However, the mechanisms of these interactions remain unknown (Zaidi *et al*., 2017). A pseudorecombination event has been detected between two distinct begomoviruses under natural conditions, between the severe ToLCNDV strain and the Varanasi strain of *Tomato leaf curl Gujarat virus* (ToLCGV) which causes severe leaf curl of tomato in India (Chakraborty *et al*., 2008). In Spain, genetic analysis showed that the new strain of ToLCNDV spreading in that country resulted from recombination events (Fortes *et al*., 2016). The effect of the pseudo-recombination event between ToLCNDV and ToLCGV on viral pathogenesis was first demonstrated experimentally, and the recombinant virus was associated with severe pathogenicity. A similar effect was also observed in a recombinant between ToLCNDV and isolates of the begomovirus *Tomato leaf curl Palampur virus* (ToLCPMV) (Moriones *et al*., 2017).

ToLCNDV infects tomato, which is the main host crop for numerous *Tomato yellow leaf curl disease* (TYLCD)-associated viruses. The possible occurrence of mixed infections by ToLCNDV and TYLCD-associated begomoviruses either in tomato or cucurbits constitutes a serious threat for these crops, because begomoviruses are prone to recombination (Fortes *et al*., 2016). The recombination event has also been shown to be frequent within SLCV isolates under natural conditions, and occurs in DNA-A and DNA-B components. Most SLCV recombinants infect hosts other than cucurbits, indicating that recombination plays a major role in virus host ranges (Hassan, 2019). In Indonesia, ToLCNDV was reported to be recombinant with the *Squash leaf curl China virus* (SLCCNV) under natural conditions. Phylogenic analysis based on the AV1 gene has shown that ToLCNDV has clustered with SLCCNV (Wilisiani *et al*., 2019).

Pseudo-recombination has been produced in the laboratory, between closely related begomoviruses such as *Tomato golden mosaic virus* (TGMV), *Bean golden mosaic virus* (BGMV), and SLCV, by reassortment of their genome components (Chakraborty *et al*., 2008). The begomoviruses WmCSV and ToLCPMV have also been shown to possibly pseudo-recombine under experimental conditions (Esmaeili *et al*., 2015). The replication protein of DNA-A of one virus bound to the DNA-B of the other to induce systemic symptoms.

The RNA virus CABYV was shown to result from a recombination event between ancestors of CABYV and

MABYV in Taiwan (Knierim *et al.*, 2010). This virus was reported to be transmitted by whiteflies in Brazil, rather than by aphids. Since whiteflies are the most frequent vectors of plant viruses, and because of the dominant crop production in Brazil, the virus was named recombinant CABYV-M1. This virus had new properties; it was spread throughout Brazil, and it was not able to infect several cucurbits (*C. lanatus, C. sativus* and *L. sativa*) which were known hosts of the common type CABYV. The recombinant CABYV was able to overcome the resistance of *C. melo* 'TGR 1551' that was reported to be resistant to common CABYV. Therefore, the virus was reclassified as *Cucurbit Whitefly Borne Yellow virus* (Costa *et al.*, 2019, 2020). Recombinations between subgroups of CMV has been widely reported under natural conditions. The different strains of CMV were classified into three main subgroups (IA, IB, and II) (Bonnet *et al.*, 2005; Ouedraogo *et al.*, 2019), notably in Spain with the prevalence of recombination events in RNA3. However, phylogenic analysis of Polish CMV isolates belonging to subgroups IA and II have revealed the prevalence of subgroup II, with detection of a new recombinant with the IA-MP/II-CP pattern (Hasiów-Jaroszewska *et al.*, 2017). CMV showed recombination between two strains (A and B), which followed the exchange of 3A and CP in RNA3 and the formation of hybrid 1a and 2a in RNA1 and 2 (Sztuba-Solińska *et al.*, 2011). Inoculations with two CMV isolates and *Tomato aspermy virus* (TAV) showed establishment of a recombination event across RNA3 in co-infected plants under experimental conditions. Precise homologous recombination had occurred at several RNA3 sites (Morroni *et al.*, 2013). In Tunisia, many isolates of CMV have shown pseudo-recombination, mostly IB-IA-IA and IB-IA-IB in pepper crops. Fifty-five of 57 isolates were able to break host resistance when tested against polygenic resistance to CMV movement in pepper, which indicates that resistance was not a good strategy for control of CMV in Tunisia (Ben Tamarzizt *et al.*, 2013). The reported recombination events in ZYMV and WMV were limited to the same species. Most recombination events reported in ZYMV were limited to P1, CI, HC-Pro, P3, CP, and NIb regions under natural conditions. Those described in WMV were in the N-terminal part of the CP and CI coding regions (Desbiez *et al.*, 2011; Maina *et al.*, 2019).

## METHODS FOR DETECTING CUCURBIT VIRUSES

### *Serological techniques: Enzyme-linked Immunosorbent Assays (ELISA)*

ELISA (Enzyme Linked Immunoabsorbent Assay) has become widely accepted as an immunodetection method. These assays provide high sensitivity, ease of use, rapidity, and the ability to quantify pathogen biomass in plant tissues and other matrices (Miller and Martin, 1988). The technique consists of the detection of viruses via their capsid proteins or of proteins coded by each virus that remain specific. The principle of this technique is based on the antibody-antigen pair, which is an immune defense where the virus plays the role of antigen. The most widely used serological technique involves Enzyme-linked Immunosorbent Assays (ELISA).

ELISA methods, including double antibody sandwich (DAS) ELISA, direct tissue blot immunoassay (DTBIA), and tissue-print (TP) ELISA, are the most commonly used, and several modifications have been made to the technique, including antigen-coated plate enzyme-linked immunosorbent assays (ACP-ELISA) (Mehetre *et al.*, 2021).

In a polystyrene plate, the wells are first coated with an anti-CP antibody. Excess antibody is then washed away leaving the antigen-anti-CP antibody complex. A second antibody conjugated antibody-CP is then applied, obtaining the antigen-antibody conjugate complex. Each antigen is thus surrounded by two antibodies, one at the base and one at the apex. Following this coupling, an enzyme reacts with an added substrate that stains the solution yellow, and the optical density of the solution is then visualized by a spectrophotometer (Miller and Martin, 1988) (Table 2).

This technique is commonly used in many diagnoses and analyses, and especially for virus detection, and the sensitive and specific technique rapidly produces results. It is also very practical, and sensitivity increases depending on the type used. However, direct and indirect types have two main disadvantages; direct types can give a false positive results and indirect types have problems of immobilization and non-specific reactions (Aydin, 2015).

### *Nucleic acid-based methods*

#### Polymerase chain reaction (PCR) and reverse transcription-PCR

PCR is a technique for *in vitro* amplification and visualization of fragments of specific genomes. Four main elements must be available, including DNA, DNA polymerase, $MgCl_2$, and primers which are the initiators of amplification (replication). Primers are comprised of approx. 10 to 30 bases. Their position in the viral genome delimits the size of the fragment to be amplified (Table 3). The PCR takes place in three phases: denaturation, hybridization, and elongation. At the level of

**Table 2.** Serological tests, based on ELISA and its modified methods, used for detection of cucurbit-associated viruses.

| Virus name | Host plants | ELISA based methods | References |
|---|---|---|---|
| *Tomato leaf curl New Delhi virus* (ToLCNDV) | Luffa<br>Tomato | Double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA)<br>Triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA) | Mantilla Paredes, 2018; Zubair *et al.*, 2020 |
| *Chickpea chlorotic dwarf virus* (CpCDV) | Chickpea | DAS-ELISA<br>Dot-blot ELISA<br>Direct antigen-coating DAC-ELISA | Kumari *et al.*, 2006 |
| *Watermelon chlorotic stunt virus* (WmCSV) | Watermelon | DAS-ELISA | Ahmad *et al.*, 2018 |
| *Squash leaf curl virus* (SLCV) | Squash | | |
| *Watermelon mosaic virus* (WMV) | Melon | DAS-ELISA | López-Berenguer *et al.*, 2021 |
| *Cucurbit aphid-borne yellows virus* (CABYV) | Zucchini<br>Watermelon | DAS-ELISA | Radouane *et al.*, 2020 |
| Zucchini yellow mosaic virus (ZYMV) | Squash<br>Melon<br>Watermelon | DAS-ELISA | Tripathi *et al.*, 2021 |
| Melon necrotic spot virus (MNSV) | melon<br>Cucumber<br>Zucchini | TAS-ELISA<br>DAS-ELISA | Miras *et al.*, 2020; Torre *et al.*, 2020 |
| Cucumber vein yellowing virus **(CVYV)** | Cucumber<br>Melon | DAS-ELISA | Desbiez *et al.*, 2019 |
| *Papaya ringspot virus* (PRSV) | Papaya<br>Melon<br>Watermelon | DAS-ELISA<br>DAC-ELISA | Hartati *et al.*, 2020; Kumar *et al.*, 2021 |
| *Cucumber mosaic virus* (CMV) | Squash | Plate-trapped antigen ELISA PTA-ELISA | Nascimento *et al.*, 2017 |

reverse transcription (RT), there is synthesis of a complementary DNA (cDNA) from one RNA strand by the action of a reverse transcriptase enzyme (DNA polymerase, RNA-dependent). This technique is mainly used for the identification and detection of RNA viruses, transforming their genomes into cDNA which is the basic material for completion of PCR tests.

Several PCR tests have been used to detect phytoviruses, such as the use of specific primers (dual priming oligonucleotide; DPO) (Table 4). The primers give high levels of specificity and sensitivity. The difference between conventional primers and DPO primers is structural; primers consist of two separate primer segments bridged by polydeoxyinosine linkers with a low melting temperatures (Kwon *et al.*, 2014).

## Loop-mediated isothermal amplification (LAMP)

The loop-mediated isothermal amplification (LAMP) method is a rapid technique for DNA amplification using specific primers, and DNA polymerases with strand displacement activity (Kuan *et al.*, 2010). The technique is highly sensitive and cost-effective, which could be used in daily routine tests, and especially *in situ* testing of crop pathogens (Waliullah *et al.*, 2020).

The LAMP method is an auto-cycling strand displacement DNA synthesis using four to six primers, which bind with high specificity to the targets, and the amplified products can then be visualized using gel electrophoresis, or by intercalating dyes such as SYBR Green I, or using a real-time quantitative measurements. LAMP is an important technology for use in laboratory or field conditions. LAMP has also addressed the limitations of qPCR and PCR, that require specific equipment and reagents that are often not available in poorly resourced laboratories or in the field (Waliullah *et al.*, 2020).

LAMP has been widely used to detected important DNA viruses, such as SLCV (Kuan et al., 2010), and for RNA viruses including *Cucurbit chlorotic yellows virus* (*Closteroviridae*; *Crinivirus*; CCYV) (Okuda *et al.*, 2015), CMV (Bhat *et al.*, 2013) and *Cucumber green mottle mosaic virus* (*Virgaviridae* ; *Tobamovirus* ; CGMMV) (Li *et al.*, 2013). Bhat *et al.*, (2013) compared the detection sensitivity of CMV on black pepper using RT-LAMP, RT-PCR and qRT-PCR. They showed that detection sensitivity of CMV with RT-LAMP was 100 times

**Table 3.** Primers used for the detection of viruses.

| Virus | Primer name | Sequence (5'–3') | Amplicon size (bp) | Annealing temperature | Source |
|---|---|---|---|---|---|
| ToLCNDV | A1-F<br>A1-R | ACCAACAGGCCGATGAACA<br>TTCCCACTATCTTCCTGTGCA | 750 | 55°C | Radouane *et al.*, 2018 |
|  | To-B1F<br>To-B1R | GAAACACAAGAGGGCTCGGA<br>GCTCCACTATCAAAGGGC GT | 677 | 55°C | Sáez *et al.*, 2016 |
| WmCSV | WmA150F<br>WmA 1350R | GTCAGTATGTGGGATCCATTGC<br>GCAAATACGATTCAACCACAACC | 1201 | 57°C | Ali-Shtayeh *et al.*, 2014 |
|  | WmB672F<br>WmB2000R | CGCCGTTGCCTGGAGGATGTTCAC<br>GCAGCACAGGCTGCCTTCACCTTC | 1329 | 65°C | Ali-Shtayeh *et al.*, 2014 |
| SLCV | SqA2F<br>SqA1R | TATCTCCCATCTTGGCAAGG<br>AGCTGTATCTTGGGCAACAGA | 601 | 55°C | Sobh *et al.*, 2012 |
| CpCDV | CpCDV-SEQ2<br>CpCDV-Tu-1145-R | CGACACATAAGGTTCAGGTTG<br>AGGCAACCCTTGGGAGTCA | 544 | 55°C | Radouane *et al.*, 2019 |
| CVYV | CV-<br>CV+ | GCGCCGCAAGTGCAAATAAAT<br>AGCTAGCGCGTATGGGGTGAC | 450 | 55°C | EPPO, 2007 |
| WMV | WMV-5<br>WMV-3 | GGCTTCTGAG CAAAGATG<br>CCCAYCAACTG TYGGAAG | 408 | 55°C | Desbiez *et al.*, 2007 |
| ZYMV | GK ZYMV F1<br>GK ZYMV R2 | ATAGCTGAGACAGCACT<br>CGGCAGCRAAACGATAACCT | 1004 | 57°C | Nagendran *et al.*, 2017 |
| PRSV | GK PRSV F<br>GK PRSV R | GCAATGATAGARTCATGGGG<br>AAGCGGTGGCGCAGCCACACT | 1267 | 61°C | Nagendran *et al.*, 2017 |
| CMV | GK CMV F<br>GK CMV R | GAGTTCTTCCGCGTCCCGCT<br>AAACCTAGGAGATGGTTTCA | 1218 | 54 °C | Nagendran *et al.*, 2017 |
| CABYV | CE9<br>CE10 | GAATACGGTCGCGGCTAGAAATC<br>CTATTTCGGGTTCTGGACCTGGC | 600 | 58°C | Wilson *et al.*, 2012 |
| MNSV | VP 51-2<br>VP 51-1 | TGGATCCGGTAGTAGGAATG<br>TTTACCCACAGTGAAGCTTCG | 405 | 47 °C | Navarro *et al.*, 2006 |

**Table 4.** DPO primer list.

| Virus | Primer name | Sequence (5'–3') | Amplicon size (bp) | Annealing temperature | Source |
|---|---|---|---|---|---|
| WMV | WMV F<br>WMV R | GGTAATTTTGTTTGGGGCGAACIIIIIAAGCATTC<br>GCGTGATCAACTAAAATGCGTGGIIIIICAGCATTCC | 623 | 63 | Kwon *et al.*, 2014 |
| PRSV | PRSV F<br>PRSV R | CGGAAATGATGTGTCAACTAGCACIIIIICTGGAGAGA<br>ATGCTTCTGCCGCGTTACIIIIITGAGCCATAATTTG | 458 | 63 | Kwon *et al.*, 2014 |
| ZYMV | ZYMV F<br>ZYMV R | GTTACAGGCTCCGGCTCAIIIIIGAAAACAGTAG<br>TCCATTAATGTCGGGTGAAGTGCCIIIIICAATGCACC | 345 | 63 | Kwon *et al.*, 2014 |

greater than that with conventional RT-PCR and 10 time more sensitive than SYBER green-based qRT-PCR.

## High-throughput sequencing tools in viral diagnosis

Since 2002, more than 800 metagenomic studies of viruses have been published with the development of high-throughput screening (HTS) (Breitbart *et al.*, 2002). This metagenomic revolution is expanding epidemiological knowledge of health-related infections, in particular by redeploying geographical sampling areas and taking increased account of wild areas. The number of species sequenced by this approach greatly increases the amount of available genetic information. Phylogenetic reconstructions that are inferred from this information can reliably infer epidemiological links between isolates at spatial and temporal scales, and allow elucidation of inter-host transmission chains.

HTS provides a key step in metagenomics that encompasses sequencing technologies. It allows the sequencing of multiple strands of DNA in parallel, resulting in greater throughput than conventional sequencing allows. As NSGs have become cheaper and more accessible, they have been used to address a growing range of biological problems, including issues related to food safety and quality (Bernardo *et al*., 2013).

HTS has provided an efficient tool for virus detection and identification in plants, which gives accurate and sensitive diagnoses of virus infections. Rodríguez-Negrete *et al*., (2019) have employed the technique to determine the viral diversity in seven states in Northern-Pacific Mexico, to characterize the begomovirus naturally existing in non-cultivated plant hosts. Their study used HTS analyses to give subsequent *de novo* assembly of important DNA signatures related to geminiviruses (80 to 100%). This showed that DNA signatures belonged to 52 geminivuruses infecting crop hosts 35 geminiviruses infecting noncultivated plants, identified in different plant species. Their study demonstrated that HTS analyses can increase knowledge of virus diversity, and assist identification and detection of novel emerging known and unknown viruses without requirement for disease etiological information (Karavina *et al*., 2020).

In Poland, Minicka *et al*., (2020) used the HTS technique for detection and identification of viruses occurring in mixed and single infections, allowing identification of 13 species, from 20 tested samples of different plant species, and identification of two new emerging viruses in Poland, *Clover yellow mosaic virus* (*Alphaflexiviridae*; *Potexvirus*; ClYMV) and *Melandrium yellow fleck virus* (*Bromoviridae*; *Bromovirus* ; MYFV), as well as a new strain of CABYV that belong to two different groups. These authors also concluded that HTS rapidly provided information about the viruses that were not detected in the region.

In France, the use of HTS analyses for the study of virus evolution has revealed the presence of undescribed variants, such as WMV and CMV on solanaceous crops, and complex virus populations within individual plants. However, spatial genetic variation of CABYV was related to landscape structure, while introduction and recurrence of WMV were mainly due to the human exchange of plant materials, giving a complex spatial pattern of genetic variation (Desbiez *et al*., 2020).

Drawbacks have been reported for HTS technology. These include the need to annotate contigs/singletons via *de novo* assembly, which could affect sequences by creation of chimeras deriving from different genomes, and the differentiation of sequences that need confirmation through cloning and sanger sequencing. However, the metagenomics analyses could greatly assist identification of genetic variability in virus populations, and facilitate study of genome evolution, to determine environmental factors that influence the generation of novel from established species (Rodríguez-Negrete *et al*., 2019).

## STRATEGIES FOR CONTROL OF CUCURBIT VIRUSES

### *Prophylaxis*

#### Vertical transmission

In Spain, crop protection is based on prevention through the use of healthy seed. The use of virus-free seeds is an important strategy for preventing introduction of virus into production sites. This is also the case for the use of nets, mainly in greenhouse crops, elimination of crop residues, and use of crop rotation (Janssen *et al*., 2003).

Hydrochloric acid treatment and drying for the disinfection of melon seeds remains the most effective way to obtain healthy seeds and limit the spread of MNSV (Dumas de Vaulx, 1970). In addition, hydrogen peroxide, hot water, and sodium hypochlorite are also used as seed treatments.

#### Horizontal transmission

Prophylactic measures also aim to prevent or limit the contact of virus vectors with cultivated plants. These include efficient weed removal near crops and avoiding overlapping crops in the same area to reduce sources of viruses.

Establishment of integrated pest management is essential for the management of cucurbitaceous pathogens. Weed control is also crucial because these plants can be reservoirs for vectors and viruses. Recourse to genetic resistance is also applied to control cucurbit viruses (Wintermantel *et al*., 2017).

For aphid vectors, the use of plastic mulches limits the spread of viruses because the plastic is aphid-repellent. However, these mulches confer limited protection; the more the plants cover the mulch surfaces, the lower is the effectiveness of the mulches. There are also rows of woven or perforated plastic that prevent winged aphids from reaching plants, but these must be removed during pollination, which allows aphids to feed on plants (Lecoq, 1992). For example, plastic mulching delayed the spread of CABYV for 2 weeks (Lecoq, 1999).

Rotations of different crops, mainly using non-host plants belonging to families other than *Cucurbitaceae*, can limit the spread of the viruses.

### *Breeding for resistance*

#### Resistance to the virus

Breeding for resistance to plant viruses is among the most effective strategy for management of diseases caused by these pathogens. In melon, MNSV was controlled by the use of resistant cultivars. The dominant TGR 1551 gene in melon offered genetic resistance against *Cucurbit yellow stunting disorder virus* (*Closteroviridae*; *Crinivirus*; CYSDV). In addition, oligo-genic resistance allowed CMV control in melon. Collection of CMV isolates between 1974 and 1978 revealed the presence of the "Song" pathotype that overcame this resistance (Sugiyama, 2013). However, resistance to CMV in melon was reported to be recessive and in most cases oligogenic, but, in the subgroup II strains of CMV which are monogenic, the resistance depends on only one gene, *cmv1*, which prevents movement of the virus and systemic infection (Pascual *et al.*, 2019).

Romay et *al*. (2019) studied the resistance to two unrelated begomoviruses, ToLCNDV and *Melon chlorotic mosaic virus* (MeCMV), to evaluate host genetic variation that could target these two viruses, and that could provide resistance breeding material and information on resistance factors for use in melon breeding programmes. They found that melon families were resistant to both viruses, suggesting that the genes involved in resistance were common. They also proposed that the resistance was controlled by the genes *bgm*-1, *Bgsm*-2 in ToLCNDV and MeCMV.

Resistance to ZYMV in melon was reported to be linked to three loci, and that it was dominant and monogenic, and also oligogenic. The three loci are mainly *Zym*-1, *Zym*-2, and *Zym*-3 and all are essential for the resistance (Danin-Poleg *et al*., 1997; Martín-Hernández and Picó, 2020).

#### Resistance to vectors

For aphids, melon has two cases of resistance to viruses: either the resistance to viruses, or to vectors conferred by the *VAT* gene. This is the case for *A. gossypii*. In the field, resistance to the CABYV conferred by the *cab1* and *cab2* genes ensures high efficacy (Boissot *et al*., 2016). However, Martín-Hernández and Picó (2020) reported that this virus could also be controlled by one dominant gene, which leads to accumulation of the virus in the inoculated host tissues, but not in systemic tissues, which was suggested to be the cause of the impairment of virus movement in the host vascular system.

#### Resistant cultivars

Several commercial cultivars have been genetically modified by the introduction of the *VAT* gene that confers resistance to *A. gossypii*, the vector of CABYV, WMV, and ZYMV. However, effectiveness of this gene is limited because these viruses are transmitted by many species of aphids other than *A. gossypii* (Boissot *et al*., 2016). For ZYMV, the use of genetic host resistance is extensive. The cucumber "*Zym*" gene confers long-lasting resistance, but this gene confers only partial resistance in melon, and this resistance can be overcome by the virus. Squash had *Zym* resistance to ZYMV, and the gene was incorporated into zucchini. This gave tolerance to the virus with expression of mild symptoms and reduced virus multiplication within host plants. However, a mutation in the P3 protein of the virus allowed overcoming of the host tolerance. Although the tolerance was easily overcome, the relative fitness of the tolerance-breaking variant was reduced compared to wild-type virus on zucchini cultivars(Desbiez *et al*., 2003). Cucumber, squash, and melon showed resistance to PRSV (Lecoq and Desbiez, 2012). In cucumber and squash/zucchini, cucumber has different levels of CMV resistance (Lecoq and Desbiez, 2012). Several efforts have been made to find resistance to WMV. Some commercial cucumber and zucchini cultivars are tolerant to WMV, but their efficiency toward the virus remains limited. CP is the only gene that has shown better resistance to WMV and ZYMV. Freedom II, a transgenic squash that contains CP genes of both of these viruses, was released in 1995 in the USA. This was the first virus transgenic crop to be commercially cultivated, and was reported efficient in the field conditions against WMV. However, other hybrids including resistance to CMV in the USA, but these could not be used in the Mediterranean region to the restrictions of genetically modified (GMO) crops in the region (Loebenstein and Lecoq, 2012).

### *Biological control*

Biological control is one of the most commonly used vector management strategies but not for eradicating diseases.

*Amblyseius swirskii* Athias Henriot (Arachnida: *Phytoseiidae*) has been the subject of a recent study for control of *B. tabaci* populations and reducing the spread of ToLCNDV in a range of crops including cucumber and pepper (Rodríguez *et al*., 2019).

The mite *A. swirskii* has limited adult *B. tabaci* by feeding on eggs and larvae. On zucchini, pre-installation of the predator on plants was assessed. Significant negative impacts of the mite on the number of emerging whiteflies adults were detected, due to colonization of the eggs by the phytoseiid predator. Control of the vector minimized plant infection by ToLCNDV (Tellez *et al.*, 2017).

Management of virus diseases associated with cucumber and transmitted by *A. gossypii* has been studied in Egypt (Eid *et al.*, 2018). A biological control trial released the parasitic aphid *Aphidius colemani* Viereck and larvae of the predatory ladybird *Coccinella septempunctata* L. Control of *A. gossypii* was carried out in two greenhouses, one using biological control and the other using conventional chemical treatments. The experiment was conducted in 2015 and 2016, to validate the results under different meteorological conditions. For summer cucumber, this study indicated that effective control was achieved with more than ten *C. septempunctata* and more than four *A. colemani* per m$^2$. Although costs of the biological controls were are high and aphid populations were not less compared to the chemicals, the cucumbers quality and yields were satisfactory.

Biological control was not evaluated as a strategy to slow the spread or reduce severity of vectors, but dissemination of nonpersistent viruses by vectors was gradually prevented. For example, aphids emit alarm pheromones that trigger and increased vector movements when they are attacked by their enemies, and this increases virus dissemination. Control of nonpersistent viruses is still not well established. Studies have concluded that the use of biological control could prevent secondary virus spread, and reduction of vector numbers could stop the spread of viruses to nearby crops (Hooks and Fereres, 2006).

For severe virus infections, biological vector control does not provide effective disease management solutions because complete vector control is required.

### *Chemical control*

Several chemical methods, using detergents, insecticides, essential oils, and combinations of these substances, have been used for management of vector pests and the diseases they transmit. Control using these materials are not always satisfactory. These treatments aim to prevent secondary damage caused by the insect vectors, including reduction of virus transmission and deposition of honeydew (Johnstone and Rapley, 1981; Gibson and Rice, 1986).

Greenhouse and field trials were carried out in the USA in 2016 assessing management of CYSDV by controlling *B. tabaci* (Castle *et al.*, 2017). Eight foliar and systemic insecticides were assessed, including the active ingredients acetamiprid, dinotefuran, pyrifluquinazon, thiamethoxam, cyantraniliprole, imidacloprid, or flupyradifurone, either as foliar or soil treatments. Virus transmission rates were reduced by less than 10% by some of the active ingredients. Foliar treatments gave good results compared to those applied to the soil, and the insecticides had the same effects in the greenhouse and in the field. Of the seven active ingredients, foliar applications of flupyradifurone, acetamiprid or dinotefuran gave the best management of the virus, by decreasing the populations of *B. tabaci*.

Limiting spread of viruses is mostly achieved by controlling vectors. Flupyradifurone is has very rapid activity against the tobacco whitefly vector of more than a hundred viruses. The trials of Castle *et al.* (2017) aimed to manage *Tomato yellow leaf curl virus* (*Geminiviridae*; *Begomovirus*; TYLCV) associated with tomato, but the results are still valid for other vegetable crops affected by *B. tabaci*. Foliar treatments of thiamethoxam or flupyradifurone reduced virus transmission by 85% because of the anti-feeding activity of the active ingredients (Roditakis *et al.*, 2017). Given the potential environmental danger linked to thiamethoxam, it should not be used at the full bloom crop development stage to limit the risk of bee poisoning (Chahbar *et al.*, 2011). Similarly, flupyradifurone could have similar harmful effects on bees and birds (European Food Safety Authority, 2015). However, these treatments remain ineffective because of the small proportion of whiteflies required to cause symptoms of viruses associated with *Tomato yellow leaf curl* (TYLCD-viruses), and because of development of resistant *B. tabaci* populations. Increasingly strict regulatory restrictions on the use of pesticides cause producers to seek alternative solutions using biological control and prophylactic systems in integrated protection systems in greenhouse crops.

Current strategies, aim to eliminate and exclude vector through the use of insecticides to reduce aphid and whitefly populations. If the frequency of treatments is high, the insecticides have not been effective. This is the case for CABYV, following the pesticide resistance developed by the vector, and also for *B. tabaci* which has become very resistant to chemical treatments at all stages of development (Willrich Siebert *et al.*, 2012).

Management of *O. bornovanus* was based on the application of a surfactant that affected zoospores of the fungus or seed treatments this study suggested a prolonged seed treatment of 144 h at 70°C (Tomlinson and Thomas, 1986). This was effective removed MNSV and increased seed germination rates (Herrera-Vásquez *et al.*, 2009).

Nonpersistent transmission of viruses presents a significant challenge for vector control because the time between acquisition and transmission is very short (a few seconds) compared to viruses transmitted by semipersistent and persistent modes (Castle *et al.*, 2017).

The use of mixtures of insecticides with different modes of action reduces the likelihood of the emergence of pesticide resistant insect strains. Combinations of insecticides/insecticides, insecticides/synergists or insecticides/repellents make it possible to produce a synergistic effects capable of increasing the duration of effectiveness of the active substances, of reducing the effective doses. These strategies may also give insecticidal action on insects with single active ingredient resistance(Baldet *et al.*, 2014).

## CONCLUSIONS

In natural conditions, there are more than 90 viruses that have been recorded infecting cucurbit crops, and the major problems are caused by ten viruses (Desbiez, 2020). This diversity of pathogens probably due to the genetic and ecological diversity of cucurbit hosts in the Mediterranean region. Cucurbits are cultivated in a variety of agroecosystems which provide variably favourable conditions for these viruses and/or their vectors.

Successful management strategies for virus diseases relies on multi-dimensional understanding of virus biologies, including epidemiology, evolution, environmental effects, and virus/plant and virus/vector interactions. Knowledge of these biological factors will facilitate future management of these diseases (Romay *et al.*, 2014).

Methods for controlling these diseases and pathogen vectors are not completely effective, and cucurbit producers require innovative control methods that are economical and easy to implement.

Sustainable approaches to improve cucurbit crop productivity through phytosanitary quality must combine complementary approaches that involve the plant hosts and the natural and anthropic environmental factors (Romay *et al.*, 2014).

Research on plant virus interactions and development of control methods is required to achieve sustainable cucurbit production. New molecular approaches, such as high-throughput sequencing metagenomic analyses, need to be applied in plant science, to understand disease resistance mechanisms, epidemiology, and virus transmission and interactions. Understanding in these aspects assist rapid diagnoses for sustainable plant management strategies by cucurbit producers in the Mediterranean region.

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