CUCURBIT CROPS AND THEIR VIRAL DISEASES IN LATIN AMERICA AND THE CARIBBEAN ISLANDS: A REVIEW

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SUMMARY

Cucurbit crops are cultivated throughout the world. Melon (Cucumis melo L.), cucumber (Cucumis sativus L.), watermelon (Citrullus lanatus (Thumb.) Mat. et Nak.), squash and pumpkin (Cucurbita spp.) are the major crops. In Latin America and the Caribbean islands (LAC) cucurbits are consumed as a part of the daily diet since pre-Columbian times, when some species such as Cucurbita pepo L., Cucurbita moschata Duch. and Cucurbita maxima Duch. were domesticated by American Indians. In LAC, cucurbit crops have become export commodities and a source of income for several countries, in addition to their role in local consumption. The increase of area devoted to cucurbit crops and the intensification of production has led to the emergence of severe viral epidemics that threaten the sustainability of these cultures. This paper reviews the cucurbit viruses described in the region and their impact. In addition, the potential of different measures to control the most frequent cucurbit viruses in LAC is discussed.

Key words: Cucurbitaceae, plant viruses, cucurbit production, Latin American countries

INTRODUCTION

Cucurbits represent one of the most important vegetables for human consumption throughout the world. Cucurbit species are members of the family Cucurbitaceae that roughly includes 120 genera and 800 species, which are predominantly tropical plants though some, such as Bryonia spp. and Alsomitra spp., are adapted to temperate climates (Teppner, 2004). Four major cucurbit crops are economically important worldwide: melon (Cucumis melo L.), cucumber (Cucumis sativus L.), watermelon (Citrullus lanatus (Thumb.) Mat. & Nak.), squash and pumpkin (Cucurbita spp.) (Robinson and Decker-Walters, 1997). Global production of cucurbits cultivated in the world is 151,212,210 tons. China is the main producer with 83,429,409 tons of melon, watermelon, cucumber and squash, while the USA is the main producer in the Western Hemisphere with 4,602,370 tons (FAOSTAT, 2012).

Cucurbit crops are often threatened by diseases of fungal, bacterial and viral origin (Sitterly, 1972) and pests, such as the pumpkin caterpillars (Diaphania spp.) and the melon fly (Bactrocera cucurbitae Coquillet), are also serious constraints to their cultivation (Peter and David, 1991; Duyck et al., 2004; Dhillon et al., 2005; Hans-Petersen et al., 2010). Aphids, whiteflies and thrips can become serious limitations to cucurbit production through the extensive damage they provoke, but also through the transmission of viral disease (Brown et al., 1995; Morse and Hoddle, 2006; Powell et al., 2006).

At least 59 viruses infecting cucurbits are known (Lecoq and Desbiez, 2012), whose outbreaks have led to significant yield and quality losses to these crops on a worldwide basis (Flock and Mayhew, 1981; Desbiez and Lecoq, 1997; Brown et al., 2001; Lecoq and Desbiez, 2012). This review examines the current situation of cucurbit production in Latin America and the Caribbean islands (LAC), with special emphasis on viral diseases that affect these crops, and the perspectives for their control.

ORIGIN OF MAJOR CUCURBIT PLANTS CULTIVATED IN LATIN AMERICA AND THE CARIBBEAN ISLANDS

Cucumber (Cucumis sativus). Cucumber is widely grown in cool temperate regions because it is better adapted to low temperatures than other cucurbits (Paris et al., 2012). Cultivated cucumbers are usually monococious. India is the centre of origin of cucumber that has been cultivated there for at least 3,000 years and introduced later in China and Europe (Leppik, 1966) and, in the 15th century, in the Western Hemisphere by Columbus (Robinson and Decker-Walters, 1997). The most closely related species to C. sativus is the southeast Asian Cucumis hystricis Chackr. (Renner et al., 2007; Sebastian et al., 2010). C. sativus is the seventh plant species whose genome (243.5 Mb) has been sequenced. This is expected to provide a remarkable increase of new findings for its genetic improvement (Anonymous, 2009).
Melon (Cucumis melo). Melon is the other important crop in the genus Cucumis. Its genome has recently been sequenced, which will contribute to further investigations involving evolution and genetic improvement (García-Mas et al., 2012). The C. melo genome has a size of 454 Mb, while its mitochondrial genome (2,740 Kb) is the largest among plant mitochondrial genomes, i.e. up to 100 times the size of a typical animal mitochondrial genome (Rodríguez-Moreno et al., 2011). The difference in genome size between C. melo and C. sativus is probably due in part to transposon amplification in the melon genome (García-Mas et al., 2012). Africa is considered as the centre of origin of melon because of the large number of African wild species (Robinson and Decker-Walters, 1997), whereas Central Asia and China are regarded as secondary centres (Leppik, 1966). This assumption was supported by the chromosome numbers: melon and 30 other African species in the genus Cucumis have a chromosome number of X = 12, whereas C. sativus has a chromosome number of X = 7 (Luan et al., 2008). However, recent phylogenetic analyses have shown that C. melo may have an Asian rather than an African origin, suggesting the Himalayan region as the ancestral area for progenitor populations of melon and cucumber. Moreover, a sister species of melon is the Australian Cucumis picrocarpus F. Muell. whose divergence from melon occurred roughly 2.8 million years ago (Sebastian et al., 2010).

Watermelon (Citrullus lanatus). Watermelon is more produced than any other cucurbit in the world with 73,313,777 tons according to latest reports. In Europe, watermelon production is slightly exceeded that of another cucurbit, cucumber (FAOSTAT, 2012). Watermelon originates from Africa (Robinson and Decker-Walters, 1997). The presumed ancestor of the modern cultivar C. lanatus includes wild annual forms referred to as C. lanatus subsp. lanatus var. caffer (Schrad.) Mansf., which are natives to the Kalahari Desert (Southern Africa). However, the finding of 5000-year-old seeds of wild watermelon in an archaeological site in southwest Libya raises new discussions about the origin, distribution and domestication history of this species (Wasylkowa and van der Veen, 2004). In Asia, watermelon was introduced to India and China in about the 9th and 12th century, respectively, in Europe by the Moors during their conquest of Spain (Dane and Liu, 2007) and in the Americas by the Spaniards and rapidly spread throughout the continent (Robinson and Decker-Walters, 1997). According to Romão (2000), a secondary centre of watermelon diversity is northeast Brazil where slave trading might have reached 18 millions people coming from Africa in two major groups, Bantu and Sudanese. The same author indicates that African watermelon ethnovarieties could be grown in the same areas, may be in slaves gardens, leading to new segregants and recombinant forms during the long period of slave trading. C. lanatus is the only cultivated species of the genus Citrullus which comprises eight species (Bisognin, 2002), among which C. lanatus subsp. lanatus (Tsamma and citron type) and C. lanatus subsp. vulgaris (sweet-dessert watermelon group) (Levi et al., 2012). Although a large number of commercial varieties of watermelon are being released each year, their genetic diversity is low, increasing the risks of pest and disease threats. Hence, the great interest to enhance genetic diversity using new germplasm coming from different geographical regions (Zhang et al., 2012).

Squash (Cucurbita maxima, C. moschata, C. pepo). The genus Cucurbita comprises 12-14 different species of American origin and a distribution ranging from the USA to Argentina (Sanjur et al., 2002). Along with corn (Zea mays L.) and beans (Phaseolus spp), squashes were domesticated in the Americas, playing a crucial role for the development of American Indian agriculture (Carter, 1946). As stated by Paris (2000), six species were originally listed by Linnaeus in the genus Cucurbita on the basis of phenotypic features. Afterwards, four of them (C. pepo, C. verrucosa, C. melopepo, C. ovifera) were re-assigned to the species C. pepo and the other two were re-located in the genus Lageneria and Citrullus. The great polymorphism exhibited by C. pepo may have led Linnaeus to identify four different species instead of a unique, but polymorphic, species. Years later, the botanist A.N. Duchesne demonstrated, on the basis of inability to hybridize and produce fertile offspring, that several forms of Cucurbita belonged to the polymorphic C. pepo and that, more interestingly, two other Cucurbita forms were unable to hybridize with C. pepo, therefore, they were considered as distinct species that were named C. maxima and C. moschata (Paris, 2000). C. pepo is the northernmost species of the three aforementioned Cucurbita, the northwest of Mexico and the south-east of the USA being thought to be domestication centres of this species (Carter, 1946; Nee, 1990; Sanjur et al., 2002). Archeological studies in Mexico provided evidence of C. pepo and other wild cucurbits cultivation as early as 8,750 BC, almost 60% of them being wild Cucurbita species and C. pepo the only cultivated species (Whitaker and Cutler, 1971). Three subspecies are recognized: C. pepo subsp. fraterna (only found in wild form), C. pepo subsp. pepo (only found in cultivation) and C. pepo subsp. texana (found in cultivation and wild form). The last two are more genetically related to each other (Gong et al., 2012). C. moschata is thought to originate from the middle American area, from which it spread southward and northward (Carter, 1946). The wild ancestor of C. moschata is unknown, though molecular DNA analyses suggest that it may be localized in lowland northern South America (Sanjur et al., 2002). Archeological studies carried out in northern Peru revealed the presence of C. maxima and C. moschata between 1,800 BC and 1,100 AD, but interestingly, these species were found to be chronologically different, C. maxima being the older one (West and Whitaker, 1979).
As suggested by this finding, *C. maxima* might have been replaced by *C. moschata* probably due to ecological and cultural factors. *C. maxima* is thought to be a native of the humid lowland of Bolivia and warmer temperate regions of South America, where *Cucurbita andreana* Naudin, the wild progenitor of *C. maxima*, was originally described (Sanjur et al., 2002). *C. maxima* was not present in North America until the 18th century when it was introduced to north-eastern USA by sailing ships from South America (Robinson and Decker-Walters, 1997). Two other species are also cultivated in America, *Cucurbita ficifolia* Bouché and *Cucurbita argyrosperma* Huber. *C. ficifolia* is common in the mountains from northern Mexico to northern Argentina and Chile (Nee, 1990). *C. ficifolia* can be used as rootstock to confer chilling tolerance and improved plant growth to cucumbers grown under low light intensity (Zhou et al., 2007). *C. argyrosperma* is little known outside Central and North America, where some cultivars are grown for their large nutritious seeds rather than for the flesh (Nee, 1990).

Another cucurbit often found in archaeological explorations carried out in the Western Hemisphere is bottle gourd (*Lagenaria siceraria* (Molina) Standl.) (Whitaker and Cutler, 1971; West and Whitaker, 1979; Whitaker, 1981; Erickson et al., 2005; Duncan et al., 2008). This cucurbit was thought to be domesticated in the Western Hemisphere due to the older archaeological evidence gathered from this part of the world (Nee, 1990). Afterwards, an African origin was proposed for *L. siceraria*, based on the diversity of wild species in the genus *Lagenaria* and the morphological and genetic characterization of a wild population of *L. siceraria* (Robinson and Decker-Walters, 1997; Decker-Walters et al., 2004). Wild species were supposed to have moved from Africa to the Americas 9,000 years ago through their fruits floating across the ocean (Decker-Walters et al., 2004). However, subsequent archaeological studies suggested that *L. siceraria* was brought to the Americas 10,000 years ago by Paleoindian populations from Asia rather than by oceanic crossing of floating fruits from Africa (Erickson et al., 2005).

**Chayote (Sechium edule (Jacq.) Sw.).** Although chayote is not one of the major cucurbit crops in the world, this plant is grown in several LAC countries such as Costa Rica, Mexico, Brazil and Puerto Rico for local consumption and export (Abdelnour and Rocha, 2008). Chayote was cultivated by pre-Columbian Aztec civilizations and its centre of origin seems to be between Mexico and Guatemala, where wild species of *Sechium* have been found (Newstrom, 1991). The genus *Sechium* was initially considered as monotypic containing only *S. edule*, but eight species have now been described in this genus (Robinson and Decker-Walters, 1997).

### PRODUCTION OF MAJOR CUCURBITS IN LATIN AMERICA AND THE CARIBBEAN ISLANDS

Estimates show that global production of cucurbits in LAC is 9,012,215 tons harvested from 549,631 ha (FAOSTAT, 2012), watermelon being the major species. As shown in Table 1, Mexico, the only Latin country in North America, is the greatest producer of cucumber among LAC countries. Interestingly, melon production in Central America is similar to that in South America, in spite of the remarkable difference in the total surface given over to this crop in either region. This fact shows the outstanding role of some cucurbits in the economy of several countries in the region, where cucurbit export is one of the significant source of income. The USA is the main importer of cucurbits to supply consumer demands during winter. Thus, Mexico exports around 30% of its melon production to the USA (Hernández-Martínez et al., 2006; García-Salazar et al., 2011), while Guatemala devotes its melon production almost totally to the USA market (de Cara et al., 2008). In Guatemala, the melon area harvested in 2000 was 5,880 ha. Ten years later, it was 22,777 ha, rising by 387.4% (FAOSTAT, 2012). In Brazil, melon exports have been favoured by the increasing development of multinational supermarket chains creating scaling-up of opportunities for growers with capacity to support initial investments, whereas small farmers lack substantial improvements in organization and technology to confront these challenges (Farina, 2000). By contrast, Argentina was the third greatest producer of squash in the world during the early 1980s, with approximately 31,000 ha harvested (Robinson and Decker-Walters, 1997) while in 2010, the harvested area was 19,600 ha so that this country dropped

### Table 1. Production of major cucurbit crops in Latin America and the Caribbean islands.

<table>
<thead>
<tr>
<th>Region</th>
<th>Melon Tons</th>
<th>Surface (ha)</th>
<th>Squash Tons</th>
<th>Surface (ha)</th>
<th>Cucumber Tons</th>
<th>Surface (ha)</th>
<th>Watermelon Tons</th>
<th>Surface (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>North America</td>
<td>561,681</td>
<td>21,418</td>
<td>522,388</td>
<td>32,100</td>
<td>477,366</td>
<td>15,653</td>
<td>1,036,800</td>
<td>44,040</td>
</tr>
<tr>
<td>Central America</td>
<td>874,781</td>
<td>39,635</td>
<td>12,310</td>
<td>5,600</td>
<td>82,567</td>
<td>3,042</td>
<td>39,145</td>
<td>15,405</td>
</tr>
<tr>
<td>Caribbean</td>
<td>85,606</td>
<td>9,374</td>
<td>446,915</td>
<td>68,967</td>
<td>127,318</td>
<td>12,231</td>
<td>65,480</td>
<td>7,829</td>
</tr>
<tr>
<td>South America</td>
<td>929,926</td>
<td>55,502</td>
<td>776,317</td>
<td>47,535</td>
<td>134,251</td>
<td>8,784</td>
<td>2,839,364</td>
<td>162,516</td>
</tr>
<tr>
<td>Total</td>
<td>2,451,394</td>
<td>125,929</td>
<td>1,757,930</td>
<td>154,202</td>
<td>824,502</td>
<td>39,710</td>
<td>3,980,789</td>
<td>229,790</td>
</tr>
</tbody>
</table>

Source: FAOSTAT, 2012; aData relative to Mexican cucurbit production.
are obligate parasites that usually depend on a vector for survival and spreading from one susceptible host to another (Hull, 2002). The knowledge of the way in which a particular virus is disseminated throughout the field is indispensable to develop adapted control strategies. Therefore, a list of the major cucurbit viruses detected in LAC is presented according to their respective vector types.

**Table 2. Cucurbit-infecting viruses in Latin America and Caribbean islands**

<table>
<thead>
<tr>
<th>Virus</th>
<th>Vector</th>
<th>Countries</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cucumber mosaic virus</td>
<td>Aphids</td>
<td>Argentina, Brazil, Chile, Costa Rica, Guadeloupe, Honduras, Martinique, Mexico, Puerto Rico, Venezuela</td>
<td>Lastra, 1968; Quiot et al., 1971; Thomas, 1981; Delgadillo-Sánchez et al., 1989; Rivera et al., 1991; Espinoza and McLeod, 1994; Yuki et al., 2000; Prieto et al., 2001; Paz-Carrasco and Wessel-Beaver, 2002; Arneso et al., 2005; Herrera et al., 2006</td>
</tr>
<tr>
<td>Papaya ringspot virus W</td>
<td>Aphids</td>
<td>Brazil, Costa Rica, Guadeloupe, Martinique, Mexico, Panama, Puerto Rico, Venezuela</td>
<td>Lastra, 1968; Quiot et al., 1971; Delgadillo-Sánchez et al., 1989; Rivera et al., 1991; Espinoza and McLeod, 1994; Yuki et al., 2000; Herrera et al., 2006</td>
</tr>
<tr>
<td>Zucchini yellow mosaic virus</td>
<td>Aphids</td>
<td>Argentina, Brazil, Chile, Costa Rica, Dominican Republic, Honduras, Guadeloupe, Martinique, Mexico, Panama, Puerto Rico, Venezuela</td>
<td>Nameth et al., 1983; Hernández et al., 1989; Espinoza and McLeod, 1994; Desbiez and Lecoq, 1997; García et al., 2000; Yuki et al., 2000; Prieto et al., 2001; Herrera et al., 2006</td>
</tr>
<tr>
<td>Watermelon mosaic virus</td>
<td>Aphids</td>
<td>Argentina, Brazil, Chile, Costa Rica, Honduras, Mexico, Puerto Rico, Venezuela</td>
<td>Lastra, 1968; Delgadillo-Sánchez et al., 1989; Rivera et al., 1993; Hernández et al., 2000; Yuki et al., 2000; Prieto et al., 2001; Paz-Carrasco and Wessel-Beaver, 2002; Herrera et al., 2006</td>
</tr>
<tr>
<td>Zucchini tigré mosaic virus</td>
<td>Aphids</td>
<td>Costa Rica, Guadeloupe, Martinique, Venezuela</td>
<td>Quiot-Douine et al., 1986; Romay et al., 2014a</td>
</tr>
<tr>
<td>Squash mosaic virus</td>
<td>Beetles</td>
<td>Brazil, Chile, Honduras, Mexico, Monserat, Puerto Rico, Venezuela</td>
<td>Lastra, 1968; Delgadillo-Sánchez et al., 1989; Thomas, 1981; Espinoza and McLeod, 1994; Prieto et al., 2001; Moura et al., 2001; Paz-Carrasco and Wessel-Beaver, 2002</td>
</tr>
<tr>
<td>Squash leaf curl virus</td>
<td>Whiteflies</td>
<td>Mexico</td>
<td>Flock and Mayhew, 1981; McCreight and Kishaba, 1991</td>
</tr>
<tr>
<td>Cucurbit leaf crumple virus</td>
<td>Whiteflies</td>
<td>Mexico</td>
<td>Brown et al., 2000</td>
</tr>
<tr>
<td>Melon chlorotic leaf curl virus</td>
<td>Whiteflies</td>
<td>Costa Rica, Guatemala, Mexico, Nicaragua</td>
<td>Brown et al., 2001; Karkashian et al., 2002; Ala-Poikela et al., 2005; Hernández-Zepeda et al., 2007</td>
</tr>
<tr>
<td>Melon chlorotic mosaic virus</td>
<td>Whiteflies</td>
<td>Venezuela</td>
<td>Ramírez et al., 2004</td>
</tr>
<tr>
<td>Tomato yellow leaf curl virus</td>
<td>Whiteflies</td>
<td>Cuba</td>
<td>Martinez-Zubiaur et al., 2003</td>
</tr>
<tr>
<td>Cucurbit yellow stuntng disorder virus</td>
<td>Whiteflies</td>
<td>Mexico</td>
<td>Brown et al., 2007</td>
</tr>
<tr>
<td>Beet pseudo-yellows virus</td>
<td>Whiteflies</td>
<td>Costa Rica</td>
<td>Hammond et al., 2005</td>
</tr>
<tr>
<td>Melon yellowing-associated virus</td>
<td>Whiteflies</td>
<td>Brazil</td>
<td>Nagata et al., 2005</td>
</tr>
<tr>
<td>Tobacco ringpot virus</td>
<td>Nematodes</td>
<td>Mexico</td>
<td>Delgadillo-Sánchez et al., 1989</td>
</tr>
<tr>
<td>Zucchini lethal chlorosis virus</td>
<td>Thrips</td>
<td>Brazil</td>
<td>Pozzer et al., 1996; Nagata et al., 1998</td>
</tr>
<tr>
<td>Melon severe mosaic virus</td>
<td>Thrips</td>
<td>Mexico</td>
<td>Ciuffo et al., 2009</td>
</tr>
<tr>
<td>Tomato spotted wilt virus</td>
<td>Thrips</td>
<td>Brazil, Chile, Puerto Rico</td>
<td>Silveira et al., 1985; Prieto et al., 2001; Paz-Carrasco and Wessel-Beaver, 2002</td>
</tr>
<tr>
<td>Melon necrotic spot virus</td>
<td>Fungi</td>
<td>Guatemala, Honduras, Panama, Mexico</td>
<td>de Cara et al., 2008; Herrera-Vásquez et al., 2010</td>
</tr>
<tr>
<td>Squash necrosis virus</td>
<td>Fungi</td>
<td>Brazil, Martinique</td>
<td>Lin et al., 1983; Lecoq, 2003</td>
</tr>
<tr>
<td>Chayote mosaic virus</td>
<td>Beetles</td>
<td>Costa Rica</td>
<td>Hord et al., 1997</td>
</tr>
</tbody>
</table>

out of the top 10 squash producers in the world. However, during the same period the Argentinan harvested area of soybean increased from approximately 2,000,000 ha to 18,130,800 ha increasing by ca. 890% becoming one of the most important sources of income (FAOSTAT, 2012).

**CUCURBIT VIRUSES REPORTED IN LATIN AMERICA AND THE CARIBBEAN ISLANDS**

At least 21 cucurbit-infecting viruses have been reported from LAC (Table 2), whose symptoms are very variable, i.e. mosaic, deformation, chlorosis, curling and yellowing of the leaves, vein clearing and vein banding, stunting of the plants and deformation of fruits (Fig. 1). Plant viruses are obligate parasites that usually depend on a vector for

**Aphid-borne viruses.** 1. *Cucumber mosaic virus* (CMV) is the type member of the genus *Cucumovirus* (family *Bromoviridae*). CMV genome size is approximately 8 kb consisting of three linear positive-sense single stranded RNA molecules (Bujarski et al., 2012) which are packaged in separate isosahedral virions. The virus is transmitted by aphids in a non-persistent manner (Nault, 1997), is divided in two subgroups (I and II) based on nucleotide sequence identity and serological properties and is reported
Fig. 1. Symptoms associated with viral diseases of cucurbit crops A. Leaf curling and stunting caused by Melon chlorotic mosaic virus (MeCMV) in melon. B. Rugose mosaic caused by Melon chlorotic mosaic virus (MeCMV) in melon. C. Mosaic and leaf deformation caused by Papaya ringspot virus (PRSV-W) in melon. D. Vein clearing and slight mosaic caused by Papaya ringspot virus (PRSV-W) in watermelon. E. Mosaic caused by Zucchini yellow mosaic virus (ZYMV) in squash. F. Severe leaf deformation and mosaic caused by Zucchini yellow mosaic virus (ZYMV) in zucchini squash. G. Mosaic caused by Cucumber mosaic virus (CMV) in melon. H. Vein banding caused by Squash mosaic virus (SqMV) in melon.
Field surveys of cucurbit viruses have shown PRSV-W as prevalent in Costa Rica (Rivera et al., 1993). In Brazil, extensive viral surveys in cucurbit fields from Northern to South-eastern regions in different years have shown that PRSV-W is widespread with a remarkable predominance (>40%) compared with other cucurbit viruses (Yuki et al., 2000; Oliveira et al., 2000; Moura et al., 2001; Halfeld-Vieira et al., 2004; Silveira et al., 2009). In contrast, PRSV-W has not been reported, so far, in the southernmost countries, Argentina and Chile, where other cucurbit potyviruses are present (García, 2000; Prieto et al., 2001).

3. Zucchini tigré mosaic virus (ZTMV). ZTMV was firstly described in Guadeloupe as the T strain of PRSV (PRSV-T) due to the particular symptoms of “tiger” stripe pattern on zucchini plants and its biological relationships with PRSV, though PRSV-T is antigenically distinct from PRSV-W (Quiot-Douine et al., 1986). However, recent sequence comparisons indicate that PRSV-T is actually a new potyvirus species closely related to but distinct from PRSV, occurring in Guadeloupe, Martinique, Costa Rica and Venezuela. ZTMV has probably long been overlooked because of its close relationship to PRSV, the lack of discriminating diagnostic tools and its high frequency of co-infections with PRSV (Romay et al., 2014a).

4. Zucchini yellow mosaic virus (ZYMV), a potyvirus first observed in Italy in the early 1970s, 10 years later was widely distributed in cucurbit crops around the world with devastating consequences (Desbiez and Lecoq, 1997). Usually, disease symptoms are severe mosaic, deformation of leaves or fruits and stunting of plants. However, one of the main features of ZYMV is the great biological variability among its strains whereby differences in host range as well as symptoms severity or nature (necrosis or wilting reactions) can be expected (Lecoq and Desbiez, 2012). Based on molecular analyses, three distinct groups of ZYMV are recognized (groups A, B and C), all isolates from the Western Hemisphere are classified in group A (Coutts et al., 2011a). In LAC, ZYMV was first detected in Mexico (Nameth et al., 1985) but current records show that it occurs in numerous LAC countries, the same as the earlier reported PRSV-W and CMV (Table 2). Prevalence of ZYMV in LAC field crops seems to be variable, while virus surveys from Mexico showed that it occurred with a frequency higher (ca. 30%) than PRSV-W, Watermelon mosaic virus (WMV) and CMV in two distinct years (Félix-Gastélum et al., 2007). In Puerto Rico and Venezuela, ZYMV incidence was comparable to that of PRSV-W, with a frequent presence of mixed infections (Paz-Carrasco and Wessel-Beaver, 2002; Romay et al., 2014b). Interestingly, both potyviruses had similar frequency but PRSV was more prevalent in cucurbit weeds than ZYMV, probably due to its longer time of adaptation to local endemic plants. In Brazil, PRSV is still the most important
cucurbit virus though an increasing frequency of ZYMV has been observed (Silveira et al., 2009).

5. Watermelon mosaic virus (WMV) is another potyvirus reported from several LAC countries (Table 2). This virus is an important constraint to cucurbit production in temperate and Mediterranean climatic conditions, and can also be responsible for severe diseases in non-cucurbits crops such as beans, pea and vanilla (Lecoq and Desbiez, 2008). However, as a whole, WMV is rare or absent in tropical regions (Lecoq and Desbiez, 2012). Three main groups of WMV have been identified based on molecular analysis, the American isolates falling into the second group referred to as G2 (Lecoq and Desbiez, 2012). Symptoms associated with WMV infections can be mosaic, vein banding, filiformism and reduction in the size of the leaves and may vary according to the host and the viral isolate. WMV is a common virus in cucurbit crops in Chile, where it was reported to cause significant yield losses (Prieto et al., 2001). Its incidence in cucurbit crops from Costa Rica, Puerto Rico, Mexico and Venezuela was estimated around 20% (Lastra, 1968; Rivera et al., 1993; Paz-Carrasco and Wessel-Beaver, 2002; Félix-Gastélum et al., 2007) although recent surveys in the latter country have disclosed a much lower (ca. 3%) prevalence (Romay et al., 2014b). By contrast, the average incidence of this virus in Brazil, which was estimated at about 10% (Yuki et al., 2000; Moura et al., 2001; Halfeld-Vieira et al., 2004) had grown to approximately 30% according to a more recent report (Silveira et al., 2009).

Whitefly-borne viruses. 1. Squash leaf curl virus (SLCV) belongs to the genus Begomovirus, family Geminiviridae. The genome of most begomoviruses consists of two circular single-stranded DNA molecules, each ca 2.7 kb in size, referred to as DNA A and DNA B. However, some begomoviruses such as Tomato yellow leaf curl virus (TYLCV), have a single genomic component similar to DNA A of bipartite begomoviruses (Stanley et al., 2005). Most begomoviruses are phloem-restricted and are transmitted by the whitefly Bemisia tabaci Genn. in a persistent manner (Navas-Castillo et al., 2011). Actually, B. tabaci is considered as a complex of at least 24 indistinguishable species (Dinsdale et al., 2010). The Middle East-Asia Minor 1 (MEAM1) whitefly, commonly referred as biotype B, is regarded as the most invasive species and efficient begomovirus vector (De Barro et al., 2011). In the mid 1980s MEAM1 was introduced in the Western Hemisphere where, within a few years, it displaced indigenous whiteflies in the USA and several LAC countries (Perring et al., 1993; Morales, 2006). SLCV was first recorded in the USA and Mexico in the late 1970s, infecting zucchini squash (C. pepo) in which it induces thickening of the veins, upward curling of the leaves, enations and stunting (Flock and Mayhew, 1981). Phylogenetic analyses indicate that SLCV belongs to the “New World” begomovirus clade and is considered as endemic to squash throughout the southwestern USA and Mexico (McCreight and Kishaba, 1991). This New World begomovirus has now spread to several countries in the Middle East (Desbiez and Lecoq, 2012).

2. Cucurbit leaf crumple virus (CuLCrV) is another begomovirus first found in California (USA) in volunteer watermelons in commercial melon fields. The symptoms displayed by infected plants were yellowing, leaf curl and crumpling (Guzman et al., 2000). During the same period, whitefly-infested pumpkins and melons from Arizona and Texas (USA), and Coahuila (Mexico) showed begomovirus-like symptoms which were associated with a new begomovirus species named Cucurbit leaf curl virus (Brown et al., 2000). This virus was recently synonymized with CuLCrV by the International Committee on Taxonomy of Viruses (ICTV) (Adams and Carstens, 2012). CuLCrV is common in melons grown in the fall planting period in southwestern United States (McCreight et al., 2008). To date, no new reports have come from Mexico or from any other LAC country.

3. Melon chlorotic leaf curl virus (MCLCuV) is a begomovirus identified in 2000 in the Zacapa Valley of Guatemala where it infects, with a 70 to 80% incidence, melons that exhibit patchy foliar chlorosis, leaf curling, and reduced fruit set (Brown et al., 2001). Zacapa Valley is a large area dedicated almost exclusively to melon production for the international market (Brown et al., 2011), which makes MCLCuV a serious threat to the economy of the country. The very severe symptoms elicited by this virus in melon and watermelon, contrast with the milder syndromes caused by SCLV and CuLCrV, both of which infect the same cucurbit species (Idris et al., 2008). MCLCuV was recorded under the name of Squash yellow mosaic virus from Costa Rica (Karkashian et al., 2002), where it is widely distributed (Hernández et al., 2012) and is also present in Nicaragua (Ala-Poikela et al., 2005), and in the Yucatan peninsula of Mexico infecting watermelon and squash (Hernández-Zepeda et al., 2007).

4. Melon chlorotic mosaic virus (MeCMV) is the most southern cucurbit begomovirus so far reported from LAC. It was found for the first time in Venezuela in melons showing mosaic and chlorosis of the leaves (Ramirez et al., 2004) and, some years later, in watermelon in association with a DNA alphasatellite molecule (MeCMA) (Romay et al., 2010). Alphasatellites are self-replicating circular DNA molecules ca. 1.3 kb in size whose encapsidation, vector transmission and movement in the plant rely on their helper virus. They had only been associated with Old World monopartite begomoviruses (Nawaz-ul-Rehman and Fauquet, 2009). However, new begomovirus-alphasatellite associations, besides that of MeCMV-MeCMA, have recently been reported in the Americas (Paprotka et al., 2010). To date, MeCMV is the major constraint to melon and
5. **Squash leaf curl virus-like (SLCV-like).** Several isolates of begomoviruses infecting cucurbits in El Salvador, Honduras and Colombia have partially been sequenced showing a close relationship to SLCV (Brown et al., 2002; Morales, 2006). Further sequencings are needed to clarify the taxonomic position of these viruses that seem to be members of the same phylogenetic group, i.e. the SCLV clade which includes also CuLCrV, MCLCuV and MeCMV.

6. **Tomato yellow leaf curl virus (TYLCV).** This virus was introduced in the Americas in the late 1980s, rapidly becoming the greatest threat to tomato production in the Caribbean (Morales and Anderson, 2001). Although TYLCV was isolated in Cuba from *C. pepo* exhibiting yellowing and curling of the leaves (Martínez-Zubiaur et al., 2003) and was also found in other cucurbits in the Middle East (Anfoka et al., 2009), there is no evidence of yield losses caused to cucurbits elsewhere.

7. **Cucurbit yellow stunting disorder virus (CYSDV).** This virus was introduced in the Americas in the late 1980s, rapidly becoming the greatest threat to tomato production in the Caribbean (Morales and Anderson, 2001). Although TYLCV was isolated in Cuba from *C. pepo* exhibiting yellowing and curling of the leaves (Martínez-Zubiaur et al., 2003) and was also found in other cucurbits in the Middle East (Anfoka et al., 2009), there is no evidence of yield losses caused to cucurbits elsewhere.

8. **Beet pseudo yellows virus (BPYV).** This virus was introduced in the Americas in the late 1980s, rapidly becoming the greatest threat to tomato production in the Caribbean (Morales and Anderson, 2001). Although TYLCV was isolated in Cuba from *C. pepo* exhibiting yellowing and curling of the leaves (Martínez-Zubiaur et al., 2003) and was also found in other cucurbits in the Middle East (Anfoka et al., 2009), there is no evidence of yield losses caused to cucurbits elsewhere.

Beet-transmitted viruses. 1. **Squash mosaic virus (SqMV).** This virus was introduced in the Americas in the late 1980s, rapidly becoming the greatest threat to tomato production in the Caribbean (Morales and Anderson, 2001). Although TYLCV was isolated in Cuba from *C. pepo* exhibiting yellowing and curling of the leaves (Martínez-Zubiaur et al., 2003) and was also found in other cucurbits in the Middle East (Anfoka et al., 2009), there is no evidence of yield losses caused to cucurbits elsewhere.
of this virus is very low in Brazil, although it has been exceptionally observed to reach 56% incidence in the field (Alencar et al., 2012). In Puerto Rico, SqMV was detected with a prevalence of 30%, whereas the infection rate in Venezuela is very low (less than 6%) (Lastra, 1968; Hernández et al., 1989; Romay et al., 2014b).

2. **Chayote mosaic virus** (ChMV) belongs to the genus *Tymovirus*, family *Tymoviridae*. Tymoviruses have a linear, positive-sense single stranded RNA genome of about 6.3 kb (Hull, 2002). Tymoviruses are transmitted mechanically and, in nature, in a semi-persistent manner and a low efficiency by beetles of the families Chrysomelidae and Curculionidae (Dreher et al., 2012). ChMV has only been described in Costa Rica infecting chayote plants (Hord et al., 1997). The host range of the virus is limited to cucurbit species, which exhibit mosaic and leaf corrugation, whereas symptomless infections are observed in other hosts belonging to botanical families such as Solanaceae and Amaranthaceae (Bernal et al., 2000). In Costa Rica, chayote had been traditionally cultivated as a backyard crop, but in the 1980s it became an important crop for the export market (Flores, 1989), which has likely favoured the development of viral diseases.

**Nematode-transmitted viruses.** *Tobacco ringspot virus* (TRSV) is the type species of the genus *Nepovirus*, family *Secoviridae*. Members of this genus have a genome organization similar to that of comoviruses, are widely distributed in temperate regions and most of them are transmitted persistently by nematodes (Sanfaçon et al., 2012). TRSV can be associated with a RNA satellite of small size, about 359 nucleotide long, which interferes with virus replication and disease symptoms (Hull, 2002). TRSV induces chlorotic spots, systemic ringspots, severe leaf deformation, mottling, and stunting in squash plants (Abdalla et al., 2012). In the mid 1980s, TRSV was found in cucurbits in Mexico (Delgadillo-Sanchez et al., 1989), but its field incidence was not assessed.

**Thrips-transmitted viruses.** 1. *Tomato spotted wilt virus* (TSWV) is the type species of the genus *Tospovirus*, family *Bunyaviridae*. Tospoviruses have spherical or pleomorphic particles and a genome comprising three molecules of negative or ambisense single stranded RNA (Plyusnin et al., 2012). Tospoviruses are transmitted by thrips in a circulative and propagative manner (Hull, 2002). Virus acquisition occurs during the first instar larval stages and viral particles are transmitted to plants during feeding of adults (Jones, 2005). TSWV has a host range of about 1100 species belonging to 85 botanical families (Parrella et al., 2003).

Although TSWV is an important pathogen of tomato, lettuce and sweet pepper rather than cucurbits (Jones, 2005) it was reported infecting these crops in Brazil, Chile and Puerto Rico (Prieto et al., 2001; Paz-Carrasco and Wessel-Beaver, 2002).

2. **Zucchini lethal chlorosis virus** (ZLCV) is a tospovirus that was first isolated in Brazil from zucchini squash and cucumbers in São Paulo state and the Federal District, respectively (Pozzer et al., 1996; Nagata et al., 1998). In cucumber, ZLCV causes mottling, yellowing, and vein banding of the leaves (Nagata et al., 1998) and it was found associated with important yield losses of marketable fruits in extensive areas of zucchini cropping (Bezerra et al., 1999). Currently, there is no evidence of ZLCV occurrence in any country other than Brazil. ZLCV is transmitted by *Frankliniella zucchini* (Nakahara and Monteiro, 1999) and its host range is mainly restricted to the family Cucurbitaceae (Bezerra et al., 1999) unlike TSWV, which has a much broader host range.

3. **Melon severe mosaic virus** (MeSMV) is a tospovirus infecting melon, watermelon, cucumber and zucchini in several states of Mexico. The virus can be mechanically transmitted to cucurbits and solanaceous plants. Although its natural vector is unknown, the western flower thrips (*F. occidentalis*) was observed in melon plants exhibiting mosaic, leaf blistering, leaf deformation, and fruit splitting (Ciuffo et al., 2009).

**Fungus-transmitted viruses** 1. *Melon necrotic spot virus* (MNSV) a member of the genus *Carmovirus*, family *Bubusviridae*, has a genome consisting of a molecule of linear positive-sense single stranded RNA of approximately 4 Kb. Several carmovirus species are soil-borne and are readily transmitted mechanically under experimental and natural conditions. MNSV is transmitted by *Olpidium bornovanus* (Sahtiyanci) Karling (Campbell et al., 1995; Rochon et al., 2012). The presence of MNSV and *O. bornovanus* was associated with melon vine decline in Guatemala (de Cara et al., 2008). In Panama, MNSV was reported to cause stem necrosis, necrotic spots on the leaves and wilting of plants in commercial melon crops (Herrera et al., 2006). The virus was also detected in cucurbits in Mexico and Honduras (Herrera-Vazquez et al., 2010) but it was not found in Venezuela (Romay et al., 2014b). MNSV has also been reported to be seed-borne in melon through a vector-assisted seed transmission mechanism (Campbell et al., 1996).

2. **Squash necrosis virus** (SqNV) is a tentative carmovirus species found in Brazil (Lin et al., 1983) and in Martinique Island (Lecocq, 2003). SqNV causes systemic necrotic spots in squash and is transmitted by some strains of *O. bornovanus* (Campbell et al., 1995).

**PERSPECTIVES FOR THE MANAGEMENT AND CONTROL OF CUCURBIT VIRUSES IN LAC**

A management program for viral diseases begins with an accurate assessment of the viral threats secured through extensive field surveys. Development of new
simple and reliable detection methods as well as the generalized use of diagnostic kits already available will allow the carrying out of extensive new surveys in LAC. This will provide an updated and comprehensive picture of cucurbit-infesting viruses in the region. The success of disease management also relies on the understanding of the epidemiological processes (Jeger, 2004). Virus epidemics involve interactions between the virus, host plants, vectors and the environment (Jones et al., 2010). Thus, by managing some of these factors a sustainable control is feasible.

The use of insecticides to reduce whitefly populations has led to a significantly fewer presence of SqVYV symptoms in watermelon crops in Florida (USA) (Adkins et al., 2011). However, insecticide treatments against aphid vectors are generally not efficient for controlling cucurbit potyviruses (Webb and Linda, 1993; Coutts et al., 2011b; Lecoq and Desbiez, 2012). Mineral oils, at weekly intervals, have been used to reduce the incidence of viruses non-persistently transmitted by aphids (Loebenstein and Raccah, 1980), as they seem to interfere with the retention of potyvirus particles on the aphid stylet, reducing viral acquisition (Desbiez and Lecoq, 1997). Nevertheless, in experimental melon fields of California (USA), mineral oil sprays did not reduce virus spread to tolerable level when inoculum pressure was high (Umesh et al., 1995).

Cross-protection is another method for plant virus control, where pre-infection with a mild strain of a virus may protect the hosts from severe challenging strains of the same virus. The mild ZYMV-WK strain has been successfully used to control severe strains of this virus in France, Italy, Israel, Taiwan, Turkey, the United Kingdom and the USA (Desbiez and Lecoq, 1997). However, ZYMV-WK was not efficient to prevent infections caused by very divergent ZYMV isolates from Réunion Island (Lecoq and Desbiez, 2012). In Israel, an efficient method was developed for inoculating the ZYMV-WK strain in cucurbit plantlets on a large scale. (Yarden et al., 2000).

Cross-protection against severe strains of PRSV was also successfully achieved using mild strains (referred to as PRSV-W-1 and PRSV-W-2) under greenhouse and field conditions in Brazil (Rezende and Pacheco, 1998). However, subsequent cross-protection assays, using the mild strain PRSV-W-1, showed that a severe strain of PRSV could still be detected in the non-inoculated upper leaves, suggesting competition for viral replication sites between PRSV strains (Freitas and Rezende, 2008). Cross-protection is an alternative to control plant viral diseases that requires long-term and extensive studies to validate the use of a viral mild strain at an economical scale without risks of strain reversion towards a more severe form.

Cultural practices that tend to reduce viral epidemics and damages can perform efficiently for many plant viruses. Such practices attempt to prevent the interaction between the host plant, the vector and the viral source. Trials in which cucurbit and grain sorghum were intercropped performed better in reducing field epidemics of WMV and PRSV than those in which cucurbit plots were surrounded with grain sorghum (Damicone et al., 2007). However, whereas this practice may be useful in small scale cultivation, its use in extensive areas (e.g. melon for export) is less practical. Plastic mulches were also shown to delay the onset of infections by thrips-, whitefly- and aphid-borne viruses (Abou-Jawdah et al., 2000; Momol et al., 2004; Adkins et al., 2011; Lecoq and Desbiez, 2012). Silver plastic mulches are more efficient than black plastic mulches to reduce vector populations (Simmons et al., 2010; Coutts et al., 2011b), but the higher cost of silver plastic mulch is a limiting factor to its wide use in some cucurbit-growing areas (Adkins et al., 2011).

Control of alternative hosts of viruses or vector populations is another strategy for reducing virus disease incidence. In tropical and subtropical regions of LAC, the efficiency of this control strategy is affected by the environmental conditions that favour the presence of weeds and cultivated cucurbits for the whole year round. However, the removal of potential reservoirs including weeds, volunteer cucurbit plants, crop remnants and plants with viral symptoms is recommended (Coutts et al., 2011b). Susceptible crop-free periods have been a useful measure to reduce the impact of TYLCV in Dominican Republic where processing tomato production was dramatically affected in the 1990’s (Salati et al., 2002). This type of measures can contribute to sustainable cucurbit production, but their implementation must take into account the impact on countries like Guatemala, Costa Rica and Honduras, where cucurbit crops are important sources of income.

The use of virus-resistant cultivars is one of the most valued and simple strategies to control plant viruses. Durable resistance to ZYMV has been introgressed in cucumber (resistance conferred by the zym gene), while a resistance in melon (Zym gene) is easily overcome (Lecoq and Desbiez, 2012). The cucumber cv. Taichung Mou Gua (TMG) that possessed the zym gene was shown to be completely resistant to 34 Venezuelan ZYMV isolates, whereas one of these isolates completely overcame the resistance of melon line PI 414723, which also possessed the Zym gene, suggesting a low durability of the melon resistance if used in the field (Romay et al., 2014b). A high level of resistance to ZYMV is also available in squash (C. moschata). It was introduced in zucchini squash (C. pepo) by interspecific crosses, but the resistance level is only partial in this host (Lecoq and Desbiez, 2012). For PRSV, resistance sources have been identified in melon, cucumber, squash and watermelon (Lecoq et al., 1998; Maluf et al., 1997; Strange et al., 2002), and commercial cucumber cultivars with resistance genes are already available (Lecoq and Desbiez, 2012). In Brazil, several sources of resistance to PRSV in squash and watermelon have been found and their inheritance determined (Maluf et al., 1997; Oliveira et al., 2003; Azevedo et al., 2012).

The crinivirus CYSDV is a relatively recent emerging plant virus (Navas-Castillo et al., 2011) so that efforts to
look for resistance sources are in progress. McCreight and Wintermantel (2011) identified a recessive gene in the melon line PI 313970 (*C. melo var. acidulus* Naudin), which conferred a high level of resistance to CYSDV. A recessive gene for resistance to CuLCrV was found in melon PI 2313970 (McCreight et al., 2008) and squash cultivars partially resistant to SLCV are commercially available (Lecoq and Desbiez, 2012). To date, there are no reports of screenings for resistance sources to MCLGaV, in spite of its presence in several countries from Latin America with intensive and extensive cucurbit production.

Virus resistance mediated by genetically modified (GM) plants is now available for controlling some plant viruses. Squash cultivars expressing the coat protein gene of CMV, WMV and ZYMV and resistant to these viruses are currently grown in the USA (Lecoq and Desbiez, 2012). However, there is still reluctance about the use of GM plants in many, and not only, LAC countries.

Finally, the success of control strategies for plant diseases or pests is based on the combination of different approaches that involve the hosts and the environmental factors, both natural and anthropic. Hence, there is a need of permanent research and development to adapt control methods to priorities for each region in order to reach sustainability of cucurbit productions.

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**REFERENCES**


Espinoza H.R., McLeod P.J., 1994. Use of row cover in canta-
lope (Cucumis melo L) to delay infection of aphid-transmit-

FAOSTAT, 2012. Statistical database (online) of Food and Ag-


Flores E., 1989. El chayote, *Sechium edule*, Swartz (Cucurbita-


sion and pathogenicity-the tails of two proteins. *Molecular Plant Pathology* 8: 139-150.


ties for Mexican cantaloupe producers. *HortScience* 46: 439-
444.


HansPetersen H.N., McSorley R., Liburd O.E., 2010. The im-
pact of intercropping squash with non-crop vegetation bord-
ers on the above-ground arthropod community. *Florida Entomologist* 93: 590-608.

Halfeld-Vieira B.A., Ramos N.F., Rabelo-Filho F.A.C., Gon-

topathology* 160: 19-25.

Hernández J., Trujillo G., Albaracin M., Zapata F., 1989. Nue-


ruses associated with native flora and cultivated plants from the Yucatan Peninsula of Mexico. *Virus Genes* 35: 825-833.


Herrera-Vásquez J.A., Córdoba-Sellés M.C., Cebrían M.C., Ros-


ulence in the SLCV clade, and host shifting by the host re-

Jeger M.J., 2004. Analysis of disease progress as a basis for evalu-


Cucurbit viruses in Latin America

Journal of Plant Pathology (2014), 96 (2), 227-242


Sebastian P., Schaefer H., Telford I.R.H., Rennera S.S., 2010. Cucumber (Cucumis sativus) and melon (C. melo) have numerous wild relatives in Asia and Australia, and the sister species of melon is from Australia. Proceedings National Academy of Sciences USA 107: 14269-14273.


