

Cucurbits

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Cucurbit viruses cause considerable economic losses worldwide. The most common viral diseases affecting this crop family are Potyviruses, Cucumoviruses, Criniviruses, Ipomoviruses, Tobamoviruses, and the emerging Begomoviruses. Four main cucurbit crops are grown worldwide, namely melon, cucumber (*Cucumis*), watermelon (*Citrullus*), and squash (*Cucurbita*). Huge natural variation is also available within each genus, providing valuable sources of genetic resistance to these diseases. Intraspecific and intrageneric diversity and crossability are key factors to select the optimum breeding strategies. Melon and cucumber are diverse species for which intraspecific resistance is available. Conversely, in *Citrullus* and *Cucurbita*, wild relatives provide the resistance diversity absent in watermelon and in *C. pepo*. Some of the classical sources used by breeders, many of which are multi-resistant, come from corresponding origin centers in Asia, Africa, and America, as well as from secondary centers of diversity. Genetic studies have identified dominant and recessive and often complex resistance. Many of the genes identified have been mapped and markers for MAS are available, but higher mapping resolutions are required to identify the corresponding genes. Only a few genes could be cloned and functionally characterized. Efforts are underway to use genome mapping and functional genomics to advance toward a genomic-assisted breeding against viral diseases in cucurbits.

Keywords: Cucurbits, Cucurbit viruses

1. General Introduction

Plant viruses are responsible for more than USD 30 billion annual losses in crops ^[1], and the economic impact of these pathogens is expected to increase under the current global warming scenario ^[2]. Since viruses are obligate intracellular parasites, the use of chemicals to control the diseases they cause is not an option. Thus, the use of genetic resistances for breeding is the most reliable and cost-effective alternative to minimize losses.

Cucurbitaceae is one of the largest vegetable families, including four of the crops within the twelve-top horticultural crops worldwide (FAOSTAT, 2020). The main cucurbits are within three genera: Watermelon (*Citrullus lannatus*), cucumber, and melon (*Cucumis sativus* and *Cucumis melo*); and zucchini, pumpkin, squash, and gourd (*Cucurbita* spp). A high number of minor cucurbits are also largely cultivated in specific regions worldwide, being basic foods in these regions with a positive effect on human health ^[3]. *Cucurbita* spp. have different origins, from southern North America to Argentina. Melon, which was thought to have an Asian origin according to recent studies, was domesticated at least twice in Asia and Africa ^[4]. Cucumber is originally from India and East Asia, and watermelon has an African origin. For a thorough review on their origins, domestication, and phylogeny, see ^[5].

Cucurbit crops may be affected by tens of viruses transmitted either by a diversity of vectors or mechanically worldwide ^[6] ^[7]. Aphid-transmitted viruses, such as the potyviruses Zucchini yellow mosaic virus (ZYMV), Watermelon mosaic virus (WMV, formerly Watermelon mosaic virus-2), Papaya ringspot virus (PRSV, formerly Watermelon mosaic virus-1), and Moroccan watermelon mosaic virus (MWMV); cucumoviruses, such as Cucumber mosaic virus (CMV); and poleoviruses, such as Cucurbit aphid-borne yellows virus (CABYV) are among the most widely distributed, causing severe epidemics in major production areas. Also, whitefly transmitted criniviruses, such as Beet pseudo-yellows (BPYV), transmitted by *Trialeurodes vaporariorum*, were more important in the past due to the displacement of this whitefly by *Bemisia tabaci*. Other *B. tabaci*-transmitted criniviruses (Cucurbit yellow stunting disorder virus, CYSDV, and the emerging Cucurbit chlorotic yellows virus, CCYV) and ipomoviruses (Cucumber vein yellowing virus, CVYV) are more damaging today. Among *B. tabaci*-transmitted viruses, begomoviruses have become a main problem in this crop family in the last decade, infecting cucurbits with varying degrees of severity. Tomato Leaf Curl New Delhi Virus (ToLCNDV) is currently the most damaging representative of this group, although Squash leaf curl virus (SqLCV), Watermelon chlorotic stunt virus (WmCSV), and Melon chlorotic mosaic virus (MeCMV) are also important. The emergence of new races of the carmovirus Melon necrotic spot virus (MNSV), transmitted by the fungus *Olpidium*, is also increasing the incidence associated with

this virus. Other viruses transmitted mechanically, such as the tobamoviruses Cucumber green mottle mosaic virus (CGMMV) and Zucchini green mottle mosaic virus (ZGMMV), are prevalent in specific areas. There are many other viruses limited to specific areas with a negligible economic impact.

The major viruses affect all the main cucurbit crops, cucumber, melon, watermelon, zucchini, and pumpkin and squash, but some viruses are more damaging in specific crops. All major cucurbits are susceptible to potyviruses. Also, all are hosts of CMV, but infections are more important in melon and cucumber, whereas watermelon shows milder infections [8]. Melon and cucumber are also more severely affected by CYSDV, whereas ToLCNDV is especially damaging in zucchini and pumpkin [7][9]. Cucumber appears to be least affected by begomoviruses, but more susceptible to CGMMV and CVYV [6][8][9]. MNSV does not affect Cucurbita species and cause only mild symptoms in watermelons [8]. Besides, some viruses are more frequent in specific growing conditions or cycles. For example, mixed infections of ZYMV and CMV are frequent in open-air fields, affecting melons and squashes and reducing fruit quality. Also, mixed infections of CYSDV and CVYV are frequent and can increase the mild effect that these viruses cause to Zucchini separately. Mixed infections of ToLCNDV with CGMMV minimize infections in zucchini and also in cucumbers. ToLCNDV causes up to 30% of the production losses in zucchini greenhouses, and severely affects pumpkin squash under open-field conditions [10]. Diverse cultural practices can reduce the impact of viral epidemics [11], but the use of resistant cultivars, in combination with actions in an integrated disease management adapted to different agroecological conditions, can be a better and more sustainable solution.

Genetic studies of resistance to viruses have advanced in the last decade as genetic and genomic information has become available in cucurbits, with reference genomes being generated for most major cucurbits, melon (454 Mbp), cucumber (237.5 Mbp), watermelon (425 Mbp), and squash (263 Mbp) [12][13][14][15]. Resistant sources were selected in the past by screening, and the available collections are now being studied in detail with genetic and genomic tools [16][17][18][19]. Often, some sources are multi-resistant, displaying resistance to one or more viruses, and even belonging to different families. Also, as it occurs in other species, race specific resistance has been found for the variable pathogens (see references below, for each species and virus). The genetics of resistance is diverse, either dominant or recessive, monogenic, and oligogenic or polygenic, including combinations of all these possibilities. New genetic studies have allowed the identification of markers appropriated for marker assisted selection and, in some cases, the genes underlying the resistance. The strategies followed are different for the different crops, depending on the variability of the species/genus, on the origin of the resistances and on the crossability relationships among the different taxa. The possibility of mechanical transmission also affects the advance of genetic studies.

Most of the breeding programs performed in the past have used the same multi-resistant sources, such as the Indian PI 414723 and PI 124112, the Korean PI 161375 and African TGR-1551 melon accessions, the Chinese TGM-1 and 02245 cucumber genotypes, the Nigerian watermelon accession PI 595203, and the African accession Nigerian local of Cucurbita moschata and accessions of the wild Cucurbita species C. ecuadorensis and C. okeechobeensis. Thus, there is a need to broaden the genetic basis of the resistance to face new viruses and new strains.

2. Natural Resistances to Viruses in Cucurbits

The range of resistance sources is diverse in the different cucurbits and in general resistances come from the same geographical regions, which coincide with the centers of origin, domestication, and diversification of the species. For example, in melon, which was domesticated at least twice in Asia and Africa, the high intraspecific variability provides resistances in Asian and African accessions of the subspecies *agrestis* readily crossable to the elite cultivars and landraces so that populations with no distorted segregations can be obtained and used for mapping purposes. In cucumber, which originated in India and East Asia, resistances, also intraspecific, have been found mainly in East Asian accessions and in minor extension in accessions from America, Europe, and India. Wild Cucumis are also resistant to many viruses, but crossability barriers prevent their use for breeding melons and cucumbers. For watermelon of African origin, most of the resistances reported for breeding have been reported in African and Asian accessions of other *Citrullus* species which can be crossed to watermelon. Also, in Cucurbita, an American crop, the tropical pumpkin (*C. moschata*) and wild Cucurbits, are the major sources of resistance for breeding the two main crops, zucchini (*C. pepo*) and pumpkin (*C. maxima*). The geographical origin of the resistances to the different viruses in Cucurbits is disperse. For example, most resistances to CMV have been found in melon and cucumber Asian accessions from Afghanistan to Japan, whereas resistance to potyviruses has been found all around the world. In all four crops, there are some multi-resistant sources. Many breeding programs have been based on a few of these multi-resistant sources, which increases the risk of resistance breakdown. The huge genetic diversity, still unexplored, within these major Cucurbits provide an excellent opportunity to identify new sources of resistance. For this, the genetic tools available in these Cucurbits, including genomic and transcriptomic sequences from references, as well as from other varieties, must speed up the search for

new resistances. In fact, cucurbit researchers have already generated high-throughput genotyping data from complete germplasm collections that would optimize their use in screening assays. To date, few genes have been mapped and cloned in melon (eIF4E for resistance to MNSV and VPS41, for resistance to CMV), and few orthologous genes have been identified in cucumber (eIF4E, which confers resistance to CVYV and the potyviruses ZYMV and PRSV-W). The availability of large marker collections, high-throughput genotyping tools, and high-resolution mapping populations will allow advances in gene mapping and identification of the underlying genes, providing markers useful for efficient marker-based selection procedures, pyramiding of resistance genes, comparative analysis of syntenic regions, genomic selection, etc. New tools, like gene editing by CRISPR/Cas, will allow these genes to be targeted in elite cultivars to introduce these resistances and to study gene function. In species where transformation is not available, other tools, like TILLING, will be useful for the generation and introduction of resistances.

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