

Review

Natural Resistances to Viruses in Cucurbits

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Abstract: 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; *Cucumis*; *Citrullus*; *Cucurbita*; resistance; virus; genetic diversity



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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, for-

merly *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) [12–15]. Resistant sources were selected in the past by screening, and the available collections are now being studied in detail with genetic and genomic tools [16–19]. 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. okechobeensis*. Thus, there is a need to broaden the genetic basis of the resistance to face new viruses and new strains. This paper summarizes the work done within the last decades in the study of genetic variability of resistance to viruses in cucurbits as well as in the understanding of the inheritance of the resistances.

2. Melon (*Cucumis melo*)

Among cucurbits, most information is available in resistance to melon viruses. This species has been traditionally divided into two subspecies, *melo* and *agrestis* [20]. Resistances have been identified frequently in accessions of the subspecies *agrestis*, mainly in the Asian groups conomon, momordica, and acidulus. Some accessions are particularly interesting, since they show resistance to several viruses. For example, the Indian accessions PI 414723 and PI 124112 are resistant to many potyviruses. Others carry resistances to viruses of different families, like the Korean accession PI 161375, resistant to CMV, MNSV, KGMMV, and BPYV; the Indian PI 313970, resistant to CYSDV, CABYV, WmCSV, LIYV, and CuLCrV; and the African TGR-1551, resistant to WMV, CYSDV, and CABYV [21]. These accessions are very powerful genetic resources for pyramiding diverse resistances in elite cultivars (Table 1).

The viruses causing most important economic losses in melon are WMV, PRSV, ZYMV, and CMV. Lately, emerging viruses like ToLCNDV have become a serious problem in some regions, spreading throughout many countries.

Table 1. Genetic resources for resistance to viruses in *C. melo*.

Species	Virus	Resistant Accession	Origin	Group	Genetic Control	Gene	References	
Melon	WMV	TGR-1551	Zimbabwe	Acidulus	Recessive	Major QTL and minor QTLs	[22]	
		PI 414723	India		Monogenic and Dominant	<i>wmv1551</i> <i>Wmr</i>	[23] [24]	
		PI 414723 PI 180280; WMR-29	India India		Dominant (NB-LRR) Dominant (NB-LRR)	<i>Prv2</i> <i>Prv1</i>	[25,26] [26,27]	
	ZYMV	PI 414723 IC 274007 IC274014	India India	Acidulus	Monogenic or Oligogenic	<i>Zym-1 to Zym-3</i>	[28,29] [30]	
		CMV	Freeman's cucumber PI161375 C-189	Japan Korea Japan	Conomon Conomon	Recessive and Oligogenic Recessive and Oligogenic	<i>cmv1</i> <i>cmv1; cmqw3.1; cmqw10.1</i>	[31,32] [33,34] [35]
	Ginsen makuwa China51		Japan China	Makuwa Chinensis	Recessive and Oligogenic Recessive and Oligogenic	<i>cmv1</i>	[32] [32]	
	Miel Blanc Pat81		China Korea	Chinensis Chinensis	Recessive and Oligogenic Recessive and Oligogenic	<i>cmv1</i>	[32] [32]	
	Ogon		China	Makuwa	Recessive and Oligogenic		[32]	
	Shiro-Uri		Japan	Conomon	Recessive and Oligogenic		[32]	
	Nanbukin		China	Makuwa	Recessive and Oligogenic		[32]	
	Queen's pocket Yamaturi		Afganistan Japan	Dudaim	Recessive against SGII strains Dominant and Monogenic	<i>Creb-2</i>	[32] [36]	
	CYSDV		TGR-1551 (PI 482420) PI 313970	Zimbabwe India	Acidulus Acidulus	Recessive and Oligogenic Recessive		[37] [38]
			CABYV	PI124112 PI 313970	India India		Recessive and Oligogenic	<i>cab-1 and cab-2</i>
	Faizabadi Phoont PI 255478			India Korea				[39] [39]
	PI 282448 PI 414723	Korea India					[39] [39]	
	TGR-1551	Zimbabwe		Acidulus	One dominant gene and at least two modifier genes		[41]	
	WM9 HSD 2445-005	India Sudan		Kakhri-Agrestis			[9] [9]	

Table 1. Cont.

Species	Virus	Resistant Accession	Origin	Group	Genetic Control	Gene	References
	CVYV	PI 164323			Dominant	<i>Cvy-1</i>	[42]
		HSD-93-20-A			Dominant	<i>Cvy-1</i>	[42]
		HSD 254			Recessive	<i>cvy-2</i>	[42]
		Ouzbeque			Dominant	<i>Cvy-3</i>	[42]
		PI 164323			Dominant	<i>Cvy-3</i>	[42]
MNSV		PI 161375	Korea	Conomon	Recessive and Monogenic	<i>nsv</i>	[43,44]
		Gulfstream			Recessive and Monogenic	<i>nsv</i>	[43]
		Doublon	France	Charantais	Dominant and Digenic	<i>Mnr1; Mnr2</i>	[45]
ToLCNDV		PI 414723	India	Momordica			[46]
		PI 124112	India	Momordica			[46]
		Kharbuja	India	Momordica			[46]
		WM-7	India	Agrestis	Polygenic	One major QTL and two minor	[47]
		WM-9	India	Agrestis	Dominant		[46]
		IC274014	India		One Recessive and two dominant genes	<i>bgm-1, Bgm-2, Tolcndv</i>	[9]
CGMMV		Phoot; Kachry	India	Momordica	Recessive and Polygenic		[48]
		Chang Bougi	Korea	Makuwa	Digenic and Recessive. Partial	<i>cgmmv-1, cgmmv-2</i>	[49]
KGMMV		PI 161375	Korea				[50]
CCYV		JP 138332	India	Momordica			[51]
BPYV		Nagata Kin Makuwa	Japan		Monogenic		[52]
		PI 161375	Korea		Monogenic		[52]
LIYV		PI 313970	India		Monogenic and dominant	<i>Liy</i>	[53]
CuLCrV		PI 313970	India		Monogenic and recessive	<i>culcrv</i>	[54]
		PI 236355	England				[54]
		MR-1, PI 124111, PI 124112, PI 179901	India				[54]

Table 1. Cont.

Species	Virus	Resistant Accession	Origin	Group	Genetic Control	Gene	References
	MeCMV	IC274014	India		Two Recessive and one Dominant genes	<i>bgm-1, Bgm-2, tolcndv</i>	[9]
	WmCSV	HSD 2445-005 PI 282448 90625, PI 124112, PI 414723	Sudan South Africa India				[55] [55] [55]
	MWMV	PI 180280, WMR-29	India				[21]
	AWFV	PI 180280, WMR-29	India				[21]
	ZYFV	PI 180280, WMR-29	India				[21]
	ZTMV	PI 180280, WMR-29	India				[21]

WMV. In the momordica accession PI 414723, resistance to WMV is controlled by a single dominant gene, *Wmr*, which courses with a reduction on virus presence but not complete resistance [24]. In the African acidulus accession TGR-1551, resistance is recessive and controlled by a major QTL, mapping in LG XI, and several minor QTLs [22]. This resistance is effective against several WMV isolates, with the reduction of virus titer and symptoms [56]. Differential expression studies have been performed to characterize the response to WMV in TGR-1551, revealing more transcriptomic changes in resistant than in susceptible plants, associated with a defense response that contrasts with the recessive nature of the resistance [57]. Fine mapping of the major QTL in LG XI, named *wmv¹⁵⁵¹*, reduced the interval to 141 Kb and confirmed the minor QTL in LG V, whose effect was significant only when *wmv¹⁵⁵¹* was heterozygous [23]. Other sources were reported as resistant to WMV, such as the oriental pickling conomon melon Freeman's Cucumber, dudaim accessions, and some other melons, but the reported level of resistance is lower compared with the two main momordica and acidulus sources, and their genetics have not been further studied [24,35].

PRSV. Three main sources of resistance to the potyvirus PRSV-watermelon strain (PRSV-W) have been reported. Two of them, the Indian accessions PI 180280, from which WMR29 was derived, and PI 180283, show allelic resistances [27,58]. In the momordica accession PI 414723, the resistance is controlled by a dominant gene, *Prv* [25]. The two better characterized alleles of this gene are *Prv1*, described in the cultivar WMR-29, which produces symptomless resistance, and the allele *Prv2*, present in the accession PI 414723, which produces systemic necrotic lesions upon infection [27,59]. Both WMR-29 and PI 414723 are also resistant to other four potyviruses, Moroccan watermelon mosaic virus (MWMV), Algerian watermelon mosaic virus (AWMV), Zucchini yellow fleck virus (ZYFV), and Zucchini tigre mosaic virus (ZTMV), suggesting that the same locus could be involved [21]. The *Prv* gene has been identified as a nucleotide-binding site and leucine-rich repeat (NBS-LRR) gene, mapping in a region of LG IX within a cluster of resistance gene homologs (RGHs), one of them being *Fom-1*, for resistance to *Fusarium oxisporum* races 0 and 2. Interestingly, *Prv* RNA suffers alternative splicing, producing two different proteins whose ratios could be changing upon pathogen attack [26], similarly to the alternative splicing suffered by the *N* gene for resistance to *Potato virus Y* in tobacco [60]. New Indian collections have been screened against potyviruses, providing additional PRSV resistant sources [30]. Other resistant sources have been reported to the PRSV-papaya strain (PRSV-P), which infects papaya and is less important in cucurbits [61].

ZYMV. Resistance to ZYMV has been found in the accession PI 414723. However, it is controversial, since it was identified as monogenic and dominant by some authors [28] and as oligogenic dominant by other authors, with three loci, *Zym-1*, *Zym-2*, and *Zym-3*, acting complementarily. All of the loci are required for the resistance [29], which probably depends on the ZYMV strain used [35]. Two of the genes have been mapped, locating *Zym-1* in LG IV (which, in the new LG ordering by Perin et al. (2002), is LG II [62]) and *Zym-2* possibly in LG VII (LG X in Perin et al. (2002)) [63]. More recently, other collections have been screened against ZYMV, identifying new sources of resistance [64]. Dhillon et al. (2007) also screened against ZYMV the new collection of Indian landraces and found that resistance to this virus was scarce, even in this collection in which PRSV resistance was quite common. Resistant plants were only found in the accessions IC 274007 and IC 274014 that showed a heterogeneous response. [30]. Resistance to ZYMV in IC 274014 was also confirmed by Romay et al. (2019) [9].

CMV. In melon, resistance to CMV is scarce, usually under polygenic control, and frequently dependent on the CMV strain used in the study. Classically, only the accessions Freeman's cucumber and PI 161375, the Korean cultivar Songwhan Charmi (SC), have been reported as resistant to CMV, being the resistance recessive [31,65]. More recently, after a larger screening of 253 accessions from different geographical regions, Diaz et al. (2003) found some more accessions and related species with heterogeneous resistance to different CMV isolates, such as the Japanese accession C189 [35]. Several studies in Asian and

Indian germplasm have found more resistances to CMV, but the strain specificity and the inheritance were either not reported [66,67] or reported only for the strain FNY [68]. The most studied melon accession is SC, which presents recessive and oligogenic resistance [69]. A single gene mapping in LG XII, *cmv1*, controls the resistance to CMV subgroup II (SGII) strains [33,70], being able to restrict the transport of the virus to the phloem [71] in a manner dependent of the movement protein (MP) of the virus. A virus carrying the MP from a SGI strain is able to invade the phloem of the plant, whereas one carrying the MP of a SGII strain will not be able to overcome the restriction to phloem loading [70]. However, at least two more QTLs are needed for resistance against subgroup I (SGI) strains, working cooperatively with *cmv1*, which indicates the complex genetic architecture of the resistance to CMV [34]. The gene *cmv1* has been cloned, encoding a Vacuolar Protein Sorting 41 (VPS41), and a putative causal polymorphism (L238R) has been identified in this accession [72]. Pascual et al. (2019) analyzed the VPS41 gene in 52 accessions of different geographic origins belonging to 15 melon groups, both from the subspecies *melo* and *agrestis* and tested for resistance to CMV SGII strains, reporting nine sources of resistance, all belonging to the conomon, makuwa, and chinensis Far Eastern group, with three of them showing the same causal mutation than SC (Ginsen makuwa, China51, and Miel Blanc) and five of them (Pat81, Freeman's cucumber, Ogon, Shiro-Uri, and Nanbukin) carrying a new polymorphism (G85E). All of them showed restriction to CMV phloem entry, indicating that restricting phloem entry is a general resistance strategy in melon and this restriction is controlled by the gene *cmv1* in all mentioned accessions [32]. There is only one study that has reported a dominant resistance to CMV, in the Japanese accession Yamaturi [36].

A dominant resistance to WMV, ZYMV, PRSV-W, and CMV is also present in the accessions PI 161375 and PI 414723, which carry the *Vat* gene [73,74]. *Vat* is a CC-NBS-LRR gene controlling the resistance to the aphid *Aphis gossypii* and located in the LG V [75]. This resistance is triggered by aphid puncturing, is *A. gossypii* clone-dependent, and points to a dual role of the *Vat* gene, both in resistance to *A. gossypii* and to virus infection when the virus is transmitted by this aphid [76].

CYSDV. Two acidulus melons have been reported as resistant to CYSDV, PI 482420 and PI 313970. Resistance to CYSDV in the African accession TGR-1551 (PI 482420), was found in a screening of 44 melon accessions [77]. Molecularly, the resistance involves a reduction in virus accumulation and restriction of virus movement in the vasculature [78]. The initial segregation analyses suggested a monogenic dominant control of the resistance. Further mapping studies, performed with a RIL population in a multi-environment assay, have confirmed the major effect of one QTL in LG V and narrowed it down to a region of 700 kb, providing molecular markers useful for MAS [23]. Resistance in the accession PI 313970 is also partial, since the virus was detected in asymptomatic tissues and is controlled by a single recessive gene [38].

CABYV. After screening a large melon collection, Dogimont et al. (1996) found some melon accessions resistant to *Cucumber aphid-borne yellows virus* (CABYV), mostly in the momordica and acidulous group from India, such as Faizabadi Phoont, PI 124112, PI 41472,3 and PI 313970, as well as from other geographical origins, such as Korea, with PI 255478, or South Africa, with PI 282448 [39]. Romay et al. (2019) confirmed the resistance of PI 414723 and also found resistance in the accessions HDS 2445-005 and WM9 from Africa and India, respectively [9]. Resistance to CABYV derived from in the accession PI 124112 is controlled by two complementary, recessive genes [40], whereas, in TGR-1551, it is controlled by one single dominant gene, but also at least two modifier genes have been detected. The virus accumulates in the inoculated tissues, but accumulation fails in the systemic tissues, which suggests an impairment of virus movement in the vasculature [41]. TGR-1551 is an especially interesting accession, since it carries resistances to WMV, CYSDV, and CABYV. The resistances are different, since it is recessive for WMV [56] and CYSDV [37,79] but is dominant for CABYV. However, despite this different genetic control, for both

CABYV and CYSDV the resistance is manifested as an impairment of viral movement in the vasculature [41,78].

CVYV. Screening of 135 melon and 12 wild *Cucumis* accessions for resistance to the Ipomovirus *Cucumber vein yellowing virus* (CVYV) found resistance only in some wild species [80]. Resistance was later studied in a collection of more than 1000 melon accessions, identifying three loci associated with the resistance, with different inheritance in different accessions. A first locus, *Cvy-1*, with three alleles: *Cvy-1⁺*, for susceptibility in Vedranta; *Cvy-1¹*, controlling resistance in the Indian accession PI 164323; and *Cvy-1²*, which controlled systemic necrosis in the African accession HSD-93-20-A. A second locus, *cvy-2*, was present in the African HSD 254 and was recessively inherited, controlling tolerance to CVYV. *Cvy-3* was a third locus, present in Ouzbeque and PI 164323 and controlling symptoms severity [42].

MNSV. Resistance to *Melon necrotic spot virus* (MNSV) in the Korean accession PI 161375 and the cultivar Gulfstream is controlled by the recessive gene *nsv* [43]. Map-based cloning of *nsv* led to the identification of an eukaryotic translation initiation factor eIF4E, mapping in LG XII, as responsible for the resistance [44]. EcoTILLING the melon eIF4E gene in 113 accessions revealed three additional sources of resistance from different origins sharing a polymorphism that correlated with resistance to MNSV [80]. A digenic dominant resistance was found in the Charentais type melon 'Doublon,' with two dominant genes *Mnr1* and *Mnr2*, the former mapping in LG XII at 19 cM from *nsv* [45].

ToLCNDV. This virus was first described in India and appeared as a severe disease in 2012 in Southeast Spain. A large screening, including melon accessions of different horticultural groups, identified five melon genotypes with variable levels of resistance, all of them originally from India and belonging to the momordica, kakri, and wild melon groups of the spp. *agrestis*. PI 414723, PI 124112, and Kharbuja, were either symptomless or recovered from the mild infection [46], whereas the accessions WM-7 and WM-9 showed higher level of resistance, with very low viral titers both in the resistant parental accessions and in the F1 hybrids with PS. The genetics of the resistance in WM-7 revealed three controlling regions, with one major locus in LG XI and two additional regions in LG II and XII [47]. The main region of LGXI has been reported as syntenic to the region where the major ToLCNDV resistance QTL found in *C. pepo* maps [81]. An additional *momordica* accession, IC204014, showed a resistance controlled by one recessive gene, *begomovirus resistance-1* (*bgm-1*) and two dominant genes, *Begomovirus resistance-2* (*Bgm-2*) and *Tomato leaf curl New Delhi virus* (*Tolcndv*), but none of them have been mapped. Interestingly, this accession was also resistant to *Melon chlorotic mosaic virus* (MeCMV), with the resistance sharing two of the genes, since it was controlled by two recessive genes, *bgm-1* and (*tolcndv*), and one dominant gene (*Bgm-2*) [9].

CGMMV. Partial resistance to *Cucumber green mottled mosaic virus* (CGMMV) was reported in the Indian momordica lines 'Phoot' and 'Kachry' with recessive and polygenic control, although the plants still showed very mild symptoms at early stages of infection [48]. The resistance in the Korean accession Chang Bougi, a makuwa type, was also partial and temperature-dependent, and was controlled by two complementary recessive genes, *cgmmv-1* and *cgmmv-2*, which was specific for the strain CGMMV-SH and affected virus movement, delaying symptoms appearance in the upper leaves but not restricting the virus [49,82]. Thus, no full resistance to CGMMV has been reported yet in melon.

Other Viruses

Resistance to the tobamovirus *Kyuri green mottle mosaic virus* (KGMMV) was found in the Indian accession PI414723 and in far Eastern accessions [83]. Indian accessions show variable response to the aphid transmitted potyvirus *Moroccan watermelon mosaic virus* (MWMV) [67]. Among the whitefly transmitted viruses, resistance to the crinivirus *Cucurbit chlorotic yellows virus* (CCYV) has been found in the Indian accession JP 138332 [51]. Tolerance to the crinivirus *Beet pseudo-yellows virus* (BPYV) is under monogenic control in 'Nagata Kin Makuwa' and PI 161375, the common source of resistance to MNSV and

CMV [52]. Resistance to the closterovirus *Lettuce infectious yellows virus* (LIYV) was found in the accession PI 313970, the same Indian acidulus resistant to CYSDV, and is controlled by a single dominant gene, *Liy* [53]. This accession is also resistant to the begomovirus *Cucurbit leaf crumple virus* (CuLCrV), with a recessive resistance controlled by a single gene, *culcro* [54]. These authors also found complete resistance to CuLCrV in the accession PI 236355 and partial resistance in other six accessions and one breeding line [54]. Resistance to the begomovirus *Watermelon chlorotic stunt virus* (WmCSV) has been described in several accessions from South Africa, Sudan, and India [55].

3. Cucumber (*Cucumis sativus* L.)

Cucumber is less variable than melon, but useful sources of resistance have been reported within the species, including accessions of the wild ancestor *C. sativus* var. *hardwickii* [84]. Resistance to major viruses comes mainly from Asian germplasm. The most interesting multi-resistant accession, the Chinese TMG1, is resistant to most of the main potyviruses and cucumoviruses affecting this crop [85]. This accession has been the most studied by far, and co-segregation of most of its resistances has been found. Many of the additional resistance sources reported to date have resistances allelic to those of TMG1. Apart from potyviruses and CMV, the whitefly transmitted CYSDV and CVYV and the tobamovirus CGMMV are more important in cucumber than in watermelon or squash. The resistance to these viruses has been found in different accessions and maps in genomic regions different from those of resistances to aphid-transmitted viruses (Table 2).

Table 2. Genetic resources for resistance to viruses in *C. sativus*.

Species	Virus	Resistant Accession	Origin	Genetic Control	Gene	References
Cucumber	ZYMV	TMG-1	China	Monogenic and recessive	<i>zym-1</i>	[86,87]
		Formosa	Brazil	Monogenic and recessive		[88]
		192-18	Japan	Recessive	<i>zym-1</i>	[87,89,90]
		G22	Japan			[89]
		A202-18	Japan			[89]
		R10	Japan			[89]
		S93-18	Japan			[89]
		Dina-1				<i>zym-1</i>
	WMV	Kyoto 3 feet	Japanese	Monogenic and dominant	<i>Wmv</i>	[93]
		TMG-1	China	Polygenic	<i>wmv-2, wmv-3</i>	[94]
		Dina-1		Polygenic		[95]
		Inbred line 02245	China	Monogenic and recessive	<i>wmv</i>	[96]
	PRSV	Inbred line 02245	China		<i>prsv</i>	[97]
		TMG-1	China	Monogenic and Dominant	<i>Prsv-2</i>	[95,98]
		Dina-1		Monogenic and incompletely dominant		[95,98]
Surinam		South America	Monogenic and recessive	<i>prsv-1</i>	[99]	
MWMV	Inbred line 02245	China	Monogenic and recessive	<i>prsv</i>	[97]	
	TMG-1	China	Monogenic and recessive	<i>mwm</i>	[98]	
ZYFV	TMG-1	China	Monogenic and recessive	<i>zyf</i>	[100]	
CMV	Chinese Long	China	Different genetic controls		[101,102]	
	TGM-1		Monogenic and Dominant		[86]	
	‘Srinagar Local-I,’ ‘Srinagar Local-II,’	Southern Himalaya (India)	Monogenic and dominant		[103]	
	‘Paprola Local’	China	Polygenic and recessive	<i>cmv6.1</i>	[104]	
	inbred line 02245		Three incompletely dominant genes		[105]	
Tokio Long Green					[106]	
Kyoto-3-Feet	Japan				[106]	
IC-277048 (var. Hardwickii)	India		Monogenic and recessive		[107]	

Table 2. Cont.

Species	Virus	Resistant Accession	Origin	Genetic Control	Gene	References
	CYSDV	PI 250147 PI 211589 PI 605923 Ames 13334	Pakistan Afghanistan India Spain	Partial and Quantitative	<i>cysdv5.1</i>	[108] [109] [109] [109]
	CVYV	C.sat-10 CE0749 Kyoto-3-Feet	Spain Japan	Monogenic, dominant and Partial Monogenic and incomplete	<i>Cscys-1</i>	[110,111] [112] [106]
	CGMMV	BGV001358; CGN19818	India	Partial		[113]
	MYSV	27028930		Quantitative	<i>Swf-1, Swf-2, Swf-3, Swf-4</i>	[114,115]

Potyriviruses ZYMV, PRSV, WMV, and MWMV. Recessive resistance to ZYMV has been described in several cucumber accessions. Resistance controlled by a single recessive gene was described in an inbred line derived from the Taiwanese cucumber ‘Taichung Mou Gua-1’ (TMG-1) [86,116] and in the Brazilian cultivar Formosa [88]. A survey of 6 Japanese and 21 European cucumber lines identified 5 Japanese slicing cucumber breeds with different degrees of resistance. ‘G22’ and ‘A192-18’ showed no virus presence, whereas in ‘A202-18,’ ‘R10,’ and ‘S93-18,’ virus multiplication was restricted to a very low level [89]. In the inbred line ‘A192-18,’ Amano et al. (2013) identified the gene *zym-1* as a single recessive locus mapping in LG VI in an interval of six candidate genes. SNPs comparison between susceptible and resistant parents suggested a *Vacuolar Protein sorting 4* (CsVPS4) as candidate gene for the *zym-1* locus [90]. The analysis of the *zym-1* locus indicates that resistance to ZYMV in TGM-1 is allelic to that found in Dina-1, an inbred line derived from the Dutch hybrid ‘Dina’ (alleles *zymv*^{TGM} and *zymv*^{Dina}, respectively) [91,92]. Also, the resistance from A192-18 (*zymv*^{A192-18} allele) is closely linked to the Dina-1 resistance. All these results suggest that resistance to ZYMV is conferred by *zym-1* through different mutations in different sources of resistance, with differing in their phenotypes and the dominance relationships between them [87,92]. Comparative genomics of cucumber TMG1-derived and melon PI 414723-derived resistance shows that these sources of ZYMV resistance are non-syntenic [117].

Several sources of resistance to WMV have also been reported in cucumber, with different inheritances. In the Japanese cultivar ‘Kyoto 3 feet,’ resistance was controlled by a single dominant gene, *Wmv* [93], whereas the Chinese inbred line 02245 carries a single, recessively inherited gene, *wmv*⁰²²⁴⁵, mapping in LG VI (Tian et al., 2016). The ZYMV resistant accessions TGM-1 and Dina-1 are also resistant to WMV [86,92] and the resistance co-segregates in these two accessions [95]. TGM-1 carries two independent factors conferring resistance [94,99]. One of them is a single recessively inherited gene *wmv-2*, mapping in LG VI and expressed in the whole plant, including cotyledons. A second resistance factor, *wmv-3*, which is closely linked to *zym-1* [99], would be the result of complex epistatic interactions with either a dominant susceptibility factor, *Wmv-4*, or a recessive resistance factor, *wmv-4*. This second factor would be expressed only in true leaves [94].

TGM-1 and Dina-1 are also resistant to PRSV-W. In TGM-1, resistance seems to be conferred by a single dominant gene, *Prsv-2* [98,118]. The resistances to ZYMV and PRSV-W in TGM-1 are tightly linked, separated by only 2.2 cM [119]. Resistance to PRSV in ‘Dina-1’ is also controlled by a single gene, incompletely dominant and co-segregating with *Prsv-2* [95]. The South American cultivar ‘Surinam’ also shows resistance to this virus [86,95], in this case controlled by a single recessive gene, *prsv-1*, [99,120], allelic to *Prsv2* [119]. In the Chinese inbred line 02245, resistance to PRSV-W is controlled by the recessive gene *prsv*⁰²²⁴⁵, mapping in the same LGVI than *wmv*⁰²²⁴⁵ [97].

The multi-resistant lines TGM-1 and Dina-1 are also resistant to two other potyviruses, MWMV and ZYFV. The resistance to MWMV in TMG-1 is controlled by a single recessive gene, *mwm*, which is tightly linked to the resistance to ZYMV [98], whereas the resistance to ZYFV is also due to a single recessive gene, *zyf* [100]. All the previously described co-segregations suggest either the existence of different alleles of the same gene conferring resistance to different potyviruses or the occurrence of a cluster of resistance genes [95].

CMV. Reports on resistance to CMV in cucumber are variable. Cucumber accessions from China, such as Chinese Long, were the first used to develop CMV-resistant varieties [101,102]. Different genetic controls, from polygenic to single dominant control, were proposed and derived from this same source [121]. Kooistra (1969) studied the inheritance of CMV resistance in material derived from the resistance source ‘Tokyo Long Green’ and proposed three incompletely dominant resistance genes [105]. Studies performed with progenies derived from the cross between these two sources have suggested that different genes controlled these two resistances [121]. The resistance to CMV in the multi-resistant accession TGM-1 is controlled by a dominant gene [86]. CMV tolerance was reported in three cucumber landraces from the lower Himalayas (‘Srinagar Local-I,’ ‘Srinagar Local-II,’

and ‘Paprola Local’), all controlled by a single dominant gene, with the two former being allelic and the latter non-allelic [103]. Recently, Shi et al. (2018) reported a quantitatively inherited recessive resistance in the multi-resistant Chinese inbred line 02245, with a major QTL, *cmv6.1*, in LG VI found in a RILs population between 02245 and the susceptible line 65 G. In the mapping interval, nine genes related with disease resistance were identified [104]. Apart from *C. sativus* sources, CMV resistance has been reported in *C. sativus* var. *hardwickii*, the wild ancestor of cultivated cucumber, with which it can still be crossed. In this case, the Indian genotype IC-277048 shows a recessive resistance controlled by a single gene [107].

Thus, resistances to ZYMV (*zymv*^{TGM}, *zymv*^{Dina} and *zymv*^{A192-18}), WMV (*wmv*⁰²²⁴⁵), PRSV (*prsv*⁰²²⁴⁵), and CMV (*cmv6.1*) have been mapped in LG VI [90,96,97]. In particular, *zym-1* and *prsv*⁰²²⁴⁵ are tightly linked [108].

CYSDV. In cucumber, resistance to CYSDV is partial. Two independent surveys screening several hundreds of cucumber accessions, including wild cucumbers, land races, traditional, cultivars, and breeding lines, from various geographical locations, identified only a few accessions, all of them showing partial resistance, with delayed infection and decreased symptoms severity [109,122]. Preliminary analysis indicated that the resistance found by Aguilar et al. (2006) is controlled by more than one recessive gene [122]. The Asian cucumber accessions PI 211589, from Afghanistan; PI 605923, from India; and the Spanish accession Ames 13334 were the most promising sources, with less severe symptoms and low virus titers in the screening performed by Eid et al. (2006) [109]. A major QTL for resistance (*cysdv5.1*), derived from the PI 250147 collected in Pakistan, was recently reported in LG V [108,123]. These are the only putative sources of resistance to CYSDV found in cucumber.

CVYV. To date, resistance to CVYV found in cucumber seems to be partial. It was first described in cv. ‘Kyoto-3-Feet,’ which is also resistant to *Cucumber mosaic virus* [106]. A survey with 46 Spanish cucumber landraces found four partially resistant genotypes showing reduced symptoms and virus accumulation [110]. Inheritance of resistance in one of them, Csat-10, showed a monogenic and dominant control [111]. The resistant accession CE0749, a CVYV-resistant Long Dutch-type cucumber, displays a monogenic and incomplete dominant resistance, with the gene behind, *Cscvy-1*, explaining more than 80% of the resistance. Fine mapping of the gene using bulk segregant analysis allowed to determine a 625 Kb region in LG V with 24 candidate genes [112].

CGMMV. Resistance to CGMMV in cucumber is scarce. In a survey with cucumber accessions and some wild *Cucumis* relatives, only two Indian cucumber accessions, BGV001358 and CGN19818, displayed partial resistance to both Asian and European strain of the virus, with mild symptoms and low viral titer [113].

MYSV. Resistance to *Melon yellows spot virus* (MYSV) strain S was found in the Thai cucumber accession 27028930 [114]. QTL analysis of a F2 population derived from this accession found four QTLs involved in the resistance, with mapping in LG1, 3, 4, and 7, explaining between 9.4% and 20.1% of the variance [115].

4. Other *Cucumis* Species

Among wild *Cucumis* species, *C. metuliferus* (Naud.) Mey. accession PI 292190 is resistant to PRSV-W and WMV and, in both cases, the resistance is controlled by a single dominant gene [124]. *C. metuliferus* is also resistant to SqMV [125], CYSDV [77], and ToLCNDV [46]. *C. anguria* shows resistance to CGMMV, controlled by one dominant gene [113,126], and to CMV [127]. *C. prophetarum*, *C. dipsaceus*, and *C. africanus*, have been described as resistant to CVYV [80], and *C. africanus* has also been described as resistant to CGMMV [78,128]. *C. zehyeri* is resistant to MNSV [80] and CGMMV [128], and *C. figarei* is resistant to CMV [129] and CGMMV [128,130]. *C. ficifolius*, *C. miriocarpus*, and *C. meeusii* are also resistant to CGMMV [128]. However, to date, none of these species have been successfully crossed with either cucumber or melon, which impairs their possibilities of being used for breeding resistances into these species (Table 3).

Table 3. Genetic resources for resistance to viruses in other *Cucumis* spp.

Species	Virus	Resistant Accession	Genetic Control	References
<i>Cucumis metuliferus</i>	PRSV; WMV	PI 292190	Monogenic and dominant	[124]
	SqMV			[125]
	CYSDV			[77]
	ToLCNDV			[46]
<i>Cucumis anguria</i>	CGMMV		Monogenic and dominant	[113,126]
	CMV			[127]
<i>C. prophetarum</i>	CVYV			Marco [78] et al., 2003
<i>C. dipsaceus</i>	CVYV			[78]
<i>C. africanus</i>	CVYV			[78]
	CGMMV			[78]
<i>C. zehieri</i>	MNSV			[80]
	CGMMV			[78]
<i>C. figarei</i>	CMV			[129]
	CGMMV			[128,130]
<i>C. ficifolius</i>	CGMMV			[128]
<i>C. miriocarpus</i>	CGMMV			[128]
<i>C. meeusii</i>	CGMMV			[128]

5. Watermelon (*Citrullus lanatus* [Thunb.] Matsum. & Nakai) and *Citrullus* spp.

Resistances within the species *Citrullus lanatus* are scarce. Most of the resistances have been found in *Citrullus* species other than *lanatus*, the close species *C. mucospermus*, *C. amarus*, and *C. colocynthis* that show different crossability relationships with watermelon [131]. *C. mucospermus* can be intercrossed to *C. lanatus*, producing highly fertile progeny, although an effect of the direction of the cross has been reported. *C. amarus* is readily crossed with both *C. lanatus* and *C. mucospermus*. However, these crosses produce skewed segregation ratios that can impair genetic analysis. The genome of *C. colocynthis* differs more than of that the two other species with the genome of *C. lanatus*, although crossings are possible with some accessions. Resistances in African accessions of these three species have been reported and used for breeding watermelons [132]. Similarly to melon and cucumber, there are some multi-resistant accessions that have been deeply studied, such as the *C. mucospermus* PI 595203 (readily crossable to watermelon) that display recessive resistance to the three potyviruses, ZYMV, WMV, and PRSV, which are most damaging to this crop, and the *C. amarus* PI 244019. In both cases, the recessive resistance has been associated to the eIF4 factor. Many other accessions are promising sources but need further characterization and more complete genetic studies (Table 4).

Table 4. Genetic resources for resistance to viruses in *Citrullus* spp.

Species	Virus	Resistant Accession	Origin	Group	Genetic control	Gene	References
<i>C. mucosospermus</i>	ZYMV	PI 482261	Zimbabwe		Monogenic recessive	<i>zym-FL</i>	[133]
		PI 595203	Nigeria	Egusi	Monogenic recessive	<i>zym-CH, zym-FL</i>	[134–137]
		PI 494528, PI 494532	Nigeria	Egusi			[138]
		PI 560016, PI 494529	Nigeria				
	PRSV	PI 244017; PI 244018; PI 244019 PI 482342; PI 482318; PI 482379 PI 485583 PI 595203	South Africa Zimbabwe Botswana Nigeria				[139] [139] [139] [139]
WMV		PI 244019, PI 255137	South Africa				[140]
		PI 189317, PI 189318	Nigeria				[140]
		PI 244018; PI 164708	India				[140]
		PI 494529; Egun	Nigeria	Egusi			[140]
		PI 306782 PI 595203 PI 494528 and PI 494532	Nigeria Nigeria Nigeria				[140] [135] [138]
<i>C. amarus</i>	ZYMV	PI 482322, PI 482299, PI 482308, PI 482261 PI 485580 PI 596662	Zimbabwe Botswana South Africa		Monogenic and recessive	<i>zym-FL</i> (in PI 482261)	[133]
	WMV	PI 244018, PI 244019, PI 255137	South Africa				[141]
	PRSV	PI 244019, PI 244018 PI 482342, PI 482318, PI 482379 PI 485583 PI 244017	South Africa Zimbabwe Botswana South Africa		Monogenic and recessive		[139,142] [139] [139] [139]
<i>C. colocynthis</i>	ZYMV	PI 386026, PI 386025, PI 386016, PI 386019, PI 386015 PI 537277	Iran Pakistan				[134,143] [143]
		WMV	PI 386024 PI 386016, PI 386025, PI 386026 PI 388770	Iran Morocco			[140] [140] [140]

Table 4. Cont.

Species	Virus	Resistant Accession	Origin	Group	Genetic control	Gene	References
	PRSV	PI 525080	Egypt				[144]
		PI 537277	Pakistan				[144]
		PI 652554	India				[144]
		Griffin 14201	India				[144]
		PI 244017, PI244019 and PI 485883	South Africa		Monogenic and recessive		[145]
		PI 244019			Dominant	PRSV-3	[142]
	CYSDV	PI 386015, PI 386016	Iran				[146]
	SqVYV	PI 386015, PI 386024	Iran				[147,148]
<i>C. lanatus</i>	SqVYV	PI 482266, PI 392291	Africa				[147,148]

Potyriviruses ZYMV, WMV, and PRSV. Reports on resistance to viruses in watermelon have focused mainly on potyriviruses. Two main strains of ZYMV cause disease in watermelon, the Florida strain (ZYMV-FL) and the China strain (ZYMV-CH). Most of the resistance to ZYMV has been found in accessions of three species related to *Citrullus lanatus*. The authors of [149] reported tolerance to ZYMV-FL, influenced by the environment, in two Nigerian egusi (currently classified as *C. mucosospermus*, a species of sub-Saharan/western Africa origin) watermelon accessions. Later, by screening a larger Nigerian egusi collection, resistance was reported in PI 494528 and PI 494532 [138], although the resistance in the latter was temperature-dependent [134]. The accession PI 595203, also known as Egun, shows high resistance to ZYMV-CH, with total absence of viral symptoms, and controlled by a single recessive gene, *zym-CH* [135]. This accession is also highly resistant to the Florida strain ZYMV-FL [134], with this resistance being controlled by a single recessive gene, *zym-FL* [136]. At present, it is not known whether both *zym-CH* and *zym-FL* are the same gene. The resistance to ZYMV-FL has been associated with a polymorphism in the eIF4E gene [137], which has allowed the use of PI 595203 to develop a watermelon inbred line homozygous for the resistant eIF4E allele and resistant to ZYMV-FL [150].

The species *C. amarus* (citron watermelon, previously known as *C. lanatus* var. *citroides*), which is native to southern Africa, is also an interesting source of resistance to ZYMV. Provvidenti (1991) found four landraces from Zimbabwe displaying resistance specific for ZYMV-FL: PI 482322, PI 482299, PI 482308, and PI 482261. Analysis of the inheritance of the resistance of PI 482261 identified a recessive control by a single gene, *zym-FL* [133]. Resistance to ZYMV-FL has also been found in PI 386026 and PI 386025, two Iranian accessions from a third *Citrullus* species, *C. colocynthis*, a bitter dessert watermelon [134].

A recent and more extensive screening of *Citrullus* accessions against ZYMV-FL confirmed the resistance of some of the previous sources and provided new resistant accessions of the three species: *C. mucosospermus*: PI 560016 and PI 494529, from Nigeria; *C. amarus*: PI 485580, from Botswana and PI 596662, from South Africa; and *C. colocynthis*: PI 537277, from Pakistan and PI 386016, PI 386019, and PI 386015, from Iran. In this screening performed with the whole USDA collection with more than 1600 accessions, the highest level of resistance was found in PI 595203 [143].

As in other cucurbits, accessions resistant to ZYMV often show resistance to other potyriviruses. PI 595203 also showed moderate resistance to WMV, controlled by at least two recessive genes [135]. The Egusi types PI 494528 and PI 494532, resistant to ZYMV, also showed tolerance to WMV [138]. Full resistance to WMV was reported after a large screening of 670 accessions in both greenhouses and field tests. The highest levels of resistance were found in *C. mucosospermus* (PI 189317 and PI 189318 from Nigeria). *C. amarus* PI 244018, PI 244019, and PI 255137 from South Africa were also resistant, but more difficult to manage due to late flowering and poor fruit set. Resistance was also found in Asian and African accessions of *C. colocynthis* (PI 386024 and the ZYMV-resistant PI 386016, PI 386025, and PI 386026 from Iran and PI 388770 from Morocco) [140].

C. mucosospermus PI 595203, resistant to ZYMV-FL, ZYMV-CH, and WMV, was also resistant to PRSV-W [139]. This study described a large survey of 1275 watermelon accessions, and identified seven *C. amarus* accessions resistant to PRSV-W, the African PI 244019 and PI 244018, both also reported as resistant to WMV, and the additional African accessions PI 482342, PI 482318 and PI 482379 (Zimbabwe), PI 485583 (Botswana), and PI 244017 (South Africa), with the last being the most resistant [139]. Levi et al. (2016) identified additional resistant accessions within *C. colocynthis* from Asia (PI 537277, PI 652554, and Griffin 14201) and Africa, (PI 525080) (Egypt) [144]. A deeper study of the genetics of PRSV-W inheritance in the accessions PI 244017, PI 244019 and PI 485883 reported control by a single recessive gene, *prv*, in the three accessions [145]. Using new genomic resources available for watermelon, the authors of [142] further characterized the resistance derived from PI 244019, identifying a major QTL in LG III, *pPRSV-3*, which explained nearly the 25% of the observed variation. Among the candidate genes mapping in the QTL interval, there is eIF4E, which, in many species, has been identified as a recessively inherited resistance

gene against potyviruses as well as against other viruses [151]. In fact, CRISPR addition to disrupt the open reading frame of this gene in cucumber led to resistance to several viruses, including PRSV-W [152]. Recent association studies performed with a collection of nearly 1000 accessions of PI watermelon and PRSV-W resistance found 15 significantly associated SNPs on multiple chromosomes [19].

Other viruses, CYSDV, and SqVYV. Only few studies have reported resistances to other viruses in watermelon. The authors of [146] reported resistance to CYSDV in the *C. colocynthis* Iranian accessions PI 386015 and PI 386016, whereas resistance to SqVYV was reported also in PI 386015, in the accessions of *C. colocynthis*; in PI 386024, also from Iran; and in the African accessions of *C. lanatus* PI 482266 and PI 392291 [147,148].

6. *Cucurbita* spp.

Cucurbita spp. are the crops, among the main cucurbits, in which genetic studies of virus resistance are the least advanced [153,154]. Similarly to the other cucurbits, the more advanced studies have related to potyviruses and cucumoviruses, and more recently, have studied whitefly transmitted geminiviruses, because these, mainly ToLCNDV, are becoming major threats for the cultivation of these crops. The virus resistance scenario in the three main domesticated *Cucurbita* is quite different. Many studies have described the lack of resistance within *C. pepo*. Resistance exists, but is scarce in *C. maxima*, whereas most of the reported tolerances or resistances are within *C. moschata*, with multi-resistant accessions, such as the African Nigerian local and the Portuguese Menina. Also, wild *Cucurbita* are promising sources but are genetically more distant from the cultivated and more difficult to use in breeding [155]. The wild *C. ecuadorensis* is the most multi-resistant and crossable to *C. maxima*, from which resistance to other *Cucurbita* crops can be transferred. The lack of intraspecific resistance in the main *Cucurbita* crop *C. pepo*, challenges the transference due to skewed segregations and complex genetics associated to genetic background effects (Table 5).

Table 5. Genetic resources for resistance to viruses in *Cucurbita* spp.

Species	Virus	Resistant Accession	Origin	Genetic Control	Gene	References
<i>C. moschata</i>	ZYMV	Nigerian Local Menina	Nigeria	Monogenic and dominant	<i>Zym-0, zym-4</i>	[156]
			Portugal	Polygenic and dominant	<i>Zym-1, Zym-2, Zym-3</i>	[157,158]
		Bolina	Portugal			[157]
		Soler	Puerto Rico			<i>zym-6</i> [159]
	WMV	Nigerian Local Menina	Nigeria Portugal	Monogenic and dominant Monogenic and dominant	<i>Wmv</i> <i>Wmv</i>	[156,160,161] [156,160,161]
PRSV	Nigerian local	Nigeria	Monogenic and recessive or oligogenic	<i>prv</i>	[156,162]	
CMV	Nigerian Local	Nigeria	Monogenic and dominant	<i>Cmv</i>	[156,160]	
<i>C. maxima</i>	ToLCNDV	Nigerian Local BSUAL-252	Nigeria Japan	Dominant		[81] [163]
	WMV	PI 419081	China			[164]
	PRSV	Zapatillo redondo	Uruguay			[164]
<i>C. ecuatoriensis</i>	ZYMV			Partially dominant and quantitative	<i>zymv^{ecu}</i>	[149,165]
	PRSV			Digenic or oligogenic		[166–168]
	WMV, CMV					[169,170]
	MWMV	PI 432441		Two recessive genes		[171]
	SqMV					[172]
<i>C. ficifolia</i>	ZYMV					[157]
<i>C. foetidissima</i>	SqMV					[172]
<i>C. okeechobeensis</i>	SqMV					[172]
	ToLCNDV					[173]
<i>C. lundelliana</i>	SqMV					[172]
	ToLCNDV					[173]
<i>C. martinezii</i>	WMV, PRSV, CMV					[169,170]

Potyvirus ZYMV, WMV, and PRSV. The first resistant source to ZYMV within *Cucurbita moschata* was reported in the African accession ‘Nigerian Local’ [149], which carries a major, partially dominant gene (*Zym-0*) and additional modifier genes [174]. The resistance was later confirmed as dominant and monogenic [156]. Paris et al. (1988) found additional sources within the same species in the Portuguese cultivars ‘Menina’ and ‘Bolina’ [157]. Studies in an intraspecific cross have reported that the resistance in ‘Menina’ was conferred by a single dominant gene (*Zym-1*). However, when the resistance from ‘Menina’ was introgressed into the *Cucurbita pepo* ‘True French,’ segregation did not fit a single-gene ratio and two additional dominant genes, *Zym-2* and *Zym-3*, were proposed [158]. Further genetic studies performed with both sources, Nigerian local and ‘Menina,’ as well as an additional source from Puerto Rico, named Soler [159], reported that six genes involved in these resistances. Resistance in Nigerian Local would involve three genes, two dominant (*Zym-0* and *Zym-4*), and the latter interacting with an additional recessive gene (*zym-5*) from susceptible cultivars. ‘Menina’ would carry the *Zym-1* locus, which would be linked to one of the Nigerian Local-dominant genes. The cultivar Soler seems to have a single recessive gene (*zym-6*) that would be linked to the dominant genes, either *Zym-0* or *Zym-4*, reported in Nigerian local, but not to *Zym-1* from ‘Menina’ [175]. The seven genes involved in resistances derived from *C. moschata* have not been cloned yet, but molecular markers for MAS have been reported for *Zym-0*, *Zym-1*, and *Zym-2*, [176]. More recent studies have validated the main role of *Zym-1* in the resistant response to ZYMV, finding new markers associated to this gene, located in chromosome 2, suggesting a CNL (coiled coil, nucleotide binding sites, leucine rich repeats) gene and an ATP-dependent RNA helicase as candidates for this gene [177]. These *C. moschata* main sources of resistance have been used in *C. pepo* breeding as the cross is partially fertile, pyramiding up to six resistance genes [160,176]. ZYMV resistance has been reported in *C. ficifolia*, the fig leaf gourd, but it has not been used for breeding *C. pepo* [157].

Nigerian Local and ‘Menina’ are also resistant to WMV and PRSV [160]. The resistance to WMV in these sources is monogenic dominant, controlled by the gene *Wmv*, which is closely linked to *Zymv-1* [156,161]. Nigerian Local shows also resistance to PRSV, controlled by a single recessive gene, *prv*, [156], although other studies have reported the participation of at least two genes [162].

Resistance to WMV and PRSV-W has been also described in *C. maxima* [178,179]. WMV resistance has been found in the Chinese accession PI 419081 [164] and in some accessions from Argentina and Europe [180]. Resistance to PRSV has been found in Zapatillo redondo, from Uruguay [164]. In some *C. maxima* sources, the resistance to PRSV seems to be controlled by two or three partially dominant or recessive genes [166,167].

CMV. CMV, like potyviruses, is transmitted by aphids and is frequently found in mixed-field infections with ZYMV, WMV, and PRSV. The multi-resistant *C. moschata* Nigerian local also shows resistance to CMV [160], controlled by a single dominant gene, *Cmv* [156]. Resistance to CMV was reported in *C. pepo* [180,181] and in some accessions of *C. maxima* from different geographical origins [178,182].

Begomovirus SqLCV and ToLCNDV. Some resistances to SqLMV have been found in *Cucurbita pepo*, *C. ficifolia*, and mainly in *C. moschata* [172]. Among the Begomovirus, ToLCNDV is the most damaging to the *Cucurbita* species. Resistance has only been found in *C. moschata* from different origins, namely the US, India, Japan, Nigeria, and Spain [173], being one of the resistant sources the multi-resistant Nigerian local. Genetic studies in the accessions PI 604506, from the US, and PI 381814, an Indian landrace, show that, in both cases, a major recessively inherited gene located in LG 8 controls the resistance in intraspecific crosses [81]. Interestingly, the candidate region is syntenic to the major region in LG 11 that controls resistance to the same virus in melon [47]. However, additional loci, segregant in the *C. pepo* background seem to be necessary to achieve high resistance levels [81]. Recent genetic studies with BSUAL-252, one of the reported *C. moschata* Japanese sources, have suggested the occurrence of an independent dominant gene [163].

Resistance in Wild Cucurbitas

A classical study screening most *Cucurbita* wild types for virus resistance showed that most of the species were resistant to CMV and BYMV [169,170]. *Cucurbita ecuadorensis* was highly resistant to CMV, ZYMV, WMV, and PRSV-W, being the most promising wild species for breeding *Cucurbita* spp. [149,169,170]. The resistance to ZYMV from *C. ecuadorensis* has been introgressed into *C. maxima* and has resulted in the development of resistant cultivars of this species [183]. It seems to be controlled by a partially dominant gene, *zymo^{ecu}*, and possibly some modifying genes [149,165]. Other studies have suggested that resistance is quantitatively inherited, with several genes with major effects, along with genes with minor effects [184]. The resistance to PRSV seems to be digenic [166,168] or controlled by a major gene with several genes with minor effect [167]. More recently, resistance to MWMV has been reported in *C. ecuadorensis*, controlled by two recessive genes, none of them related to eiF4E translation factor [171]. Other *Cucurbita* species, like *C. foetidissima* and *C. martinezii* (syn *Cucurbita okeechobeensis* subsp. *martinezii*), also carry resistances against WMV, PRS, V and CMV [169,170]. Resistance to begomoviruses has been found in *C. ecuadorensis*, *C. okeechobeensis*, *C. foetidissima*, and *C. lundelliana* (for SqLCV) [172] and in *C. lundelliana* and *C. okeechobeensis* for ToLCNDV, although, in this case, only under mechanical inoculation [173].

7. Conclusions and Perspectives

Here we exhaustively reviewed the current knowledge on natural resistances to viruses on the main four Cucurbitaceae crops, melon, cucumber, watermelon, and pumpkin and squash, as well as in wild relatives of the genera *Cucumis*, *Citrullus*, and *Cucurbita*. 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 *Cucurbitas*, 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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