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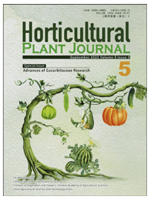

Breeding melon (*Cucumis melo*) with resistance to powdery mildew and downy mildew

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ABSTRACT

Melon (*Cucumis melo* L.) production is often restricted by a plethora of pests and diseases, including powdery mildew and downy mildew caused respectively by the fungal species *Podosphaera xanthii*/*Golovinomyces orontii* and oomycete species *Pseudoperonospora cubensis*. Many efforts have been directed on identification of resistant sources by screening (wild) melon germplasm. In the current review, we summarized such efforts from various publications of the last 50 plus years. Resistance to powdery mildew has been identified in 239 melon accessions and downy mildew resistance in 452 accessions of both *C. melo* and the wild relative species *C. figarei*. Among the resistance sources, *C. melo* var. *cantalupensis* accessions PMR 45, PMR 5, PMR 6, and WMR 29 as well as *C. melo* var. *momordica* accessions PI 124111, PI 124112, and PI 414723 have been considered as the most valuable germplasm because multiple resistance genes have been identified from these accessions and are widely used in melon resistance breeding. Further genetic mapping in a number of resistant sources has enabled identification of 25 dominant genes, two recessive genes and seven QTLs conferring powdery mildew resistance, as well as eight dominant genes and 11 QTLs for downy mildew resistances. Based on the reported sequences of associated markers, we anchored physically (many of) these genes and QTLs to chromosomes of the melon cv. DHL92 genome. In addition to presenting a comprehensive overview on powdery mildew and downy mildew resistance in (wild) melon germplasm, we suggest strategies aiming at breeding melon with durable and broad-spectrum resistance to pathogens and pests.

Keywords: *Cucumis melo*; Melon; Powdery mildew; Downy mildew; Resistance; Breeding

1. Introduction

Melon (*Cucumis melo* L.) belonging to the Cucurbitaceae family is a worldwide economic important horticultural crop. It is highly appreciated for its edible fruits that can be consumed either immature (not sweet) or in most cases, mature (high sugar content and thus sweet) (Pitrat, 2008, 2016; Grumet et al., 2021). Melon displays a great genetic diversity, which is exhibited in many aspects, such as fruit size, shape, color, ripening behavior (i.e., climacteric and a non-climacteric type), peel texture (smooth-skinned to netted), and sex determination (i.e., monoecious and andromonoecious) (Garcia-Mas et al., 2012; Zhao et al., 2019).

Based on phenotypic variations on flower (i.e., sex expression, sepals, and hypanthium and ovary hairs) and fruit traits (i.e., size, shape, exocarp, mesocarp, placentas and seeds), melon has been classified into 19 botanical groups including feral and (non-) cultivated types. They are *C. melo* var. *conomon*, *makuwa*, *chinensis*, *momordica*, *acidulus*, *cantalupensis*, *inodorus*, *ibericus*, *cassaba*, *tibish*, *chandalak*, *ameri*, *flexuosus*, *chate*, *dudaim*, *chito*, *agrestis*, *indicus* and *kachri* (Pitrat, 2016; Pitrat et al., 2000). Among them, *C. melo* var. *chito*

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is not domesticated and thus represents a feral type. *C. melo* var. *agrestis* is domesticated, but not cultivated (Pitrat, 2016). Melon cultivars belonging to the *cantalupensis* (known as cantaloups and galia), *inodorus* (honeydew), and *ibericus* (Piel de Sapo) groups are economically the most important and most consumed.

Melon cultivation in open fields is confined to the tropical and subtropical countries with warm temperature. In less favourable climates during cool seasons, melon is also widely grown in greenhouses (Burger et al., 2010). These different cultivation practices are challenged by a plethora of pests and diseases caused by different pathogens. Some of the common pests and diseases in melon production are listed in Table 1. In this review, emphasis has been placed on two of them, i.e. powdery mildew and downy mildew, with the aim to summarize the results of the last 50 plus years on identification of resistant melon accessions and their use in introgression breeding.

2. Powdery mildew

Powdery mildew is one of the most important plant diseases worldwide and commonly occurring in different cucurbit crops. The disease is caused by biotrophic fungi (Erysiphales) that are able to infect leaves, stems, flowers and fruits, significantly downgrading both the quality and quantity of fruits (Křístková et al., 2009). Three species are reported to affect cucurbits namely, *Leveillula taurica*, *Golovinomyces orontii* and *Podosphaera xanthii*. The most common one in cucurbits is *P. xanthii*, whereas *L. taurica* is of minor economic importance (Glawe, 2008; Lebeda et al., 2016). The first report of powdery mildew in melon dated back to the 1920s in California, the USA with *P. xanthii* (*Erysiphae cichoracearum*) (Jahn et al., 2002) being the causal agent. Nowadays, the disease is reported over the world (Table 2). Relatively high temperatures and humidity seem to be optimal for *P. xanthii*. On the other hand, *G. orontii* requires lower temperatures and is flourishing in colder climates and more Northern latitudes (Jagger, 1926; Jahn et al., 2002). *G. orontii* was predominant powdery mildew in cucurbits until 1958. The shift of predominance between the two powdery mildew species could be a true evolution of the pathogen but could also be attributed to misidentification of the pathogen throughout the world (Cornell University, https://www.vegetables.cornell.edu/pest-management/disease-factsheets/cucurbit-powdery- mildew/; Jagger, 1926; Jahn et al., 2002).

2.1. *Disease cycle and symptoms*

Powdery mildew infection initiates when an ascospore (sexual spore), or more often, a conidium (asexual spore) lands on plant surfaces (e.g. leaves, stems, cotyledons) (Fig. 1). After germination of the conidium, a germ tube is formed and elongates into a swollen hyphal structure called appressorium. Appressoria provide turgor pressure to the penetration pegs for the fungus to breach the host epidermal cell. After entering the plant cells, *P. xanthii* forms haustoria. In addition to the uptake of nutrients, haustoria play a key role for the delivery of molecules (e.g. effectors) to maintain a biotrophic relationship with the host. From growing hyphae, conidiophores are formed, which carry new airborne conidia ready for the next round infection. The hypha develops on top of plant surfaces (leaves, stems, cotyledons) producing white powdery spot formations (Fig. 1), resulting in a significant inhibition of photosynthetic ability of the plant (Jagger, 1926). The less frequent sexual disease cycle appears with merging of compatible mating hyphae and the production of chasmothecia.

2.2. *Podosphaera xanthii races*

Research groups from various countries have identified 21 *P. xanthii* races on melon (Table 3). The first three race, Race 1, 2 and 3, were identified in the USA prior to the 1980s (Jagger and Scott, 1938; Thomas, 1978). Since 1984, 18 new races have emerged in different regions, including three more races in the USA (McCreight and Coffey, 2011), five in France (Bertrand and Pitrat,

Table 1 Some common pests and diseases of melon (*Cucumis melo*)

Class	Disease name	Pathogen	Country	Reference
Bacterium	Bacterial fruit blotch	*Acidovorax avenae* subsp. *citrulli*	Worldwide	Bahar et al. (2009)
	Internal fruit rot	*Pantoea ananatis*	Japan	Kido et al. (2008)
Fungus	Anthracnose	*Colletotrichum orbiculare*; *C. lagenarium*	Worldwide	Kuan et al. (2011); Damm et al. (2013)
	Powdery mildew	***Leveillula Taurica, Golovinomyces orontii, Podosphaera xanthii***	**Worldwide**	Cohen et al. (2004); Kuzuya et al. (2006)
	Fusarium wilt	*Fusarium oxysporum* f. sp. *melonis*	Worldwide	Wechter et al. (1995)
	Monosporascus root rot	*Monosporascus cannonballus*, *M. eutypoides*	Worldwide	Castro et al. (2019)
Nematode	Root-knot nematode	*Meloidogyne* spp.	Worldwide	Guan et al. (2014)
Oomycete	**Downy mildew**	***Pseudoperonospora cubensis***	**Worldwide**	Lebeda and Cohen (2011)
Virus	Cucurbit yellow stunting disorder	cucurbit yellow stunting disorder virus	Worldwide	Marco and Aranda (2005)
	Cucumber green mottle mosaic	cucumber green mottle mosaic virus	Worldwide	Dombrovsky et al. (2017)
	Leaf curl	tomato leaf curl New Delhi virus	India, South Asia Mediterranean Basin, Europe, North America	Fortes et al. (2016); Romay et al. (2019)
Pest	Melon-cotton aphid	*Aphis gossypii* (Homoptera: Aphididae)	Worldwide	Capinera (2000)
	Leafminer	*Liriomyza trifolii* (Diptera: Agromyzidae)	Worldwide	Dogimont et al. (1999)
	Melon fruit fly	*Bactrocera cucurbitae*	Worldwide	Dhillon et al. (2005)
	Cucumber beetles	*Diabrotica* spp., *Acalymna vittatum*	North America	Sasu et al. (2010); Weber (2018)
	Red pumpkin beetle	*Aulacophora foveicollis* (Coleoptera: Chrysomelidae)	South Asia	Rashid et al. (2014)

Table 2 Powdery mildew species infecting cucurbits

Species	Occurrence in Cucurbits	Favored conditions	Reference
Leveillula taurica	Mexico, Libya, Russia, USA, Greece, Bulgaria, Japan, Kenya, Lebanon, Romania, Senegal, Morocco	Wide range of environmental conditions. Usually, warm and dry conditions for cucurbits	El-Ammari (1983); Palti (1988); Forster (1989); Sokolov and Sokolova (2010); Beltrán-Peña et al. (2018)
Golovinomyces orontii	Italy, Czech Republic, Iran, Hungary, Belarus, Bulgaria, Germany	Low temperatures, cold climates	Pirondi et al. (2016)
Podosphaera xanthii	China, India, Argentina, Israel, South Korea, Japan, Mexico, Russia, Thailand, USA, Italy, Myanmar, Spain, Egypt, Iraq, Libya, France, Greece, Czech Republic	Relatively high temperatures and humidity	Jagger (1926); Palti (1988); del Pino et al. (2002); Delhey et al. (2003); Liang et al. (2007); Voytyuk et al. (2007); Rajamuthiah and Mylonakis (2014); Li et al. (2019); Xu et al. (2020)

1989), three in the Czech Republic (Lebeda et al., 2004) and seven in Asia (Hosoya et al., 2000; Liu et al., 2010a; Hong et al., 2018). In Fig. 2 (upper panel), the time line of emerging new races and their spreading is presented.

2.3. *Yield loss and control methods*

Powdery mildew can lead to significant yield losses under conditions favorable to the melon pathogen (http://ipm.illinois.edu/diseases/series900/rpd925/). The main control measure remains the application of fungicides. However, resistance of *P. xanthii* to various systemic fungicides has been frequently reported since 1967, when the first *P. xanthii* race resistant to benomyl was identified (Schroeder and Provvidenti, 1969). Today, Sterol demethylation inhibitor fungicides (SDMI) are used effectively against powdery mildew in cucurbits. The main advantage for the use of this class is that it requires polygenic changes of the pathogen to become resistant (Pérez-García et al., 2009).

Further, several biological control agents are used against powdery mildew in cucurbits, including *Bacillus* bacteria (e.g. *B. subtilis*, *B. amyloliquefaciens*, *B. pumilus*), epiphytic fungi (e.g. *Pseudozymaaphidis*) and other mycoparasitic microorganisms (e.g. *Gliocladium catenulatum)* (Gafni et al., 2015; Ni and Punja, 2021).

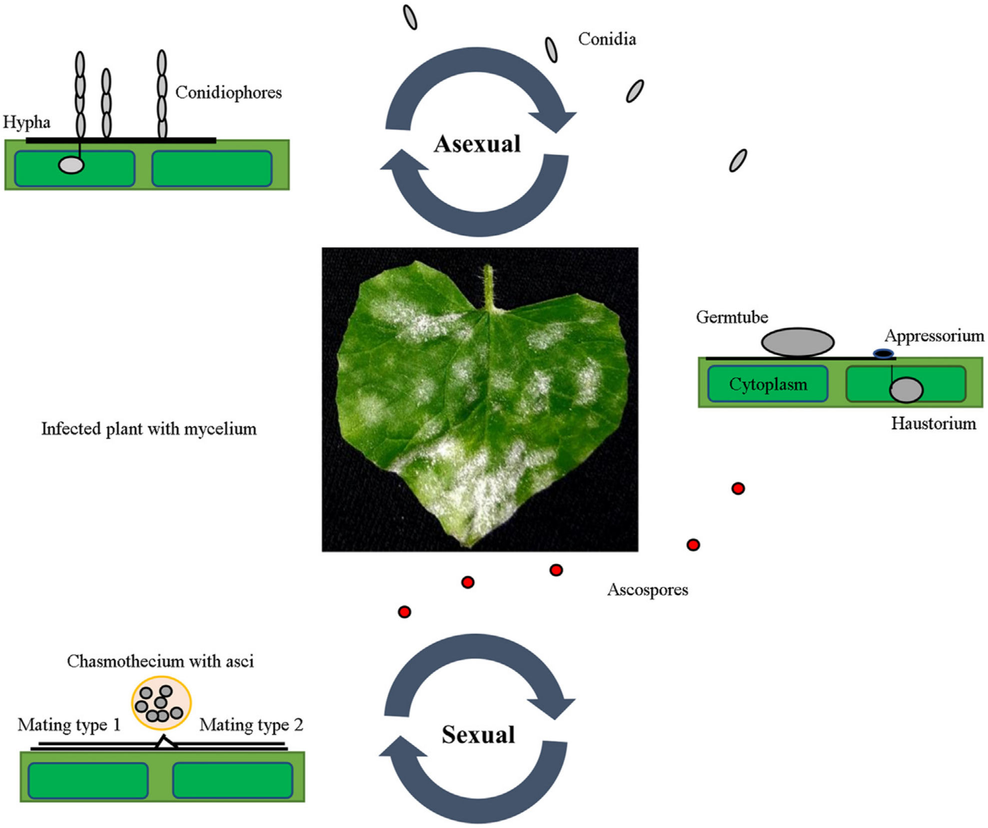


Fig. 1 Sexual and asexual infection cycles of *Podosphaera xanthii*

Asexual: Conidia from infected leaves land on plant tissue. An appressorium is formed at the end of an elongated germ tube. A haustorium is subsequently formed in plant cell. Finally, conidiophores are formed on the invading hyphae. Sexual: The sexual disease cycle occurs less often and appears when two compatible mating hyphae merge to produce sphaerical structures called chasmothecia. Chasmothecia produce asci with ascospores which are dispersed to start an infection similar to conidia.

Table 3 Previously identified sources of *Cucumis* species resistant to *Podosphaera xanthii* races

Cucumis groups/species[a]	*Podosphaera xanthii* races[b]																				
	0	1	2	2F	2U.S.	3	3.5	4	5	6	Ch1	G	H	KN1	KN2	N1	N2	N3	N4	S	Not known
C. melo		42	8	5	3			14	1		1					2	3				5
C. melo var. *acidulus*		2		1	1	1	2		1											1	6
C. melo var. *agrestis*		1	1						1												
C. melo var. *ameri*																					2
C. melo var.*cantaloupensis*	7	7		6	2	1	1	3	2	2			1		2	6	3	3	3		6
C. melo var. *ibericus*		1																			
C. melo var. *inodorus*		3																			1
C. melo var. *kachri*																					1
C. melo var. *makuwa*																					2
C. melo var. *momordica*	4	9		4	3	9	5	4	9	2		3		2	2						13
C. africanus		1	1																		
C. anguria anguria		1	1																		
C. prophetarum		1	1																		
C. zeyheri		1																			

Note: Resistant *C. melo* accessions to *P. xanthii* races were summarized from the following publications: Floris and Alvarez (1996); Pan and More (1996); Hosoya et al. (2000); McCreight (2003), (2006); Wu et al. (2004), (2008); Alvarez et al. (2005); Fukino et al. (2008); Liu et al. (2010b); McCreight and Coffey (2011); Sales Júnior et al. (2011); Wang et al. (2011); Yuste-Lisbona et al. (2011); Guan et al. (2014); Nunes et al. (2015); Li et al. (2017); Rabelo et al. (2017); Hong et al. (2018); Manchali et al. (2019); Thakur et al. (2019).

[a] *C. melo* denotes taxonomy groups that were not shown in the corresponding reports. Detailed information of resistance source per group is provided in Table S2.

[b] *P. xanthii* races not mentioned in the original publication were categorized as not known.

Apart from application of chemical plant protection products and biological control agents, plant breeding has made great efforts towards producing resistant varieties.

2.4. *Genetic resources of powdery mildew resistance*

With various screening and assessment methods (Table S1), *C. melo* germplasm collections including traditional/modern cultivars, breeding lines, and landraces as well as wild relatives have been screened for powdery mildew resistance (Table S2). In total, 239 accessions were considered powdery mildew resistant to different races (Table 3). In addition, we summarized 568 susceptible accessions reported in 16 studies (Table S3), with the aim to avoid redundant screenings in future studies.

It is worth mentioning that accessions PMR 5, PMR 6, and WMR 29 belonging to *C. melo* var. *cantalupensis* as well as accessions PI 124111, PI 124112, and PI 414723 corresponding to *C. melo* var.

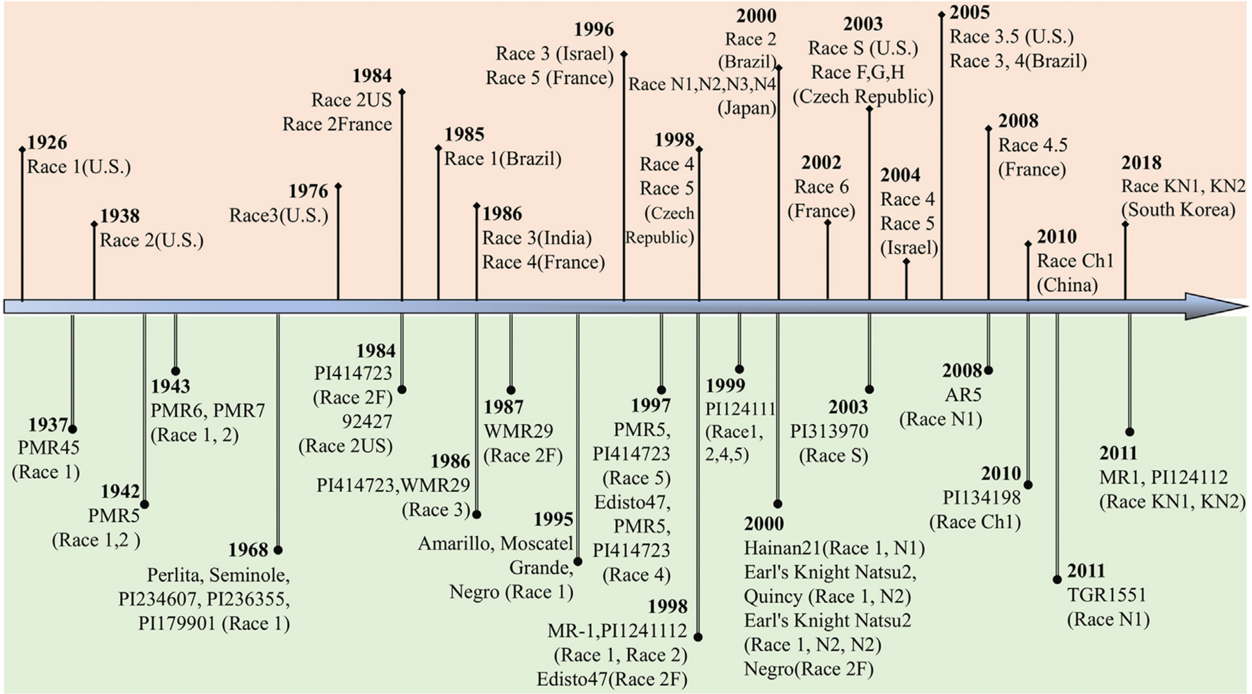


Fig. 2 *Podosphaera xanthii* races emerging year and resistance breeding history of melon

Upper panel: the time line showing the years when new races were first reported and the reported races appeared in new areas. Lower panel: the time line showing the years when resistant melon lines were introduced into cultivation and the resistance spectrum.

momordica showed resistance to multiple races (Fig. 3) and have been explored in resistance breeding (Fig. 2, lower panel). PMR 45 carrying the dominant gene *Pm-1* (Table S4) was the first powdery mildew resistant variety released 11 years after the official report of race 1 (Bohn and Davis, 1964; Harwood and Markarian, 1968; Kenigsbuch, 1992). On year after introduction of the powdery mildew resistant variety, the resistance in PMR 45 was broken by the next emerging race, race 2. A few years later, variety PMR 5, resistant to both races 1 and 2, was released (Epinat et al., 1992). This resistant cultivar carries several resistance genes (*Pm-1*, *-2*, and *-D*, Table S4) and provided good protection against *P. xanthii* for more than three decades until a new race 3 was identified in the USA in 1976 (McCreight and Coffey, 2011) and in India in 1986 (Kaur and Jhooty, 1986). Melon accession PI 414723 (with resistance loci *Pm-7*, *-x*, *-x1,5*, and *-x3*, Table S4) originating from India, was identified in 1986 as an effective source to combat race 3 (Fazza et al., 2013). One decade later in 1996, races 4 and 5 were first observed in France (Bertrand, 2002). Immediately afterwards in 1997, cultivars PI 414723 and PMR 5 were tested to be resistant to both races, while Edisto 47 (with resistance loci *Pm-Edisto47-1*, *-2*, Table S4) was effective to race 4 (del Pino et al., 2002; Rabelo et al., 2017). In 2000, races N1, N2, N3, and N4 were reported in Japan (Hosoya et al., 1999), and the first variety AR 5 (with resistance QTLs CMBR111 and CMBR8-CMBR120, Table S4) showed resistance to race N1 was released in 2008 (Fukino et al., 2008). Later, race N1 resistant variety TGR 1551 (with resistance QTL, Pm-R, Table S4), was released in 2011 (Yuste-Lisbona et al., 2011). Race S and accession PI 313970 being resistant to this race, were reported simultaneously in 2003 (McCreight and Coffey, 2011). Different from other resistance sources, one recessive gene, designated *pm-s*, was identified in accession PI 313970 that delivers resistance to *P. xanthii* race S (McCreight and Coffey, 2011). Recently in 2018, races KN 1 and KN 2 were both first reported in South Korea, and their resistant accession PI 124112 (carrying several *Pm*-genes including *Pm-4*, *-5*, *-V*.1, and *-XII*.1, Table 4) and variety MR1 (with a QTL, *Bpm12.1*, Table S4) derived from PI 124111 also have been selected in the same year (Fig. 2) (Hong et al., 2018).

So far, 25 dominant resistant loci, two recessive loci/genes and seven QTLs have been identified from a number of resistance sources (Tables S4 and S5; Fig. 4). The dominant loci are mostly clustered on chromosomes 2 and 5, indicating a potential allelic relationship of the ones in the same cluster. Four QTLs namely QTL1 (Fukino et al., 2008) on chromosome 2 and qCmPMR-12, QTL2, BPm12.1 (Fukino et al., 2008; Li et al., 2017; Cao et al., 2021) on chromosome 12 co-localize with the genomic positions of several resistance loci (Fig. 4). Next to dominant resistance genes and QTLs, recessively inherited resistance genes have also been identified in melon wild species *C. chate* accession C18 and *C. melo* var. *acidulus* accession PI 313970 (Hong et al., 2015; McCreight and Coffey, 2011). A loss-of-function mutant of a *MLO* (*mildew resistance locus O*) homolog was responsible for powdery mildew resistance to *P. xanthii* race 1 in accession C18 (Hong et al., 2015). In accession PI 313970, one recessive gene, designated *pm-s*, was identified as conditioning resistance to *P. xanthii* race S (Fig. 3) (McCreight and Coffey, 2011). Whether *pm-s* encodes a loss-of-function mutant of the *MLO* allele remains to be investigated.

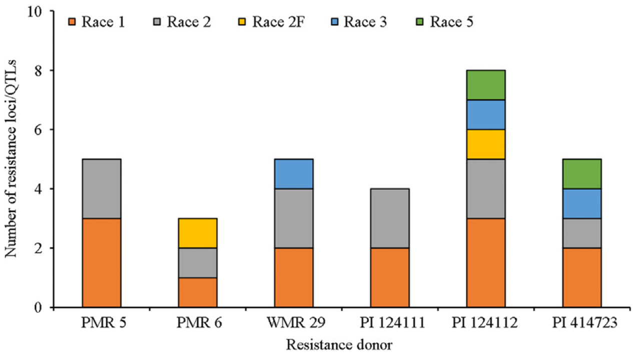


Fig. 3 Number of resistance loci/QTLs identified in *C. melo* var. *cantalupensis* (PMR 5, PMR 6, and WMR 29) or *C. melo* var. *Momordica* (PI 124111, PI 124112, and PI 414723) accessions with broad-spectrum resistance to different *P. xanthii* races

2.5. *Podosphaera xanthii* effectors

The dominant resistance for powdery mildew identified so far is shown to be short-lived since it can be easily broken by new emerging races (Fig. 2). The emergence of new resistance breaking strains is an evolution of the pathogen at the molecular level. Pathogens including *P. xanthii* secrete a large array of effector molecules that manipulate the host mechanisms for a successful disease establishment. For example, the pathogen effectors intervene with the PAMP-triggered immunity (PTI) to suppress host defense. PAMPs are pathogen-associated molecular patterns including various types of pathogen-derived molecules from nucleic acids to proteins, lipids and carbohydrates. Upon perception of PAMPs, plant patter recognition receptors (PRRs) trigger rapid PTI responses. It is possible that many QTLs identified in melon for powdery mildew resistance could encode PRRs. Mostly likely, the dominant genes may encode resistance proteins that recognize specific powdery mildew effectors leading to effector-triggered immunity (ETI) (Pedersen et al., 2012; Rajamuthiah and Mylonakis, 2014; Toruño et al., 2016). Traditional breeding is focusing on introgression of resistance genes from wild relatives in commercial varieties. However, due to evolutionary changes the pathogen effector often loses the ability to be recognized by a specific resistance protein leading to compromised resistance.

Research on *P. xanthii* effectors is limited due to the obligate biotrophic lifestyle of the pathogen. Knockout of genes that lead to loss of virulence also make the pathogen non-viable. Only recently, studies on the epiphytic transcriptome of *P. xanthii* have been published, aiming to identify candidate effector proteins. Authors identified 137 secreted proteins with 53 being candidate effector proteins as they showed similarity to previously identified fungal pathogen effectors and included the N-terminal conserved motif Y/F/WxC known to be present in many candidate effector proteins of other powdery mildew species (Vela-Corcía et al., 2016). Host induced gene silencing (HIGS) was performed by the same group later on and revealed that six of these candidates were required for powdery mildew pathogenesis (Martínez-Cruz et al., 2018). PHEC27213 is one of these six candidates, and was a highly expressed haustorial candidate effector, belonging to lytic polysaccharide monooxygenases (LPMOs) that catalyse chitin oligosaccharides. Chitin is a fungal component and chitin oligosaccharides are PAMPs acting as

Table 4 Ten major pathotypes of *Pseudoperonospora cubensis*

Pathotype	Country (year)	Plant Species	Reference
1	C1, Japan (1987)	*C. sativus, C. melo* var. *reticulatus*	Thomas (1987)
2	C2, Japan (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon*	Thomas (1987)
3	M1, Japan; M2, Japan (1987) 83, 85, Israel (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus*	Thomas (1987)
4	C, the USA (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, Citrullus lanatus*	Thomas (1987)
5	T, the USA (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, C. lanatus, Cucurbita maxima*	Thomas (1987)
6	Unpublished isolates, Israel (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, C. maxima, Cucurbita moschata, Cucurbita pepo* subsp, *pepo, Lagenaria vulgaris*	Cohen et al. (2003)
7	Harbin 10P, China (1987)	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, C. maxima, C. moschata, C. pepo* subsp, *pepo, L. vulgaris, Luffa cylindrica, Luffa accutangula*	Cohen et al. (2003)
8	Unpublished isolates, Vietnam	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, L. vulgaris, L. cylindrica, L. accutangula, Benincasa hispida, Mormodica balsamica*	Cohen et al. (2003)
9	Unpublished isolates, Russia	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, C. lanatus, C. maxima, C. moschata, C. pepo* subsp. *pepo, L. vulgaris, L. cylindrica*	Cohen et al. (2003)
10	Luf-2, Ash-1, India	*C. sativus, C. melo* var. *reticulatus, C. melo* var. *conomon, C. melo* var. *acidulus, C. lanatus, C. maxima, C. moschata, C. pepo* subsp. *pepo, L. vulgaris, L. cylindrica, L. acutangula, Luffa aegyptica, M. balsamica, B. hispida, Trichosanthes cucumerina, Humulus lupulus*	Cohen et al. (2003)

important elicitors to trigger PTI. PHEC27213 is able to suppress this chitin-associated PTI to promote *P. xanthii* virulence (Polonio et al., 2021).

3. Downy mildew

Downy Mildew is one of the main foliar diseases in cucurbit crops affecting over 40 cucurbit species including melon (Palti and Cohen, 1980). The disease is caused by the obligate biotrophic oomycete *Pseudoperonospora cubensis*. In the 19th century, the pathogen was originally classified into the *Peronospora* genus. The change in taxonomy occurred after the observation that the *Pseudoperonospora* species had the ability to produce zoospores unlike the ones belonging to the *Peronospora* genus (Savory et al., 2011).

The disease outbreak is favored by high relative humidity and temperatures of 15–20 °C when germination of infective spores is optimal. *P. cubensis* has a wide host range and poses serious problems in warmer regions where melon cultivation takes place all year and the hosts are always present for the perpetuation of the inoculum (Savory et al., 2011).

3.1. *Disease cycle and symptoms*

Downy mildew infection initiates when zoospores are released from germinated sporangia (asexual spores) on a susceptible host under wet conditions (Fig. 5). Sporangia can be dispersed by travelling with wind currents over long distances or by rain splash and infected agricultural equipment. Interestingly, Cohen et al. (2014) reported that *P. cubensis* may be transmitted by seeds since the pathogen was detected in ovaries, fruit seed cavities and seed embryos of various cucurbit crops. Encysted zoospores produce the penetration hypha that enters the leaf tissue through stomata and forms intercellular hyphae with haustoria. Infected leaves exhibit chlorotic and angular lesions on the adaxial side that are limited by the veins. As disease progresses, chlorotic lesions become necrotic and eventually necrosis expands in the whole leaf (Savory et al., 2011). The sexual cycle which includes the production of oospores is extremely rare due to the cultivation length of those crops.

3.2. *P. cubensis genetic variability and effectors*

Depending on the ability to cause disease in different sets of cucurbit species, *P. cubensis* has been divided into 10 pathotypes (Table 4). The pathotypes have been firstly officially identified by Thomas (1987), who summarized the pathotypes of *P. cubensis* by testing isolates that were collected from Japan, Israel and the USA on 13 representative Cucurbitaceae host species from seven genera including *Benincasa*, *Citrullus*, *Cucumis*, *Cucurbita*, *Lagenaria*, *Luffa*, and *Mormordica* (Table 4). Based on their differential reactions, five distinct pathotypes of *P. cubensis* were identified, including pathotypes 1 and 2 from Japan, 3 from Israel, as well as 4 and 5 from the USA. It is worth mentioning that all five pathotypes were able to infect cucumber (*Cucumis sativus*) and muskmelon (*C. melo* var. *reticulatus*). Pathotype 1 was not able to infect other hosts than these two aforementioned hosts, whereas pathotypes 2–5 had expanded their host ranges including *C. melo* var. *conomon* (pathotypes 2–5), *C. melo* var. *acidulus* (pathotypes 3–5), *Citrullus lanatus* (pathotype 4–5) and *Cucurbita maxima* (pathotype 5) (Thomas, 1987). A similar approach followed by Cohen et al. (2003) in Israel revealed a sixth pathotype which has a broader range of cucurbit hosts in comparison to pathotype 3 (Cohen et al., 2003). In 2012, Cohen (2015) collected isolates and described it as pathotype 7 in China. Pathotype 8 and pathotype 9 were found in Vietnam and Russia, respectively in 2013 (Thomas et al., 2017), and pathotype 10 was observed in India in 2014 (Cohen et al., 2015).

Experimental evidence suggests that there are more pathotypes existing in Europe. Lebeda et al. (2004) used a differential set of cucurbits including 12 representatives from six genera,

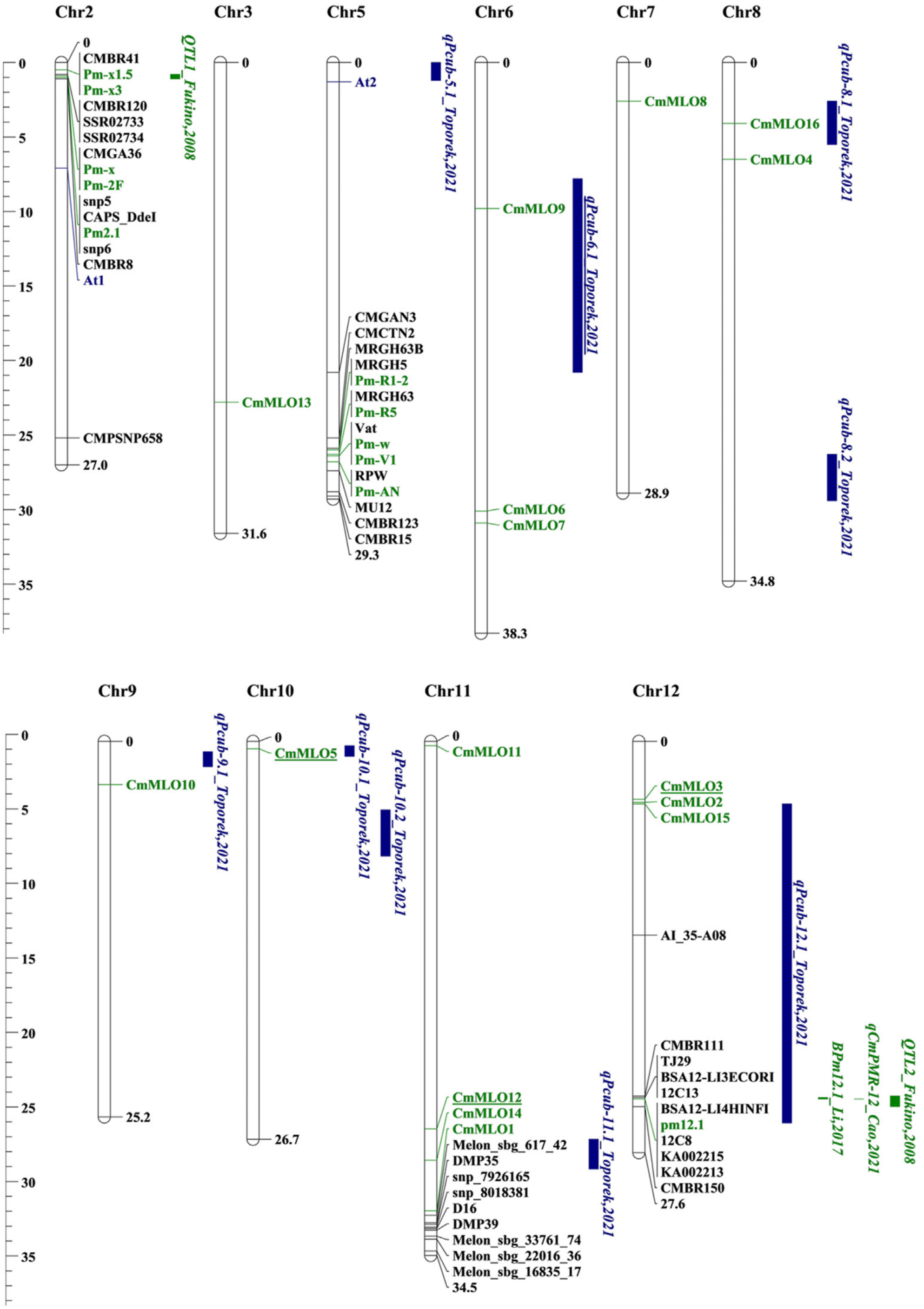
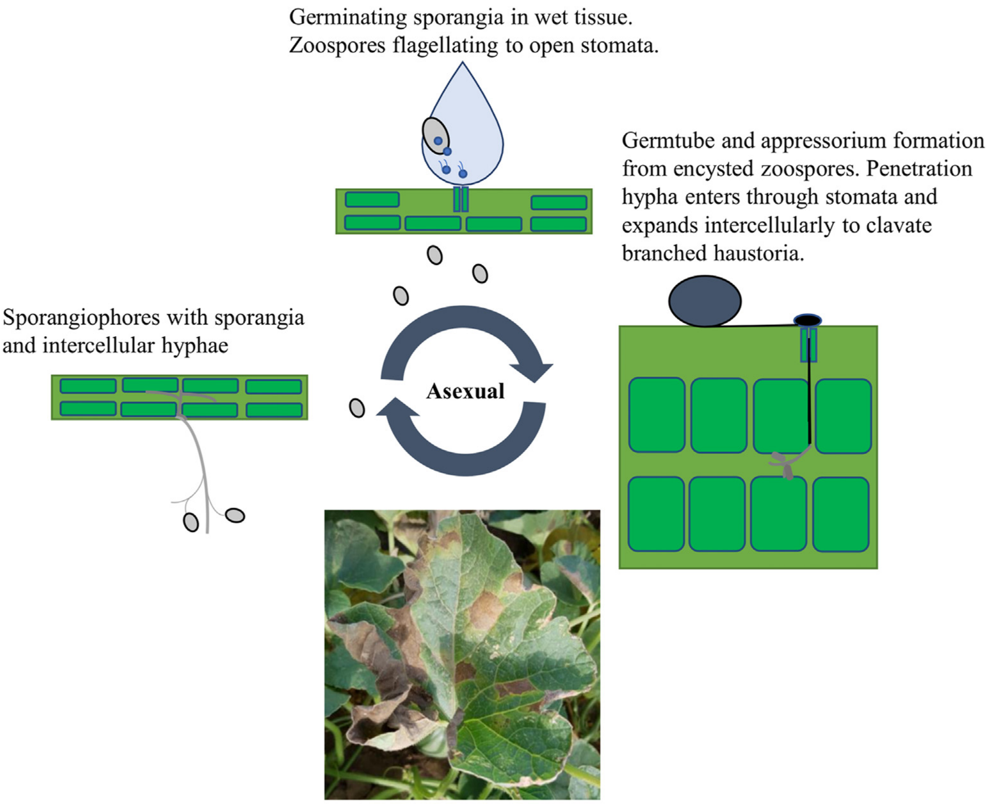


Fig. 4 Physical positions at the Megabase scale of *MLO*-like genes, previously described resistance genes, QTLs, and resistance-linked molecular markers (black) to powdery mildew disease (green), and downy mildew disease (blue) on the chromosomes of *Cucumis melo* according to the *C. melo* L. cv. DHL92 genome sequence database (CuGenDB, http://cucurbitgenomics.org/)

QTLs/genes were mapped by retrieving the reported sequences of associated markers and primer pairs (Table S5). *In-silico* mapping was performed using BLASTN. QTL (Italic) for resistance are displayed as bars and the original names given by the authors first describing them are maintained. The *MLO*-like genes that clustered in a neighborhood joining tree together in Clade V are underlined.

Benincasa, *Citrullus*, *Cucumis*, *Cucurbita*, *Lagenaria* and *Luffa* to identify pathogenic variability of 22 *P. cubensis* isolates collected from four European countries (Czech Republic, Spain, France, and the Netherlands). These 22 isolates which differed from pathotypes 1 to 5 described by Thomas (1987) were further categorized into 13 pathotypes. Later during 2003–2010, according to the classification system of Lebeda et al. (2004) by including more cucurbit species and genotypes, the amount of recognized



Leaf infected with *Pseudoperonospora cubensis*

Fig. 5 Typical *Pseudoperonospora cubensis* disease cycle
Sporangia are germinating under wet conditions on a susceptible host tissue. Zoospores are formed which flagellate into the stomata. After germtube and appressorium formation penetration hyphae expands intercellularly and clavate branch haustoria. Finally, sporangiophores are formed on the elongated hyphae.

pathotypes rapidly extended to nowadays 67. As many of the pathotypes were rather rare, the 10 pathotypes of *P. cubensis* presented in Table 4 are considered the major ones (Cohen et al., 2015).

Oomycetes release effectors in cytoplasm where they interact with effector targets encoded by plant genes to promote disease by suppressing PTI and/or ETI. Cytoplasmic effectors of oomycetes are two types: a, RXLR types which are restricted to *Peronosporales* and b, Crinkler (CRN) types which are present in all oomycetes. RXLR effectors are comprised of a signal peptide in their N terminal followed by a conserved RXLR-(d) EER motif which is responsible for translocation of the protein into the host cell. Most CRN effectors instead have a LXLFLAK motif, which plays the same role as RXLR motif. The domain downstream of the RXLR and LXLFLAK domain are responsible for the interactions of the effectors with host cell proteins (Morgan and Kamoun, 2007; Mestre et al., 2016). Most RXLR effectors exhibit sequence divergence between downy mildew species as a result of different adaptative strategies required for different hosts (Ai et al., 2020). Nevertheless, conserved RXLR effectors have been reported. HaRxL23 and PsAvh73 effectors from *Hyaloperonospora arabidopsidis* and *Phytophthora sojae* respectively are two conserved effectors that could suppress PTI in *Nicotiana benthamiana* and *Arabidopsis thaliana* and ETI in soybean (Deb et al., 2018). Conservation between effectors could mean that they might share similar effector targets in different hosts. One example is that RxLR24 effectors from *P. brassicae* and *Phytophthora infestans* were found to interact with the same host factor inhibiting the secretion of antimicrobial compounds in *A. thaliana* (Tomczynska et al., 2018).

P. cubensis secretes at least 32 identified RXLR effectors through haustoria into the cytoplasm of host cells to promote its virulence (Tian et al., 2011). Apart from RXLR, prevalent in *P. cubensis* are the QXLR effectors (Tian et al., 2011). Moreover, Savory et al. (2012) have shown that alternative splicing of non-effector genes from the Drug/Metabolite Transporter (DMT) superfamily in *P. cubensis* can make them fully functional effector proteins. These results indicate that the pathogen is in an evolutionary process of improving its molecular machinery in view of the arms race with the plant. Further research on the host mechanism of the previously identified effectors would be a good step towards understanding *P. cubensis* - host interactions and breeding for durable resistance.

3.3. *Yield loss and control methods*

The downy mildew outbreak in 1984 and its further expansion the years after in Central Europe made the disease for the first time a very serious economic threat for cucumber production in Europe (Olczak-Woltman et al., 2011). Although similar large-scale downy

Table 5 Previously identified sources of *Cucumis* species resistant to *Pseudoperonospora cubensis* pathotypes

Cucumis groups/species[a]	*Pseudoperonospora cubensis* pathotypes[b]		
	3	4	Not known
C. melo	1	142	154
C. melo var. *acidulus*			7
C. melo var. *agrestis*			1
C. melo var. *ameri*			3
C. melo var. *cantaloupensis*	1		99
C. melo var. *chandalak*			5
C. melo var. *chate*			2
C. melo var. *conomom*			3
C. melo var. *indicus*			2
C. melo var. *inodorus*			1
C. melo var. *kachri*			1
C. melo var. *momordica*	3	3	24
C. figarei			1

Note: Resistant *C. melo* accessions to *P. cubensis* pathotypes were summarized from the following literatures: Sambandam et al. (1979); Swamy et al., (1981); Epinat and Pitrat (1989); Thomas and Jourdain (1992); Somkuwar and More (1993); Epinat and Pitrat (1994); Pan and More (1996); Lebeda, 1992; More (1999); Thomas (1999); Angelov and Krasteva (2000); More et al. (2002); Wu et al. (2002); Lebeda et al. (2007); Wu et al. (2008); Shashikumar et al. (2010); Goswami et al. (2011); Malik (2012); Albuquerque et al. (2015); Manchali et al. (2019); Thakur et al. (2019).

[a] *C. melo* denotes taxonomy groups that were not shown in the corresponding reports. Detailed information of resistance source is provided in Table S7.

[b] *P. cubensis* pathotypes not mentioned in the original publication were categorized as not known.

mildew epidemics on European melon have not been recorded so far, the problem is still lurking in the dark since the pathogen destroys plants and downgrades the quality of the produced fruits. Besides breeding for downy mildew-resistant cucurbit cultivars, chemical protection is one of the most common ways of controlling the disease. Fungicides used for downy mildew can be fully systemic (Phenylamides, Carbamates), partially systemic (Cinnamic acids, Complex III respiration inhibitors) and non-systemic (Dinitroanilines, Inorganic copper fungicides) (Lebeda and Cohen, 2011). As expected, downy mildew resistant to many systemic fungicides appeared all over the world soon after the introduction of fungicides. A classic example is the report in 1979 on *P. cubensis* isolates resistant to the systemic fungicide Metalaxyl in Israeli greenhouses (Reuveni, 1980). After that incidence, metalaxyl-resistant downy mildew isolates have been reported in many other countries like Greece, Italy, Australia and Czech Republic (Urban and Lebeda, 2006). Strobilurin fungicide resistant downy mildew isolates are another typical example. Following the introduction and expansion of these isolates in Japan, they became one of the most common fungicide-resistant strains for downy mildew (Ishii et al., 2001). On the other hand, contact fungicides which are contrary to the specialized single site inhibitor fungicides targeting the pathogen at multiple sites, are less likely to generate resistant populations. However, the efficiency of contact fungicides is generally less and they should be used in combination with systemic ones. An integrated management program that includes multiple product applications and preventative measures such as minimization of the exposure of leaves to wet conditions can further reduce the risks and lead to better downy mildew control.

3.4. *Genetic resources of resistance*

In order to identify resistant sources, worldwide efforts have been carried out to screen *C. melo* accessions and their wild relatives using several screening and assessment methods (Table 5 and Table S6) (Epinat and Pitrat, 1989; Pan and More, 1996; Angelov and Krasteva, 2000; More et al., 2002; Lebeda et al., 2007; dos Santos et al., 2009; Shashikumar et al., 2010; Goswami et al., 2011).

In total, 452 resistant accessions were identified in *C. melo* species as well as the wild relative species *C. figarei* (Table 5 and Table S7). For the majority of the resistant sources, the corresponding pathotypes were not reported. Various resistant accessions were effective against pathotype 3 (5 accessions) and 4 (145 accessions). In addition, we summarized susceptible accessions from 13 studies (Table S8). Among these accessions, three of them were susceptible to pathotype 3, nine to pathotype 4, and 110 accessions susceptible to un-reported races.

Resistance loci and QTLs against *P. cubensis* have been identified in a small number of accessions, including PI 124111, PI 124111F, PI 124112, PI 414723, and 5-4-2-1 (Thomas, 1988; Epinat and Pitrat, 1989; Angelov and Krasteva, 2000; Perchepied et al., 2005; Lebeda et al., 2011; Savory et al., 2011) (Table 6). Resistance in accession PI 124111 and its derived F_7 progeny PI 124111F (*C. melo* var. *momordica*) was based on two complementary incomplete dominant genes *Pc*-1 and *Pc*-2 (Cohen and Eyal, 1995; Thomas, 1988; More et al., 2002). Resistance in PI 124111F to six *P. cubensis* pathotypes has been attributed to two glyoxylate aminotransferase-encoding genes *At1* (located on chromosome 2) and *At2* (located on chromosome 5) (Fig. 4), which are mainly expressed in leaf and seed (Taler et al., 2004). Their abundant expression was required for complete resistance to *P. cubensis* in PI 124111F (Taler et al., 2004; Savory et al., 2011).

Resistance in PI 124112 was controlled by two complementary incomplete dominant loci *Pc*-4 and *Pc*-5 (Kenigsbuch, 1992). In addition, several QTLs for pathotype 3 have been detected in a recombinant inbred line population derived from PI 124112 (Perchepied et al., 2005). Partial resistance to pathotype 3 in PI 414723 was conditioned by *Pc*-3 (Kenigsbuch, 1989). In the segregating F_2 and backcross generations derived from the resistant parental line 5-4-2-1 and susceptible parental line K 15-6, a dominant type of inheritance for downy mildew resistance was

Table 6 Resistance loci/genes and QTLs for downy mildew resistance

Genes/QTLs[a]	Donor	Pathotype	Inheritance mode	Reference
Pc-1	PI 124111,		Two complementary incompletely dominant	Cohen and Eyal (1987);
Pc-2	PI 124111F			Thomas (1988)
Pc-3	PI 414723	3	Partial resistance	Epinat and Pitrat (1989)
Pc-4	PI 124112		Incompletely dominant	Kenigsbuch (1992)
Pc-5			*Pc-5* is dominant in presence of *M-Pc-5*, recessive in the absence of *M-Pc-5*	Angelov and Krasteva (2000)
M-Pc-5	5-4-2-1			
pcXII.1, pcIV.1, pcVI.1, pcVI.2, pcVIII.1, pcII.1, pcXI.2, pcXI.1, pc16.1, pc24.1, pc32.1	PI 124112	3	Partial resistance	Perchepied et al. (2005)
At1	PI 124111F			Savory et al. (2011);
At2	PI 124111F			Taler et al. (2004)

Note: [a] Resistance genes are in italics.

conferred by *Pc-5* in 5-4-2-1 combined with a modifier *M-Pc-5* in K 15-6 that is expressed only in the presence of *Pc-5* in 5-4-2-1 (Angelov and Krasteva, 2000) (Table 6).

3.5. *Introgression breeding for powdery mildew and downy mildew resistance*

Genetic resources PI 124111, PI 124111F, PI 124112, and PI 414723 have been considered as the most valuable germplasm and are widely used resistant sources in melon breeding programs for both powdery mildew and downy mildew. PI 124111 originates from India and it was identified at the Horticultural Field Station in the USA, somewhere in the period from 1938 to 1948 (Thomas, 1988). Various lines and cultivars have been developed using PI 124111 as resistance donor including line MR-1 (derived from 90319, an inbred line of PI 124111) and PI 124111F (Lebeda et al., 2011) (Fig. 6). PI 414723 has a distinct breeding pedigree which was originally derived from PI 371795 (McCreight et al., 1992).

Variety Phoot (*C. melo* var. *momordica*) has been a core source of downy mildew resistance. For example, at least two lines were

Table 7 Previously reported susceptibility genes for downy mildew and powdery mildew in several crops

Disease	S-gene	Function	Crop	Reference
Downy mildew	*DMR1*	Homoserine kinase: amino-acid pathways and metabolite biosynthesis	*Arabidopsis thaliana*	Van Schie and Takken (2014)
	DMR6	(2OG)-Fe(II) oxygenase, participates in salicylic acid homeostasis	*A. thaliana*	Van Damme et al. (2008)
	AGD5	GTPase-activating protein at the *trans*-Golgi network	*A. thaliana*	Schmidt et al. (2014)
	MKP1	Mitogen-Activated Protein Kinase Phosphatase 1, regulates the production of reactive oxygen species during immune responses	*A. thaliana*	Escudero et al. (2019)
	TCP14	Leaf-specific expressed transcription factor	*C. sativus*	Zheng et al. (2019)
	NUP133	Nup133 nucleoporin family protein	*A. thaliana*	Ried et al. (2019)
	AAP	Amino-acid permease gene, transport of amino-acid in the cell	*A. thaliana*, *C. sativus*	Berg et al. (2020)
	STAYGREEN	Magnesium dechelatase, key regulator in chlorophyll degradation	*C. sativus*	Wang et al. (2019)
Powdery Mildew	*PMR4*	Callose synthase, salicylic acid signaling	*Solanum lycopersicum*, *A. thaliana*	Santillán Martínez et al. (2020); Nishimura et al. (2003)
	PMR5	Unknown function	*A. thaliana*	Vogel et al. (2004)
	PMR6	Pectate lyase, affects pectin accumulation in cell wall	*A. thaliana*	Vogel et al. (2002)
	EDR4	Negative regulator of defense, by regulating relocation of *EDR1*	*A. thaliana*	Wu et al. (2015)
	MLO	Membrane proteins with transmembrane domains involved in a variety of physiological processes. negative regulation of vesicle-associated and actin-dependent defense pathways	*Hordeum vulgare*, *A. thaliana*, *S. lycopersicum*, *Pisum sativum*, *Fragaria vesca*, *Capsicum annuum*, *Triticum aestivum*, *C. sativus*, *Rosa hybrida*, *Nicotiana tabacum*, *C. melo*, *Vitis vinifera*, *Malus domestica*	Jørgensen (1992); Consonni et al., 2006; Bai et al. (2008); Humphry et al., 2011; Cheng et al. (2013); Jiwan et al. (2013); Zheng et al. (2013); Wang et al. (2014); Berg et al. (2015); Qiu et al. (2015); Fujimura et al. (2016); Pessina et al. (2016a, 2016b)

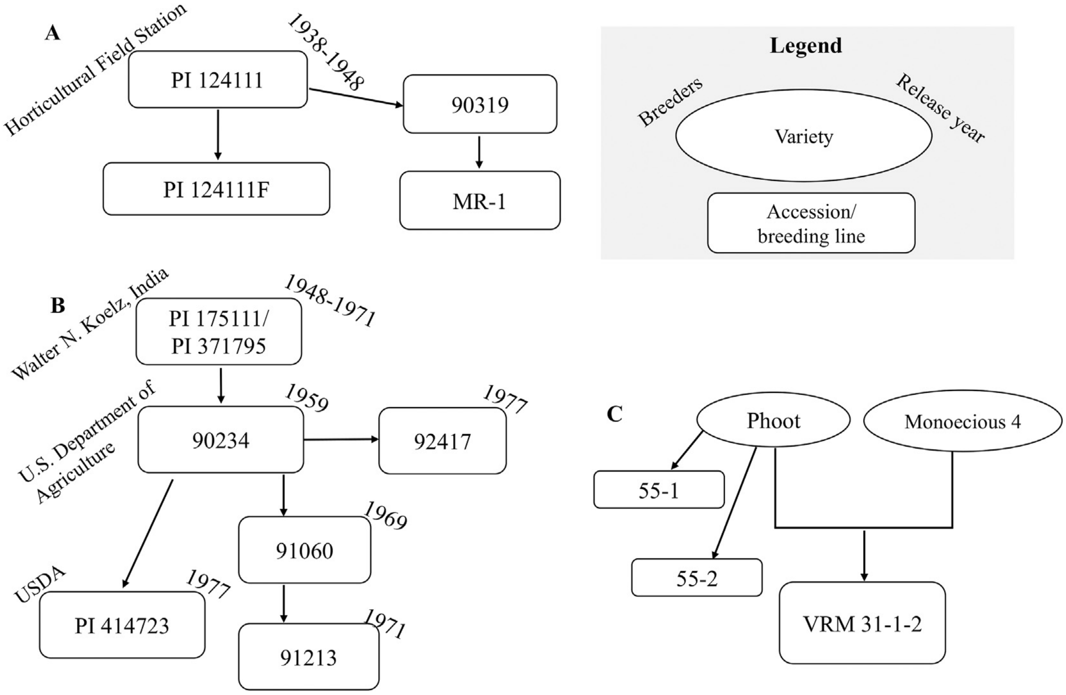


Fig. 6 Pedigree trees of resistant lines and cultivars

A. PI 124111 and its derived breeding lines; B. PI 371795 is the parental accession of PI 414723; C. Variety Phoot and its derivatives. Top right indicates how to interpret Fig A through C.

derived from Phoot including 55-2 and 55-1 (Fig. 6) (Sambandam et al., 1979; Somkuwar and More, 1993). Lines 55-2 and 55-1 derived from Phoot showed higher downy mildew resistance than those of accessions PI 124111F and PI 124112 (More et al., 2002). VRM 31-1-2 ($F_{7\text{-}9}$ generation of the cross between Phoot and Monoecious 4) were resistant to both downy mildew and cucumber green mottle mosaic virus (CGMMV) (Fig. 6). Unlike PI 124111F, VRM 31-1-2 had higher yield and acceptable commercial quality (Pan and More, 1996). Other resistance resources have been identified in India, including cultivars Budama 1, Budama 2, Budama 3, EX-1, Phoontee Goomuk, Annamalai, Nakka Dosa Kaya and FM 1. However, information on their pedigree is not available (Sambandam et al., 1979).

3.6. *Novel resistance breeding strategy by loss of function of susceptibility genes*

Although resistance can be obtained by introgression of major resistance genes (*R* genes) from wild species into elite varieties, this has rarely been durable due to the evolutionary arms race with the ever-evolving pathogens. Durability could be improved by stacking more *R* genes. Hence, other sources/forms of resistance are highly needed. An alternative approach is to explore recessive resistance conferred by impaired susceptibility genes (S-genes) in the host (Pavan et al., 2010). All plant genes required for pathogen survival and proliferation as well as supporting compatibility can be considered S genes (Van Schie and Takken, 2014).

Multiple examples of S genes have been reported over the last years for downy mildew and powdery mildew in several crops (Table 7). For downy mildew, well-known examples are the *DMR1* and *DMR6* genes, encoding a homoserine kinase protein and a (2OG)-Fe(II) oxygenase, respectively (Van Damme et al., 2008; Van Schie and Takken, 2014). Additional to downy mildew, silencing of the two genes led to resistance to a number of different pathogens in both tomato and potato (Huibers et al., 2013; Sun et al., 2016, 2022). For powdery mildew, S genes have been identified in various crops and with many different functions (Table 7). The use of impaired *MLO* genes in plant breeding for powdery mildew resistance is considered a very successful example of the S gene concept. Each plant species harbors a certain number of *MLO* homologues classified into seven phylogenetic clades. Members of clade IV in monocots and V in dicots are described as susceptibility factors toward pathogens causing the powdery mildew disease (Kusch and Panstruga, 2017). In several plant species, such as *Arabidopsis* (Consonni et al., 2006), wheat (Wang et al., 2014), tomato (Bai et al., 2008), pepper (Zheng et al., 2013), pea (Pavan et al., 2011), apple (Pessina et al., 2016a, 2016b), rice (Elliott et al., 2002), and rose (Kaufmann et al., 2012), recessively inherited powdery mildew resistance was found to be caused by naturally occurring mutations in *MLO* homologs of clade IV or V. In cucumber, three Clade V *MLO* genes namely *CsaMLO1*, *CsaMLO8*, and *CsaMLO11* were proven to play a major role in susceptibility to powdery mildew (Berg et al., 2015, 2017). Following this approach, the search for *MLO*-like proteins in the melon genome available at the Melonomics melon genomic database (https://melonomics.net) yielded 16 putative members of the MLO family (Iovieno et al., 2015). These *MLO*-like genes are scattered among eight chromosomes. Chromosomes 6 (*CmMLO6*, *CmMLO7*, and *CmMLO9*), 8 (*CmMLO4* and *CmMLO16*), 11 (*CmMLO1*, *CmMLO11*, *CmMLO12*, and *CmMLO14*), and 12 (*CmMLO2*, *CmMLO3*, and *CmMLO15*) appear to contain more than one *MLO*-like genes (Fig. 4). While the other four chromosomes including 3 (*CmMLO13*), 7 (*CmMLO8*), 9 (*CmMLO10*), and 10 (*CmMLO2*) contain one *MLO*-like gene. Three putative MLO proteins (*CmMLO3*, *CmMLO5*, and *CmMLO12*) from melon were positioned in clade V and these underlying genes are considered as candidate genes for susceptibility to powdery mildew (Fig. 4).

S genes are shown to be conserved among species. This feature provides the potential to identify melon orthologs of the known S genes and consequently to perform allele-mining in crops when sequences and/or transcriptomics data are available. During the last decade, the genome of diverse accessions that represent the full spectrum of melon diversity has been re-sequenced, together with multiple wild species (Sanseverino et al., 2015; Zhao et al., 2019; Demirci et al., 2021). Analyzing the re-sequenced genomes enables to identify allelic variation (of known S genes) occurring in melon genetic pool and to advance breeding for melon crop improvement.

4. Conclusions

Here, we have described two important diseases, powdery mildew and downy mildew, in melon production. Host resistance is generally the most favourable control method when considering environmental, economic and social reasons. To achieve durable and broad-spectrum resistance to powdery and downy mildews in melon, tools that facilitate disease evaluation need to be further developed. For example, methods for high-throughput and accurate artificial inoculation as well as disease scoring in order to unambiguously measure the resistance level. In view of resistance-breaking and lack of good dominant resistance sources to these two diseases, we recommended to utilize impaired susceptibility genes as an alternative strategy for melon resistance breeding. We expect that a strategic combination of dominant R genes/QTLs with mutant alleles of S genes will aid to the sustainability of disease resistance in melon.

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Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.hpj.2022.07.006.

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