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Review

Management of Soil-Borne Fungi and Root-Knot Nematodes in Cucurbits through Breeding for Resistance and Grafting

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Abstract: Soil-borne pathogenic fungi (SBPF) and root-knot nematodes (RKN) co-exist in the rhizosphere and are major pathogens causing root diseases in cucurbits. Current knowledge on soil-borne pathogens of cucurbit crops grown under protected cultivation, their host-pathogen interactions, and mechanisms of resistance has been reviewed. Plant resistance is an effective and sustainable method to control soil-borne diseases and the available resistant cultivars and rootstocks to key soil-borne pathogens are reported. The importance of proper pathogen diagnosis in the right choice of cultivar or rootstock is highlighted because of the specificity in the response of the cucurbit crops to fungal and nematode species and races. Plants protect themselves through common mechanisms of resistance against SBPF and RKN including hardening of their cell walls, pathogenesis-related (PR) proteins, and production of antimicrobial molecules. The activity of some enzymes, such as peroxidases and phenylalanine lyase, is increased after pathogen infection and is higher on SBPF and RKN resistant than susceptible cucurbits. Plant hormones such as salicylic acid, jasmonic acid, and ethylene are involved in the response of cucurbits to SBPF. Most mechanisms of resistance to RKN affect post-infection development of the nematode, which results in a delay or disruption of the life cycle. Traditional and biotechnological tools used for breeding for resistance in cucurbits are described. Grafting is an effective non-host resistance method to control primarily Fusarium wilt but not to control RKN. However, new rootstocks with resistance to both pathogens have been developed recently and their effects on fruit quality and yield stability need additional studies. The impact of grafting on yield in pathogen-infested soils is discussed.

Keywords: cucumber; breeding; *Fusarium*; grafting; melon; *Meloidogyne*; pumpkin; watermelon; zucchini

1. Introduction

The botanical family Cucurbitaceae includes several economically important vegetable crops cultivated worldwide in a variety of climates and environmental conditions. They comprise calabash or bottle-gourd (*Lagenaria* spp.), cucumber (*Cucumis sativus*), gourds (*Cucurbita* spp.), luffas (*Luffa* spp.), melons (*Cucumis melo*, *Cucumis metuliferus*, and *Momordica charantia*), pumpkins, squashes (*Cucurbita* spp.), watermelon (*Citrullus lanatus*), vegetable marrows, and zucchini (*Cucurbita* pepo), and also species used for medical and ornamental purposes and some weeds.

The worldwide production of cucurbits was estimated in 234,143,923 tons from a harvested area of 8,315,995 ha in 2018 [1].

Numerous pathogens are associated with cucurbitaceous crops even though those causing disease in the root system are primarily soil-borne pathogenic fungi (SBPF) and plant-parasitic nematodes (PPN). These pathogens share the same habitat in the rhizosphere, disrupt the vascular system of the host plant, and interfere with physiological processes involved in water and nutrient uptake.

Management of soil-borne diseases has strongly relied on the use of chemical soil disinfestation. However, a shift from chemical to non-chemical means of control is underway to ensure environmentally safer measures to accomplish international regulations. Alternative control methods include biosolarization, biological control, biopesticides, and cultural management. Biosolarization (soil solarization plus addition of fresh organic amendments under the plastic films) reduces soil pathogen populations effectively when soil temperatures reach at least 40–45 °C for 4–6 weeks but availability of organic material and technical impediments for its application in greenhouses limit their use. Several biological control agents based on species of *Bacillus*, *Gliocladium*, *Pseudomonas*, *Purpureocillium*, and *Trichoderma* are commercialized against SBPF and PPN and provide increased cucurbit growth and yield. Besides, some biopesticides based on essential oils, plant extracts, and plant or microbial metabolites are in the market as plant protection products against soil-borne diseases. However, all these alternative methods show lower efficacies in suppressing soil-borne diseases than soil chemical disinfestations and can provide only a partial control [2]. On the other hand, plant resistance is an effective, sustainable, and economic method to control soil-borne diseases, and it is the first option in integrated disease management when resistant cultivars are available. However, gene-mediated resistance to soil-borne pathogens has not been identified so far for many cucurbits.

The Cucurbitaceae family offers a remarkable genetic diversity due to their geographical origins, species domestication, vegetative and reproductive characteristics, and a range of adaptations to most climatic conditions, which represents a powerful resource for all types of studies. Such diversity has been used to explore sources of resistance or tolerance to key soil-borne pathogens [3–5]. The genome sequences of several cucurbit species are now available [6] and they will be useful to identify genes related to resistance traits. Grafting cucurbits have been investigated as a management option for SBPF and PPN [7,8].

The purpose of this review was to examine current knowledge on plant resistance to pathogens co-existing in the rhizosphere of selected cucurbit crops, the mechanisms involved, and traditional and biotechnological tools used for breeding for resistance with special emphasis on progress of grafting.

2. Soil-Borne Diseases in Cucurbitaceous Crops

2.1. Soil-Borne Fungi

In protected cultivation, all cucurbits can be dramatically affected by soil fungi causing damage to root and crown tissues. Soil-borne pathogenic fungi and oomycetes such as *Phytophthora* spp. and *Pythium* spp. could share symptoms in root, crown, or stem tissues, whose damage usually lead to browning, scars, girdled stem, stunt, loss of root density, wilting, decay, damping-off, and rots of roots and crown even though each pathogen have characteristic structures and symptoms that allow their recognition [9]. Cucurbits are affected by vascular wilt diseases caused by different *formae speciales* of *Fusarium oxysporum* that are morphologically similar, but generally host-specific. This fungus is currently the most important SBPF affecting cultivated cucurbits. Vascular pathogenic *Fusarium* spp. *formae speciales* cause asymmetrical brown vascular discoloration in the crown or stem, and the plant may be partially affected depending on the vascular tissues involved. The continuous use of resistant plants against Fusarium wilt has led to the emergence of new races overcoming the resistance and even for the appearance of new *formae speciales*, which makes the development of durable resistance more difficult. For example, *F. oxysporum* f. sp. *melonis* (FOM) is pathogenic to melon and cucumber [10] with races 0, 1, 2, and 1.2. Race 1.2 strains overcome two dominant resistance genes (*Fom-1* and *Fom-2*) and

are further divided into two types depending on the symptoms they cause, yellowing or wilting [11,12]. *Fusarium oxysporum* f. sp. *niveum* (FON) races 0, 1, 2, 3 causes vascular wilt in watermelon and squash. *Fusarium oxysporum* f. sp. *cucumerinum* (FOC) affect cucumber, melon, and watermelon with 0, 1, 2, and 3 races. *F. oxysporum* f. sp. *lagenariae* that causes disease in *Lagenaria siceraria*, *Cucurbita ficifolia*, and *C. maxima*, and other *formae speciales* like *F. oxysporum* f. sp. *luffae* affecting *Luffa aegyptiaca* and melon, *F. oxysporum* f. sp. *momordicae* in *Momordica charantia* and *F. oxysporum* f. sp. *benincasae* in *Benincasa hispida* [13]. *Fusarium oxysporum* f. sp. *radicis-cucumerinum* (FORC) is pathogenic to cucumber, melon, watermelon, *C. pepo*, and *L. aegyptiaca*, but without known races. FORC infection cause damages on roots and mainly the basal stem but is not a typical vascular pathogen. For another non-vascular important species, *F. solani* f. sp. *cucurbitae*, there are two races (race 1 and 2) described, which can be classified depending on their ability to produce fruit rot [14,15].

Pythium spp. [16], *Rhizoctonia solani* [17] and *Acremonium cucurbitacearum* [18] are polyphagous damping-off pathogens that induce water-soaked lesions. *Macrophomina phaseolina* [19,20] and *Phomopsis* spp. [21] produce pycnidia (fruiting body structures of the fungus) on lesions and cause necrosis on crown and roots of cucumber, melon, and watermelon adult plants. *Phytophthora capsici* [22] and *Fusarium solani* f. sp. *cucurbitae* [15] cause damages localized on the stem base on a wide range of greenhouse cucurbits. *Monosporascus* spp. [23] are involved in vine decline, which is a syndrome specifically linked to fruit growth and ripening in melon and watermelon. *Monosporascus cannonballus* produce perithecia (fruiting body structures of the fungus) on dead roots. *Olpidium bornovanus*, which only produces slight root necrosis by itself, causes the vine decline syndrome in combination with Melon necrotic spot virus (MNSV) [24]. *Verticillium dahliae* directly invade the xylem without root or crown damages [9]. Besides, each pathogen could especially affect specific plant tissues or plant development stages. For instance, *A. cucurbitacearum* was more frequent on roots from young plants while *M. cannonballus* was more evident at later stages [25,26].

Likewise, all these SBPF are distributed worldwide [27] and can cause plant death in the main intensive cucurbit crops and lead to significant or complete yield losses despite the virulence varying between hosts and pathogen strains [9]. Furthermore, there are disease outbreaks, due to less crop rotation or banning of fungicides, in addition to the emergence of more aggressive strains of pathogens such as FON race 3 in 2010 [28], or the re-emergence of *P. capsici* in Italy [29].

2.2. Plant-Parasitic Nematodes

Nematodes associated with cucurbits include *Belonolaimus*, *Criconema*, *Criconemoides*, *Dolichodorus*, *Hemicriconemoides*, *Hemicycliophora*, *Helicotylenchus*, *Heterodera*, *Hoplolaimus*, *Longidorus*, *Meloidogyne*, *Nacobbus*, *Paratylenchus*, *Paratrichodorus*, *Pratylenchus*, *Rotylenchus*, *Rotylenchulus*, *Tylenchorhynchus*, and *Xiphinema*. Of these, the genus *Meloidogyne* (root-knot nematodes, RKN) is by far the most important due to its worldwide distribution, potential damage, and economical importance [30,31].

Meloidogyne spp. are polyphagous obligate sedentary endoparasites that disrupt the vascular system of the host plant. Nematode infection starts when second-stage juveniles (J2) penetrate the roots, migrate through the intercellular space to enter the vascular cylinder, and induce the formation of feeding sites. Upon feeding-site development, the J2 become sedentary with consecutive molts to third- (J3), fourth-stage juveniles (J4), and adult females. The presence of galls in the roots is the main sign associated with RKN infection. Galls are formed by the hyperplasia of the root cortical cells. Maximum yield losses due to RKN were estimated in 88% for cucumber, 53% for zucchini, and 35% for watermelon [30] and economic losses about €2.3 million per cropping cycle in 17,500 ha of greenhouse-grown cucurbits in Southern Spain, which represents 5 % of the market value received by farmers [31].

When assessing RKN resistance, two concepts should be considered: the suitability of the plant to reproduce the nematode (host status) and the damage suffered by the plant due to nematode parasitism (host sensitivity) [32,33]. Furthermore, the competence of the nematode to form galls (pathogenic potential) but also to reproduce (parasitic success) defines two different but complementary functional

traits, which are linked and affect host sensitivity and host status, respectively. Both traits are useful for phenotyping cucurbitaceous crops for their RKN resistance.

The suitability of a host plant for a specific nematode is expressed as the ability of the plant to reproduce the nematode, and it is measured by its reproduction factor (Rf = Pf/Pi), that is, the ratio of final population densities at the end of the crop (Pf) to the pre-planting population densities (Pi). Hence, susceptible host plants show a Rf > 1 whereas resistant or non-host crops register a Rf < 1.

Cucurbit crops are all hosts to *Meloidogyne* spp. but differ in host suitability. In general, there is a large variation in Rf among cucurbits that could be useful for nematode management since less susceptible hosts (low Rf) would reduce the Pf, and, consequently, the risk of damage to the subsequent crop in the rotation. Thus, lower Rf are recorded on watermelon and zucchini than on melon, cucumber, and bottle gourd in this order [34,35]. A great variation in Rf was found among 15 cucumber cultivars in response to *Meloidogyne incognita* infection but none was found to be immune or highly resistant. Cucumber 'Long Green' was reported as resistant (Rf < 1), four cultivars as moderately resistant (Rf:1–2), and the remaining ones showed several susceptibility levels [36]. Eight out of 15 melon genotypes were classified as resistant to *Meloidogyne javanica* (Rf < 1) and promising for use in melon breeding programs, but none was resistant to *M. incognita* [37].

Most plant genotypes show different host suitability depending on the infecting RKN species, suggesting that the interaction between the host plant and the nematode species is highly specific. Therefore, accurate identification of RKN species is necessary for the choice of the cucurbit crop. For example, zucchini genotypes were less suitable to reproduce *M. incognita* than *M. javanica* and, therefore, zucchini was considered a source of resistance to *M. incognita* because it restricted nematode proliferation by supporting fewer egg masses and less fertile females [38–40]. The poor host status of zucchini for *M. incognita* with low to moderate Rf values (0.5–9.1) has been shown under different environmental conditions [41]. In contrast, zucchini was susceptible to *M. javanica* [30]. On watermelon, *M. javanica* had less ability than *M. incognita* to form galls and reproduce [42,43]. Most *M. javanica* J2 invading the roots did not develop beyond the J3 stage [35,44]. *Meloidogyne javanica* produced fewer galls and egg masses on *L. siceraria* than *M. incognita* [45]. On cucumber, *M. javanica* Rf was five-fold greater than that of *M. incognita* [46]. *Luffa cylindrica* and *Luffa acutangula* showed reduced root galling and fewer egg masses when infected by *M. javanica* than *M. incognita* [45].

Host sensitivity is measured as the damage suffered by the plant when infected by nematodes. Host plants to which the nematode multiplies but suffer little damage are termed tolerant. The degree of root galling indicates the pathogenic potential (ability to cause disease) of the nematode in a host and measures the disease severity. The pathogenic potential represents the fraction of the nematode inoculum that induces galls [45]. The parasitic success measures the successful development of the nematode inoculum until the reproductive stage [47].

As pathogens, *M. incognita* showed higher pathogenic potential than *M. javanica* on a range of cucurbit genotypes. However, *M. javanica* had higher parasitic success than *M. incognita* [45,46,48] (Figure 1). Pathogenic potential and parasitic success were highly correlated in *M. javanica*-infected cucurbits due to the high correspondence between total galls per root system and galls with egg masses (>90%) (Figure 1b). In contrast, the pathogenic potential of *M. incognita* was not correlated with the parasitic success due to the large number of galls that did not generate egg masses [45] (Figure 1a).

Although zucchini reduced *M. incognita* population build-up, it might suffer greater damage due to extensive root galling and a larger size of individual galls. By contrast, zucchini would be more tolerant to *M. javanica* damage because of reduced root galling and a smaller size of individual galls. Thus, it would stand higher Pi before affecting crop growth and yield [39].

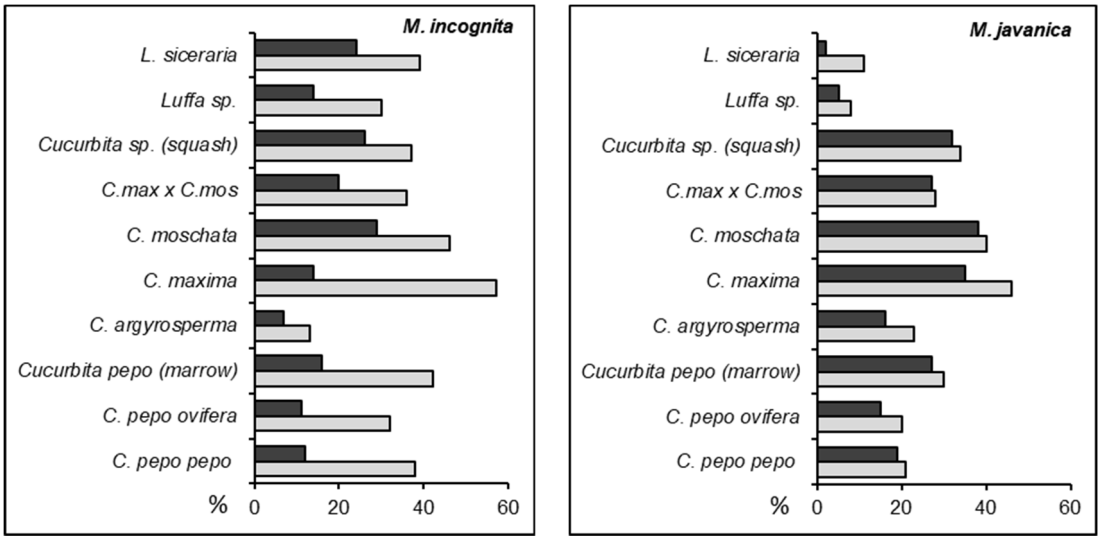

Figure 1. Parasitic success (egg masses × 100/250 J2 inoculum) (dark grey) and pathogenic potential (total galls × 100/250 J2 inoculum) (light grey) of *Meloidogyne incognita* (**a**) and *M. javanica* (**b**) on several cucurbitaceous genotypes.

Watermelon was more tolerant to *M. javanica* than *M. incognita*, as indicated by their tolerance limit (the nematode density below which there are no yield losses) [49] that was 20 J2/100 cm^3 soil for *M. javanica* and 4 J2/100 cm^3 soil for *M. incognita* [50,51]. Despite the susceptibility of watermelon genotypes to RKN (Rf > 1), their Rf were low to moderate in comparison to other susceptible hosts [35,52,53]. Watermelon cultivation in *M. javanica*-infested fields decreased the Pf [35,50,54] owing to the poor host status of the crop and the damage suffered by the plant [36]. The expected negative relationship between progressively higher Pi and the Rf, typically occurring in good host plants [55], was not observed in *M. javanica*-infected watermelons [44]. Moreover, J2 emergence from newly formed eggs was lower from watermelon (21%) than from other susceptible hosts (55%) [43]. Watermelon showed stunted top growth for 8 out of 13 weeks of the cropping cycle and this early stunting was responsible for 27% fruit yield losses [51]. All this together point at the hypersensitivity of watermelon to RKN infection [44,53].

3. Mechanism of Resistance to Soil-Borne Diseases

Passive defense in plants against pathogens begins with the perception of conserved molecular patterns associated with microbes or pathogens (PAMP) by the pathogen recognition receptors (PRR) in plants. The pathogen-secreted effectors that inactivate the recognition by the plant become avirulent factors (AVR) when they are recognized by resistance proteins ("R" genes), producing a cycle between plant defense responses and the counterattack of the pathogen [56], described as the zig-zag model [57]. While single AVR genes recognized by their corresponding R gene were identified, more complex interactions between AVR and R genes are reported [58].

Plants protect themselves against SBPF and PPN through common mechanisms including hardening of their cell walls, pathogenesis-related (PR) proteins, and production of antimicrobial molecules with an essential role of the plant hormones (Table 1).

Table 1. Main pathogenesis-related proteins and molecules involved in resistance against soil-borne diseases in cucurbits.

Resistance Mechanism		Crop	Pathogen	References
Cell wall hardening and vascular blocking				
Lignin	Lignification of plant cell walls, deposition around appressoria	All cucurbits	*Colletotrichum* spp.	[59]
Suberization and tylosis	Block vessels by suberin and tylose	*C. sativus*	FOC	[60]
		C. melo	FOM	[61]
			Monosporascus cannonballus	[25]
		Cucurbita spp.	*Acremonium cucurbitacearum*	[25]
		C. lanatus	FON	[62]
Enzymes				
Peroxidases	Hypersensitive response, lignification, phenolics, and glycoproteins cross-linking, suberization, and phytoalexin production	*C. sativus*	FORC	[63]
			Meloidogyne javanica	[64]
		C. melo	FOM	[65]
		C. lanatus	FON	[66]
		C. metuliferus	*Meloidogyne incognita*	[67]
		M. charantia	*Meloidogyne incognita*	[68]
Chitinase	Cell wall chitin hydrolysis	*C. sativus*	*Rhizoctonia solani*	[69,70]
			Thielaviopsis basicola	[69]
		C. melo	FOM	[65,71]
		C. lanatus	FON	[66,72]
β-1,3-glucanase	Cell wall β-1,3-glucans hydrolysis	*C. sativus*	*Pythium aphanidermatum*	[73]
			Rhizoctonia solani	[70]
		C. lanatus	FON	[66]
Phenylalanine ammonia lyase	Phenolic compounds biosynthesis	*C. sativus*	*Rhizoctonia solani*	[70,74]
		C. melo	FOM	[71]
		C. lanatus	FON	[72,75]
		C. metuliferus	*Meloidogyne incognita*	[67]
		M. charantia	*Meloidogyne incognita*	[68]
Polyphenol oxidase	Phenolic compounds oxidation to quinones	*C. sativus*	FORC	[63]
			Meloidogyne javanica	[64]
		M. charantia	*Meloidogyne javanica*	[68]
Lipoxygenase		*C. sativus*	*Rhizoctonia solani*	[70]
Signal molecules				
Salicylic acid	Systemic acquired resistance	*C. sativus*	*Rhizoctonia solani*	[70]
		C. melo	*Pythium aphanidermatum*	[76]
			Rhizoctonia solani	[77]
		Cucurbita spp.	*Phytophthora capsici*	[78]
		C. lanatus	FON	[66]
Jasmonic acid	Induced systemic resistance	*C. sativus*	*Rhizoctonia solani*	[70]
		C. melo	FOM	[65]
			Monosporascus cannonballus	[79]
Ethylene	Induced systemic resistance	*C. sativus*	*Rhizoctonia solani*	[70]
			Fusarium solani	[70]
		C. melo	FOM	[65]
Antimicrobial molecules				
Phytoalexins	Affect pathogen metabolism and reproduction directly	*C. sativus*	*Pythium aphanidermatum*	[80]
Defensins	Cysteine-rich peptides with antifungal/bacterial activity	*C. melo*	*Fusarium oxysporum*	[81]
		C. lanatus	FON	[72]

Fusarium oxysporum f. sp. *cucumerinum* (FOC), *F. oxysporum* f. sp. *melonis* (FOM), *F. oxysporum* f. sp. *niveum* (FON), *F. oxysporum* f. sp. *radicis-cucumerinum* (FORC).

3.1. Soil-Borne Fungi

Non-host resistance to fungi can be produced by lignin accumulation. For example, *Colletotrichum lagenarium* germinated and produced appressoria on cucumber, muskmelon, pumpkin, squash, and watermelon, but only pumpkin and squash prevented its penetration by lignin deposition in the upper and lateral host epidermal cell walls around appressoria [59].

Susceptible muskmelon and resistant pumpkin (*C. maxima*) roots infected by *A. cucurbitacearum* showed a suberized layer in the epidermis. Additionally, for *M. cannonballus*, few changes were observed in infected tissues even though pumpkin showed a slight suberin deposition in the epidermis. Tyloses were formed in the lumen of the xylem vessels of muskmelon and pumpkin, as a response to infection by *M. cannonballus* and *A. cucurbitacearum* [25]. Furthermore, during cucumber infection by FOC, tylose is formed in both resistant and susceptible varieties, but its activation is faster in the resistant ones [60]. This could explain the limited expansion of FOC hyphae in resistant plant vessels [61]. Tylose-mediated response to FOM [61] in melon and FON [62] in watermelon-resistant genotypes has also been described with tylose deposition taking place earlier in resistant varieties [61].

Plant hormones such as salicylic acid, jasmonic acid, and ethylene are involved in the response of cucumber to R. solani [70]. The activity of various R-proteins such as the enzymes peroxidase (POX), chitinase, and β-1,3-glucanase is increased during watermelon defense against FON [66,72] and the expression of chitinase, β-1,3-glucanase, POX, and phenylalanine ammonia-lyase (PAL) is higher in FON-resistant than susceptible cultivars [72,75], but no significant changes occurred in the polyphenol oxidase (PPO) expression [72]. Similarly, differences in the enzymatic activity of POX and PPO have been observed in cucumber hybrids with FORC resistance [63] and higher expression of chitinase and PAL in resistant melons to FOM race 1.2 [71]. The hormonal and enzymatic responses are closely related, as noted in melon challenged against different pathogens, where a relationship between ethylene and methyl jasmonic action was observed in chitinase or POX activities [65].

In addition, defense mechanisms can be enhanced by biotic and abiotic agents that promote systemic acquired resistance (SAR, based on PR-proteins, and salicylic acid accumulation) or induce systemic resistance (ISR, independent of salicylic acid, based on jasmonic acid and ethylene) [82]. Biotic agents such as *Paenibacillus* spp., *Pseudomonas* spp., *Actinoplanes* spp., *Micromonospora* spp., *Streptomyces* spp. increase chitinase, and glucanase activity and other related PR-proteins in cucumber, improving resistance to *R. solani*, *F. oxysporum* f. sp. *radicis-cucumerinum*, or *P. aphanidermatum* [83,84]. *Bacillus subtilis* increased the enzymatic activity of POX, PPO, and PAL in cucumber in the presence of *F. oxysporum* f. sp. *cucumerinum* [85]. In addition, changes in salicylic and jasmonic acid levels and POX activity were associated with increased resistance in *Trichoderma*-treated soils [86]. Abiotic agents such as silicate and β-aminobutyric acid derivates can also increase enzymatic activities and phytoalexin accumulation in squash [78].

Plants could synthesize phytoalexins de novo and accumulate them rapidly at infection sites. In cucumber, phytoalexin-related compounds were isolated from roots and leaves exposed to *Pythium aphanidermatum* showing that the overall defense response is not based on a single phytoalexin, but it is chemically complex and organ-specific [80]. Plant defensins are small, stable, cysteine-rich peptides that could act against fungal pathogens. Transcript levels of watermelon *CIPDF2.1* and *CIPDF2.4* defensins-like genes were higher in resistant cultivars during FON infection [72].

Many of the mentioned mechanisms of resistance have been linked with resistance genes, summarized in Table 2 from the cucurbit gene cooperative gene list [87]. The most widely described resistance genes in cucurbits for soil-borne diseases are those associated with *Fusarium* spp., even though there are other examples such as the melon vine decline resistance gene (*Mdv*) in *C. melo* [26] or the *P. capsici* resistance genes (*Crr*) in *Cucurbita* spp. [88]. None of the genes presently known confer resistance to all the *formae speciales* of *F. oxysporum*, but some genes confer specific resistance to each *forma specialis* in cucumber, melon, and watermelon.

Table 2. Resistance genes related to soil-borne fungal pathogens in cucurbitaceous crops.

Gene Name	Description	References
Cucumis sativus		
Foc	Resistance to FOC races 1 and 2 in 'Wis 248'. Controlled by a single dominant gene.	[89,90]
qFoc6.1	Resistance to FOC, one of two linked QTLs.	[91]
qFoc6.2	Resistance to FOC, one of two linked QTLs.	[91]
Cucumis melo		
Fom-1	Resistance to FOM race 0 and 2.	[92]
Fom-2	Resistance to FOM race 0 and 1.	[92]
Fom-3	Same phenotype as *Fom-1* but segregates independently.	[93]
fom1.2a	Resistance to FOM race 1.2.	[94]
fom-4	Resistance to FOM race 0 and 2. Likely associated with *Fom-1*.	[95]
Mvd	Melon vine decline resistance in 'Pat 81'. Semi-dominant gene for partial resistance to *Acremonium cucurbitacearum* and *Monosporascus cannonballus*.	[26]
Forc-1	Dominant gene that confers resistance with *forc-2* to FORC in 'Hemed'.	[96]
forc-2	Recessive gene that confers resistance with *Forc-1* to FORC in 'Hemed'.	[96]
Citrullus lanatus		
Fo-1	Dominant gene for resistance to FON race 1.	[97]
Cucurbita spp.		
Crr-1 *Crr-2* *Crr-3*	Three complementary dominant genes from *C. lundelliana* and *C. okeechobeensis* subsp. *okeechobeensis* for resistance to *Phytophthora capsici*.	[88]
Other cucurbits		
F1,2y	Dominant gene that confers resistance to FOM race 1,2y in *C. anguria*.	[98]

Information extracted from Cucurbit breeding cooperative gene list [87] and Elkabetz et al., 2016 [96]. *Fusarium oxysporum* f. sp. *cucumerinum* (FOC). *F. oxysporum* f. sp. *melonis* (FOM). *F.* oxysporum f. sp. *radicis-cucumerinum* (FORC). *F. oxysporum* f. sp. *niveum* (FON).

3.2. Plant-Parasitic Nematodes

Genetic resistance to root-knot nematodes in cucurbits crops has not been identified, according to our knowledge except for a *M. javanica* recessive gene (*mj*) from *C. sativus* var. *hardwickii* [99,100], but this is not available in commercial cultivars.

Zucchini has shown resistance to *M. incognita* but not to *M. javanica* or *M. arenaria* [30,38,39] even though the genetic base of the resistance is presently unknown. Evidence suggests this resistance is not governed by a major dominant gene because cell necrosis associated with the hypersensitive response does not occur in zucchini [101], but it may have a quantitative nature [40]. Malfunction of the *M. incognita* giant cells and abnormal growth of the surrounding tissues caused early deterioration of 74% of the *M. incognita* feeding sites before life-cycle completion [101]. Consequently, only 26% of the total *M. incognita* population within the roots reached the egg-laying female stage in contrast to 96% of the *M. javanica* population. The increased frequency of undersized individuals, immature females, and empty galls showed a failure of *M. incognita* to develop. Critical events differentiating the resistant and susceptible response to *M. incognita* and *M. javanica* were the transition from J4 to females and the reduced fertility of the egg-laying females [101].

Recombinant Inbred Lines (RILs) from a cross of *C. pepo* subsp. *pepo* 'Murcia MU-CU-16' × *C. pepo* subsp. *ovifera* 'Scallop UPV-196' were evaluated in search for sources of resistance. The nematode differentiated the *C. pepo* genotypes at the subspecies level due to lower egg mass production on the subsp. pepo than ovifera [40]. In addition, zucchini 'Murcia MU-CU-16' discriminates *M. incognita* from *M. javanica* in terms of egg masses, eggs per gram of root, and Rf, whereas scallop 'Scallop UPV-196' did so only in eggs per gram of root and Rf. *Meloidogyne incognita* and *M. javanica* differed in pathogenic potential and parasitic success on the RILs, depending on the RKN-line combination. Five lines suppressed *M. incognita* reproduction traits by more than 90% and were considered as resistant to

this RKN species. The transmission to descendants of differences in resistance and susceptibility will be useful to define breeding processes for zucchini resistance more accurately. All the RILs were susceptible hosts for *M. javanica*, which confirmed the lack of resistance to this nematode species on zucchini [40]. The parents of this RIL population were both susceptible to *F. solani* and *P. capsici* [102].

Mechanisms of resistance restricting RKN parasitism on cucurbits include reduced root invasion rates, delayed nematode development, J2 migration from the roots, increased maleness, and reduced female fecundity (Table 3). An increase in root biomass in response to RKN infection was associated with resistance in *Cucumis hystrix* [103] and *Citrullus amarus* (ex-*C. lanatus* var citroides) [104]. The hypersensitive response leading to cell death, typically associated with the presence of dominant resistance genes, has only been observed in *C. metuliferus* [67,105]. Changes in enzymatic activity as a defense response to the RKN attack occur rapidly after nematode infection and the activities of some enzymes such as POX and PAL were greater on resistant *C. metuliferus* than susceptible bitter gourd or cucumber [67,68].

Table 3. Mechanisms of resistance to root-knot nematodes in cucurbitaceous crops.

Crop	Root-Knot Nematode	Observation	References
C. amarus	*M. incognita*	Root fibrosity	[104]
C. lanatus var. *lanatus*	*M. javanica*	Reduced root invasion rates Delayed development Life cycle disruption at the J3 stage Reduced J2 emergence from eggs No effect on female fecundity	[35,44]
C. africanus	*M. incognita*	Delayed development Life cycle disruption at the J2 stage Maleness	[33]
C. hystrix	*M. incognita*	Increased lateral roots	[103]
C. melo var. *texanus*	*M. incognita*	Reduced root invasion rates Delayed development J2 emigration Empty galls No effect on female fecundity	[106]
C. metuliferus	*M. incognita*	Reduced root invasion rates Delayed development J2 emigration from the root Reduced female fecundity Hypersensitive reaction	[67,105]
C. myriocarpus	*M. incognita*	Failure J2 to establish a feeding site Life cycle disruption at the J2 stage Maleness	[33]
C. sativus	*M. hapla*	Empty galls Maleness	[107,108]
C. foetidissima	*M. incognita*	Reduced root invasion rates Delayed development Reduced female fecundity	[109]
C. pepo subsp. *pepo*	*M. incognita*	Malfunction of feeding sites Life cycle disruption at the J4 stage Empty galls Reduced female fecundity	[101]

4. Methods of Genetic Control

4.1. Traditional Breeding

Traditional breeding has been successful in domestication, searching for resistances, or the development of more practical plant archetypes, which have improved yield and quality of the fruits. However, biotechnological tools have become essential in breeding programs to accelerate any adaptation process. Traditional breeding includes screening large collections of wild plants, already existing in nature or plant accessions in germplasm banks, to phenotype their resistance response [11,105,110]. Candidates can be used directly as new cultivars, or for hybridization and grafting purposes. Resistance has been identified by direct screening to *M. cannonballus* [111], FOM race 1 and 2 [11], FOM race 1.2 [12,112], FON [113], FORC [63], *P. capsici* [114], *M. phaseolina* [20], *A. cucurbitacearum* [18], and to the nematode *M. incognita* [38,115]. Despite these advances, only cucurbit cultivars and rootstocks with resistance to some Fusarium and Verticillium pathogens (FOM 0, FOM 1, FOM 2, FON, FOC, FORC, VA) are available commercially for industrial use in greenhouse crops [116].

Analysis of F1 and F2 and backcrosses obtained by crossing resistant and susceptible genotypes allowed finding the dominant/recessive nature and the number of genes involved in the resistance. *Phytophthora capsici* susceptible/resistance segregation from *Cucurbita* spp. cultivars indicated that resistance is conferred by three dominant genes [88]. A similar study was carried out for FORC. Susceptible melon 'Dulce' was crossed with a resistant accession 'Hemed'. F1 and backcrossing to 'Hemed' produced resistant plants, showing segregation that correlates with 'Hemed' resistance, conferred by two genes with one dominant (*Forc-1*) and one recessive (*forc-2*) [96]. For *M. phaseolina*, seven out of 97 accessions of *C. melo* showed resistance, one cantaloup ('Can-NyIsr') and six exotic accessions from Africa, Asia, and Eastern Europe ('Dud-CUM296Georg', 'Dud-QPMAfg', 'Ac-TGR1551Zimb', 'Con-Pat81Ko', 'Ag-15591Ghana', and 'Ag-C38Nig') that previously showed resistance to other SBPF [26,117]. The response of F1 progenies from resistant × susceptible crossings varied from susceptible to highly resistant, suggesting differences in the genetic basis of the resistance in the different selected sources. For example, resistance derived from 'Can-NyIsr' seemed to be recessive, as the F1 behave as the susceptible parental, while 'Ag-15591Ghana' and 'Ag-C38Nig' F1 generations suggested dominance of the resistance genes, even though further studies with segregant populations are needed to determine the genetic control of each resistance [20]. In addition, the resistance of *C. melo* subsp. *agrestis* 'Pat 81' to *A. cucurbitacearum* and *M. cannonballus* seems to be controlled by a single dominant gene according to segregation analysis [26]. The final objective of these methods is to incorporate these genes into breeding programs for their introgression in commercial or domesticated cultivars. For example, a selection for improved melon root systems conferring resistance and tolerance to vine decline was successfully conducted in 'Pat 81' × 'Piñonet' backcrossing with 'Pat 81' [117], and it led to a vine decline tolerant 'Piel de sapo' line and other melon lines with high tolerance [118].

4.2. Biotechnological Tools

Biotechnological tools have been used for indirect screening for pathogen resistance. They include the use of molecular markers, omic analysis, mutagenesis, transgenic plants, and, more recently, clustered regularly interspaced short palindromic repeats (CRISPR) systems [119]. However, techniques such as the in vitro plant tissue culture could be useful when combined with others. For example, tissue culture has been used to produce mutants to improve tolerance to FOM in melon [120]. Transformation mediated by Agrobacterium tumefaciens is a tool for producing whole transgenic plants or pathogens [121] or for CRISPR modifications [122].

4.2.1. Molecular Markers

In genetics, a molecular marker is a polymorphism in a certain location within the genome that could be associated with specific germplasm or traits. Molecular markers can lead to a quantitative trait locus (QTL) when they are associated with a phenotypic trait, such as disease resistance, even though

the phenomenon of resistance cannot be completely measured through QTL because its complexity, involving different unknown genes and the environmental implications during the disease process. Nevertheless, the importance of markers in breeding, when they are highly associated with a trait of interest, is their use as tools to perform marker-assisted selection breeding (MAS) or to be incorporated into resistant gene introgression programs by taking into account that the markers are often plant germplasm-dependent [123,124] and that, occasionally, it will need more than one marker to detect a gene (e.g., two molecular markers to the *mj* gene were developed with 97% accuracy in segregating populations in cucumber only when they are used in combination [125]). Numerous marker types have been used in cucurbit resistance breeding: single nucleotide polymorphisms (SNP), random amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), sequence characterized amplified region (SCAR), and cleaved amplified polymorphic sequences (CAPS) [126], among others.

Three RAPD markers were polymorphic between different melon accessions that were linked to the Fom-1 locus. In order to increase specificity, they were converted into SCAR markers [123]. These markers were more universal than the CAPS markers developed for the same gene [124], even though these CAPS makers are more tightly linked to the *Fom-1* gene. However, Brotman et al. [124] concluded that their markers are not useful for identifying FOM resistance, while Oumouloud et al. [123] advocated the combined use of RAPD and CAPS markers developed for effective use in MAS for FOM races 0 and 2. Another two CAPS markers were close to *Fom-1* gen in melon (from P11 × MR-1), and further analysis correctly predicted the genotype [126]. Nevertheless, all these studies pointed out that the markers associated with *Fom-1* have a gene-pool-specific use, and that there might be different alleles for resistance to races 0 and 2 that originated independently in different lineages of the melon phylogeny. Similarly, tightly linked RAPD markers for the *Fom-2* gene were found [127], and converted to CAPS and restriction fragment length polymorphisms (RFLP) markers, which showed high correlation (>80%) to the susceptible phenotype [128,129], while other amplified fragment length polymorphism (AFLP) markers demonstrated a high correlation between the genotype and the resistance phenotype [130]. Further studies using these markers for different germplasm indicated that the expected resistance ratio did not correspond with the inoculation tests, even though they were capable of discriminating between the homozygosis/heterozygosis genotypes for the *Fom-2* gene [131]. Another RAPD maker was proven to be linked to the resistant gene *Fo-1* against FON race 1 in *C. amarus* [132]. Different simple sequence repeats markers were tested in a cucumber population (derived from 9110Gt × 9930 crosses) showing that resistance to Fusarium wilt in 9110Gt was quantitative with one major QTL, *Foc2.1*. An SSR marker linked to *Foc2.1* was validated in diverse germplasms, showing an accuracy rate of 87.88% for selecting resistant materials [91].

Single nucleotide polymorphisms (SNPs) markers are more abundant, stable, amenable to automation, and increasingly cost-effective than other molecular markers [133]. The use of new tools like next generation sequencing (NGS) and bioinformatics has led to genotyping-by-sequencing (GBS), which is linked to the SNPs screening (GBS-SNP) [133]. A major QTL (*qFon2-9*), which could be used in FON race 2 resistance, was mapped using a high-density genotyping-by-sequencing-single nucleotide polymorphisms linkage map on *C. amarus*. However, this major QTL only explained less than half of the phenotypic variation by itself and it is only effective with multiple markers tightly linked to this QTL [134]. Other studies showed that Qfon1 locus on chromosome 1 is a viable candidate for marker assisted selection in watermelon for *F. oxysporum* f. sp. *niveum* race 1 resistance, which were correlative to 38.4% of the phenotypic variation [135]. In addition, two inbred cucumber lines, 'Superina' (susceptible) and 'Rijiecheng' (resistant), were used to detect quantitative trait locus on cucumber for Fusarium wilt. The inheritance studies showed two pairs of additive-dominance-epistatic major genes (*fw2.1* QTL) and additive-dominance polygenes as the optimal model for resistance to FOC on cucumber [136].

4.2.2. Omics Analyses

Cucurbitaceae species contain a significantly lower number of nucleotide-binding site-leucine rich repeats (NBS-LRR) genes, closely related to resistance, than other plant species of a similar genome size [137,138]. A total of 411 disease resistance genes were identified in the melon genome, 81 represented nucleotide-binding site (NBS), leucine rich repeats (LRR), and toll/interleukin-1-receptors (TIR) domains, and 79 R genes were non-randomly distributed in the melon genome [139]. In watermelon, 44 NBS-LRR (18 NBS-LRR-TIR and 26 NBS-LRR-Coiled coil) were identified and, among the 197 receptor-like genes identified in its genome, 35 encode receptor-like proteins lacking a kinase domain in addition to the extracellular LRR and TrD (transmembrane domains) [140].

Sequence analysis can also be used to focus on specific genes. Monogenic resistance to FOM has been described against races 0, 1, and 2. Due to the relevance of these genes, many studies aimed at finding molecular markers [126]. *Fom-2* encodes (predicted) a nucleotide-binding site-leucine rich repeats type R protein of the non-TIR subfamily with a coiled-coil structure within the LRR region rather than in the N-terminal, in contrast to most members of this class. The *Fom-2* physical region contained retroelement-like sequences and truncated genes, suggesting that this locus is complex [141]. Differential gene expression analysis focusing on single genes or families has been performed as well. Differentially expressed genes were observed during *M. cannonballus* infection, suggesting that jasmonic acid could be partially responsible for the variability observed in resistant melon cultivars [142]. Genes *β-1,3-Glucanase*, *CHIT1*, *PAL1*, *PR1*, and *LOX1* were analyzed to describe an improved disease response in cucumber against *R. solani* [70], and genes of the WRKY family responded to external inducements such as salicylic, jasmonic acid, or a pathogen in resistant and susceptible cucumber genotypes during *Phytophthora melonis* infection [143]. Concerning proteomics, 15 proteins with several biological functions were found in FOC-resistant cucumber roots, and the participation of jasmonic signaling components and LRR family proteins was observed during the infection [144]. From a broader perspective, all data related to the cucurbits' genome and transcriptome sequences are in constant updating [6], which allows making genetics associations to know all the genetic variations that can be associated with a trait. In addition, the knowledge of resistance genes in other crops [145] could always be used for cucurbits because of gene homology [146].

Transcriptome profiling of *C. metuliferus* infected by *M. incognita* showed the involvement of hormone biosynthesis and cytoskeleton-related genes in the resistance response as well as many pathogenesis-related genes and RKN effectors [67,147]. Additionally, infection of *C. metuliferus* by *M. incognita* had a significant effect on both micro-RNAs' (miRNAs) expression and their corresponding targets in resistant and susceptible plants but with differential expression. Four out of ten selected miRNA-target pairs exhibited inverse expression patterns between miRNAs and their targets [147].

4.2.3. Mutagenesis and Targeting Induced Local Lesions in Genomes (TILLING)

The natural process of mutation can be accelerated artificially by physical and chemical approaches [148]. For example, a mutation in the *FonSIX6* avirulent gene (for FON race 1) significantly enhanced FON virulence in watermelon, suggesting that the mutant ΔFon1SIX6 protein allowed evasion of R protein-mediated host resistance [149].

When mutant production and analysis are used in conjunction with large-scale mutation detection like NGS, it is known as TILLING (Targeting Induced Local Lesions in Genomes). Ecotype TILLING (EcoTILLING) [150] is a similar process but is based on locating mutations in natural germplasm. TILLING is a particularly useful tool to produce random mutants that can be used as germplasm for different studies and could be reused since the genome is better described [6]. It is a widely used tool in modern breeding and has been successfully used in various cucurbits crops such as zucchini [151], cucumber [152], or melon [153], but it has not been oriented toward soil-borne diseases.

4.2.4. Transgenic Plants

There have been some attempts to produce transgenic cucumbers with chitinase gene to increase resistance to pathogens through the incorporation of R proteins, but without much success [69], as for the transformation of glucanase and chitinase genes in watermelon [121]. Defensins transformation from *Wasabia japonica* showed a stable integration and expression in melon that conferred increased levels of resistance to Fusarium wilt [81]. This technique is commonly used in conjunction with other types of analysis such as comparative genetics research of different FOM strains and genetic transformation of the fungus revealed that the *AVRFOM2* (a FOM avirulence gene) interact with the melon *Fom-2* resistance gene [154].

4.2.5. CRISPR

CRISPR (clustered regularly interspaced short palindromic repeats) gene editing is a technique that makes punctual and directed changes in the genome. The recognition sequence (sgRNA) of the region to be modified can be designed, and the linked endonuclease (CRISPR associated protein, 'Cas') cut the target sequence, whose repair will produce the mutation. In plants, it is necessary to work with pluripotent cells that can develop into complete tissues or a whole plant, causing the modification to be present throughout the entire organism. For this reason, CRISPR is linked to in vitro culture methods since it is inserted through *Agrobacterium tumefaciens* or particle bombardment normally. In cucurbit diseases, this technique has been focused on virus resistance [155,156] and there are few examples of resistance to soil-borne pathogens. One is a CRISPR/Cas9-mediated editing of the *Clpsk1* gene for resistance to FON in watermelon [122]. Interactions between phytosulfokine and FON were analyzed and it was found that the transcript of *Clpsk1* was significantly induced upon FON infection. The knockout of the *Clpsk1* gene conferred enhanced watermelon resistance to FON. Therefore, CRISPR mediated gene modification is an effective approach.

4.3. Grafting

Grafting deserves specific comments since this technology has been extensively used in cucurbits to control soil-borne pathogens, primarily Fusarium wilt caused by FOC, FOM, and FON on cucumber, melon, and watermelon, respectively, and improvements are continuously under development. Rootstocks afford increased vigor and yield, even in the absence of pathogens, and provide tolerance to abiotic stresses such as low temperature and salinity. Rootstocks can include intraspecific selections that exploit specific major resistance genes and interspecific or intergeneric selections that exploit non-host resistance mechanisms or multigenic resistance [8]. Currently, the traits receiving more attention in rootstock development are resistant to soil-borne pathogens and cold tolerance. Grafting studies can be linked to the identification of molecular markers.

4.3.1. Grafting Cucumber

Cucumber benefits from grafting because it is highly susceptible to Fusarium wilt and RKN, which causes significant yield losses throughout the world [46,157]. Grafting cucumber onto *C. maxima* can control *P. aphanidermatum* in greenhouses [158]. Damping-off infection was not observed in cucumber grafted onto the squash hybrids 'Titan' and 'Hercules' [16]. *Benincasa hispida* was effective against cucumber black root caused by *Phomopsis sclerotioides* [159]. Additionally, squash hybrids (*C. maxima* × *C. moschata*), *C. moschata*, *L. siceraria*, and *C. metuliferus* showed high resistance to FOC and high compatibility with cucumber [7]. Resistant sources for FORC included *C. ficifolia*, *C. moschata*, and squash hybrids that were good candidates for cucumber grafting [160].

Cucumber grafted onto *B. hispida*, *C. maxima*, *L. siceraria*, or the squash hybrid 'Ercole No. 6001' showed lower root galling and RKN numbers than un-grafted plants regardless of the growing season (autumn or spring) they were cultivated [115]. Cucumber grafted onto 'Ercole No. 6001' or *B. hispida* increased growth and total yield and reduced nematode numbers in comparison to un-grafted

cucumber [161]. The squash hybrids 'Strong Tosa' and 'RS841' enhanced vegetative growth and increased yield when compared to un-grafted cucumber. Nonetheless, grafted and un-grafted plants showed similar root galling and nematode reproduction [162] (Table 4). Root galling increased with time after planting and the greatest difference was recorded for the squash hybrids that had 25–50% and >75% of the roots galled at 43 and 70 days, respectively. Less root galling at midseason likely accounted for the increase in cucumber yield onto the squash hybrids [162].

Table 4. Effect of grafting cucumber, melon, and watermelon onto squash hybrid (*Cucurbita maxima* × *Cucurbita moschata*), *Lagenaria siceraria*, and *Cucumis metuliferus* rootstocks in comparison to ungrafted plants on disease severity (root galling), nematode reproduction traits, and crop yield in root-knot nematode-infested soils.

Rootstock	Scion	Root-Knot Nematode	Reproduction	Root Galling	Yield	References
C. maxima × *C. moschata* 'Strong Tosa'	*C. sativus* 'Adrian'	*Meloidogyne* sp.	NS	NS	Increased	[162]
	C. melo 'Athena'	*M. incognita*	Increased	NS	Reduced	[163]
	C. lanatus 'Fiesta'	*M. incognita*	Increased	Increased	Reduced	[4]
	C. lanatus 'TriX313'	*M. incognita*	Increased	Increased	NS	[164]
C. maxima × *C. moschata* 'RS841'	*C. sativus* 'Adrian'	*Meloidogyne* sp.	NS	NS	Increased	[162]
	C. sativus 'Dasher II'	*M. incognita*	Increased	NS	NS	[165]
	C. lanatus 'Sugar Baby'	*M. javanica*	Increased	Increased	Reduced	[42]
C. maxima × *C. moschata* 'Ercole No. 6001'	*C. sativus* 'Hesham'	*M. incognita*	Reduced	Reduced	Increased	[115]
	C. sativus 'Sinai'	*M. incognita*	Reduced	Reduced	Increased	[115]
L. siceraria 'Emphasis'	*C. sativus* 'Adrian'	*Meloidogyne* sp.	NS	NS	NS	[162]
	C. lanatus 'Fiesta'	*M. incognita*	NS	Increased	NS	[4]
	C. lanatus 'Tri-X 313'	*M. incognita*	Increased	Increased	NS	[164]
	C. lanatus 'Palomar'	*M. incognita*	Increased	NS	Reduced	[163]
L. siceraria	*C. sativus* 'Hesham'	*M. incognita*	Reduced	Reduced	Increased	[115]
	C. sativus 'Sinai'	*M. incognita*	Reduced	Reduced	Increased	[115]
C.metuliferus	*C. melo* 'Durango'	*M. incognita*	Reduced	Reduced	Increased	[166]
	C. melo 'Arava'	*M. incognita*	Reduced	Reduced	NS	[167]
	C. melo 'Honey Yellow'	*M. incognita*	Reduced	Reduced	NS	[167]
	C. melo	*M. incognita*	Reduced	Reduced	Increased	[105]

NS: Not significant.

Cucumber grafted onto the squash hybrid 'RS841' showed higher RKN reproduction and Rf than the un-grafted plants. More than 75% of the root systems were galled in both grafted and un-grafted plants. Yield losses ranged from 63% to 83% and did not differ in plots with grafted and un-grafted cucumber (Table 4). Therefore, rootstock 'RS841' did not show resistance or tolerance to RKN [165]. The squash hybrids 'Shelper' and 'Excite Ikki' yielded similarly but only 'Shelter' increased yield compared to un-grafted cucumbers [46]. Grafting reduced *M. javanica* Rf on both rootstocks as compared to un-grafted cucumber but did not affect *M. incognita* Rf. These two squash hybrids were susceptible to *M. incognita* and *M. javanica* owing to Rf > 1, but both RKN species produced similar root galling in un-grafted and grafted cucumber. Nonetheless, the un-grafted cucumbers were more tolerant to *M. javanica* than *M. incognita* infection because cucumber yield was similar despite being five-fold higher Rf for *M. javanica* than *M. incognita* [46].

4.3.2. Grafting Melon

The squash hybrids are effective against all races of FOM, including 1,2 pathotypes [168,169] and they had no negative effect on yield or fruit quality. In addition, *C. moschata*, *C. metuliferus*, and *Sycios angulatus* have shown high resistance to FOM and high compatibility with oriental melon [7].

Melon grafted onto squash hybrids did not wilt when compared to 80% and 70% wilting of un-grafted melon inoculated with *M. phaseolina* in field conditions. Although necrosis could occur in the scion tissue above the grafting union, the melon yield was not affected. This colonization pattern indicated that the pathogen could penetrate the rootstock, but its development is suppressed. However, if the pathogen reaches the susceptible scion, disease can develop [19]. *Cucumis metuliferus*

and *C. melo* subsp. *agrestis* in its crossing with susceptible 'Piel de Sapo' melon showed high resistance to *M. cannonballus* [170]. A screening for rootstock candidates showed the lowest Acremonium disease severity on *C. maxima*, *L. acutangula*, and *B. hispida* [18].

Melon is also highly susceptible to RKN and suffers considerable yield losses. Grafting melon onto *C. moschata* reduced root galling compared to un-grafted plants but Pf values did not differ from un-grafted plants [166]. The squash hybrid 'Shintoza' did not prevent yield losses caused by M. arenaria to oriental melon [171]. The squash hybrid 'Tetsukabuto' did not reduce root galling or RKN densities when compared to un-grafted melon but increased yield. Rootstocks 'Tetsukabuto' and *C. metuliferus* provided similar yields [163].

Cucumis metuliferus has been proposed as a rootstock for melon because it effectively reduced RKN reproduction and disease severity and increased melon growth [163,166] in comparison to un-grafted melon under different experimental conditions [5,68,105,163,166,167] (Table 4). Specialty melons such as Honeydew and Galia grafted onto *C. metuliferus* exhibited less root galling and lower RKN soil densities than un-grafted melon. However, yields were not different between grafted and un-grafted factors [167] (Table 2). Melon 'Paloma' grafted onto *C. metuliferus* BGV11135 reduced root galling and increased yield when compared to un-grafted plants in the spring as well as the summer plantings [105]. However, root galling was lower in the spring than the summer but only on the un-grafted melons whereas the yield of the grafted plants was higher in the spring than the summer. These results reflect the influence of the growing season in the host-nematode interaction irrespective of grafting. Similar effects of the growing season have been reported in zucchini infected by *M. incognita* [172].

Fruit quality traits, however, might be affected in some melon scion-*C. metuliferus* combinations. Flesh firmness and total soluble solids content decreased in the 'Arava'-*C. metuliferus* combination but did not affect the honeydew-*C. metuliferus* combination [167]. Fruit weight and length were increased in the 'Piel de Sapo' melon 'Finura'-*C. metuliferus* combination, but these changes did not reduce the commercial value of the melon fruits because the market accepts a wide range of fruit sizes and variability in the shape of this melon type [105]. Changes in traits associated with flesh quality (°Brix, flesh firmness, and flesh color) might be associated with a more advanced ripening state of the fruits and these effects could be reduced by adapting the harvesting period to each scion-rootstock combination [7].

4.3.3. Grafting Watermelon

The squash hybrids are effective against Fusarium wilt due to their non-host resistance to FON. Other rootstock candidates for watermelon are *C. moschata*, *B. hispida*, *S. angulatus*, *C. metuliferus*, and *Luffa* spp., which showed both high compatibility and resistance to FON 0, 1, and 2 races [7,173,174]. In Spain, routine grafting of watermelon onto squash hybrids 'Brava', 'Shintoza', and 'RS-841' to control Fusarium wilt may have controlled indirectly *Acremonium collapse* [18]. *Lagenaria siceraria* is also used as rootstock for watermelon due to its moderate resistance to FON and high compatibility [7,173]. In addition, *L. siceraria* has resistance against *P. capsici* crown rot but the squash hybrids are susceptible [175]. A clear example of the importance of proper diagnosis of the pathogen for the choice of rootstock due to the specificity of the host-pathogen interactions. Few works have tested squash hybrids for their resistance to *F. solani* f. sp. *cucurbitae* with contradictory results [176].

However, the squash hybrids are all susceptible to RKN. In fact, they support higher root galling and nematode reproduction than un-grafted watermelon [4,43,104,177]. Grafted watermelon increased Rf by 50 folds in RKN-infested commercial plastic greenhouses [43]. *Meloidogyne javanica* reproduction traits on squash hybrids were higher than those of *M. incognita*, as opposed to the observations on un-grafted watermelon due to the higher parasitic success of *M. javanica* than *M. incognita* on the squash hybrids. Furthermore, 96% of the *M. javanica* individuals inducing galls generated egg masses in contrast to 57% of the *M. incognita* [30]. Although *Lagenaria siceraria* is susceptible to *Meloidogyne* spp. [3,4,48,68], it has tolerance to RKN-infection in comparison to other cucurbit crops because of lower disease severity despite high Rf [34]. *Lagenaria siceraria* supported lower RKN reproduction than some

squash hybrids but reproduction was higher than on un-grafted watermelon [43,104,163]. Grafting onto *L. siceraria* did not increase watermelon yield when compared to un-grafted plants [4,104,163].

Grafting watermelon onto watermelon rootstocks would be a better option than on the interspecific squash hybrids or intergeneric rootstocks (i.e., *L. siceraria*) because of improved scion-rootstock compatibility and elimination of the undesirable effect on fruit quality observed on some watermelon-squash hybrid combinations [7]. In addition, some but not all plant introduction lines of *C. amarus* have shown simultaneous resistance to FON race 2 and *M. incognita* [104,134,178], and, therefore, they would be the preferred choice for fields infested with both pathogens. The RKN-resistant *C. amarus* showed higher efficiency in nematode and disease suppression than un-grafted watermelon [4,104,179]. The commercial rootstock *C. amarus* 'Ojakkyo' was more effective in reducing root galling and RKN egg production than *L. siceraria* 'Emphasis' and the squash hybrid 'Strong Tosa' [4,104]. Rootstock *C. amarus* 'Robusta', resistant to FON [180], also reduced root galling and nematode reproduction in comparison to un-grafted watermelon or squash hybrid-grafted plants in *M. javanica* and *M. incognita*-infested fields [43,179]. The 'Sugar Baby'-'Robusta' combination showed similar growth performance to the un-grafted plants with no influence on fruit quality traits [180]. Nonetheless, 'Robusta' and the squash hybrid 'Super Shintoza' differed in their response to FON and *M. incognita* when both pathogens infested the field. Both rootstocks exhibited resistance to Fusarium wilt but 'Super Shintoza' was susceptible to *M. incognita* whereas 'Robusta' was tolerant. The rootstock 'Robusta' supported lower disease severity and showed higher root dry weight than un-grafted watermelon, followed by 'Super Shintoza.' The yield was greater in grafted than un-grafted watermelon and higher on 'Robusta' than 'Super Shintoza' at high (4166 plants/ha) but not at low plant densities (2083 plants/ha) [180]. However, 'Robusta' is susceptible to Melon Necrotic Spot Virus transmitted by *O. bornovanus* [181] and should not be used in soils infested with these pathogens.

Meloidogyne incognita and FON do not interact on watermelon [177], and, therefore, the presence of one of these pathogens would not aggravate the disease caused by the other. Yield losses caused by FON on un-grafted watermelon (55%) were like those caused by *M. incognita* on grafted watermelon (49%). However, similar yield losses occurred in treatments inoculated with both pathogens [177]. The benefit of grafting watermelon would be apparent in soils infested with the fungus, but not with the nematode. *Citrullus amarus* 'Carolina Strongback', which is resistant to both FON and M. incognita, showed a higher incidence of Fusarium wilt than the squash hybrid 'Carnivor' but RKN root galling was higher on 'Carnivor' than 'Strongback' or un-grafted watermelon, which did not differ from each other [177]. Grafting onto squash hybrids could lead to increased nematode problems in RKN-infested soils. The cultivated area to watermelon in Spain has increased by 37%. Approximately 95% of the watermelons are routinely grafted [43,182]. This has been concomitant with the increased concern about nematode problems and their perception has worsened according to farm advisors [31].

The wild watermelon *C. africanus* and wild cucumber *C. myriocarpus* reduced *M. incognita* reproduction and root galling with no effect on watermelon yield components. They have been proposed as watermelon rootstocks because they are compatible and retained their resistance when grafted onto commercially susceptible watermelons [33,183]. Planting the wild species in advance of the cultivated watermelon optimized the stem diameter by overcoming the anatomical differences between scion and rootstock, which resulted in increased inter-generic compatibility [184]. The resistance of these wild *Cucumis* was primarily related to the failure of J2 to establish feeding sites, inhibition of J2 development, and conversion of J2 to males [183]. Furthermore, ground fruits of *C. myriocarpus* used as soil amendments had nematicidal activity [185]. Hence, crop residues could be incorporated into the ground after harvest as part of an integrated RKN management to further reduce the residual RKN population densities in the soil.

4.3.4. Other Possible Rootstocks

Liu et al. [5] found that 12 out of 53 accessions of *Cucumis* were resistant to FOM and five to M. incognita. Of these, *C. pustulatus* was resistant to both pathogens and highly compatible with

cucumber, melon, and watermelon. Grafted plants increased plant growth and yield with no adverse effect on fruit quality in comparison to un-grafted plants in a greenhouse heavily infested with M. incognita. Therefore, *C. pustulatus* was proposed as a rootstock to manage RKN on cucumber, melon, and watermelon [5] even though the effect of *C. pustulatus* on nematode reproduction needs to be determined. In addition, *C. africanus*, *C. anguria*, *C. prophetarum*, *C. subsericeus*, and *C. zeyheri* were highly resistant to FOM race 1, 2, whereas most accessions of *C. dipsaceus*, *C. meeusei*, *C. pustulatus*, and *C. sagittatus* were susceptible [186].

Cucumis melo var. *texanus* reduced *M. incognita* root penetration rates, migration of J2 from the roots, and delayed rate of nematode development (Table 3), which resulted in lower reproduction on *C. melo* var. *texanus* than a susceptible melon. Accessions of C. melo var. texanus varied in their response to *M. incognita* and eight out of 22 accessions showed similar RKN reproduction levels to that of *C. metuliferus* used as a resistant control [106].

Cucumis hystrix showed a level of resistance to *M. incognita* similar to *C. metuliferus*. Both *C. hystrix* and *C. metuliferus* produced more lateral roots and fewer, smaller galls than the susceptible cucumber. Interspecific progenies derived from the cross between *C. hystrix* and *C. sativus* showed similar resistance to the resistant parent *C. hystrix* [108].

Momordica balsamina (bitter gourd) has shown non-host resistance to *M. incognita* because it reduced the Rf at progressively higher Pi with no effect on plant growth and negligible root galling. This bitter gourd can be an alternative vegetable crop for RKN management in heavily RKN-infested areas. *Momordica balsamina* has nutritional, medicinal, nutraceutical, and pesticidal attributes that are potentially attractive to various industries [187].

4.3.5. Effect of Grafting on Disease Severity and Crop Yield in Root-Knot Nematode-Infested Soils

The benefit of grafting in promoting crop yield in RKN-infested soils depends primarily on the pre-planting nematode densities in soil and the susceptibility of the crop. Grafting has provided variable results in nematode suppression and promotion of yield increases. Thus, the squash hybrids 'Strong Tosa' and 'RS841', and *L. siceraria* were equally susceptible or more susceptible to RKN than un-grafted cucumber, melon, and watermelon plants (Table 4). These rootstocks did not show disease tolerance since root galling was similar or higher than that of the un-grafted plants. Yield increases were only recorded on grafted cucumbers [162] likely due to their extreme susceptibility to the nematode but were not observed either on grafted melon [167] or watermelon [104]. The choice of rootstock may affect yield when grafted plants are challenged to similar Pi levels. The 'Sugar Baby'-'RS841' combination experimented 12% and 45% yield losses at Pi < 1 and Pi = 70 juveniles/250 cm^3 soil, respectively, but only a 3% loss was recorded in the 'Sugar baby'-'Titan' combination at Pi = 69 juveniles/250 cm^3 soil [43].

Grafting melons onto the RKN resistant rootstock *C. metuliferus* increased yield due to suppression of nematode reproduction, and reduced plant damage in some but not all the experiments. Similarly, inconsistent yield increases also occurred when watermelon was grafted onto *C. amarus* [4,103]. Nonetheless, grafting cucurbits onto the RKN resistant or tolerant rootstock could be useful for RKN management in continuous vegetable cropping systems because nematode build-up by continuous cropping will be slowed down, which, in turn, will reduce the selection pressure for virulent individuals within the nematode population able to overcome the rootstock resistance.

5. Conclusions

Soil-borne diseases are a major threat to the preservation and expansion of cucurbit crops worldwide. SBPF and RKN constraint profitability of cucumber, melon, watermelon, and squash fruits. Soil disinfestation with chemicals has been extensively used in the past, but the application of toxic compounds in the soil implies collateral environmental and health risks. This makes plant resistance the preferred method to prevent damages and yield losses associated with soil-borne pathogens. Different sources of resistance have been described. However, hybridization with cultivated cucurbit

crops has shown low success on many occasions. Grafting has proven to be the best solution for specific soil-borne diseases in order to increase pathogen tolerance associated with the more vigorous root system. However, new sources of resistance are demanded due to incompatibility issues between rootstocks and scions, market demands, emergence of new pathogen races able to overcome plant resistance, or introduction of new pathogens to the region. Additionally, commercially available rootstocks do not show crossed resistance to key soil-borne pathogens, and there are few resistant rootstocks for RKN and root rot fungi.

In the last decade, research has focused on the mechanisms of resistance and breeding tools for resistance to soil-borne diseases of cucurbit crops. The current knowledge can lead to an improvement of breeding and the obtainment of new resistant cultivars. New biotechnological tools are available to complement traditional breeding programs. The combination of biomolecular and histopathological techniques can link the gene function with the interaction between host and pathogen/parasite for different pathosystems. In this respect, Fusarium wilt diseases and RKN have been extensively studied, while root rot diseases need more research. Genotyping by sequencing can lead to the identification of molecular markers like SNPs that can be associated with resistances (QTL) in a much more reliable and simpler way. Advances in the resistance of non-cucurbit species to polyphagous pathogens/parasites are useful due to the similarity of resistance gene domains in common between cucurbit and non-cucurbit species. Thus, searching for homologous resistance genes in cucurbits is a worthy tool to be further explored. TILLING, which is an unexplored resource for soil-borne diseases, can provide abundant mutant material to find resistance genes, but also genes involved in the compatibility between rootstocks and scions should be a matter of study using the tools reviewed in this article, as the grafting technology shows a long-term solution for the pathological issues, as approached in this article.

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