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

Alejandro Ayala-Doñas 1, Miguel de Cara-García 1, Miguel Talavera-Rubia 2 and Soledad Verdejo-Lucas 1,*

1 Institute for Research and Training in Agriculture and Fisheries, IFAPA La Mojonera, Autovía del Mediterráneo, Salida 420. Paraje San Nicolás, La Mojonera, 04745 Almería, Spain; alejandro.ayala@juntadeandalucia.es (A.A.-D.); franciscom.cara@juntadeandalucia.es (M.d.C.-G.)

2 Institute for Research and Training in Agriculture and Fisheries, IFAPA Alameda del Obispo. Av. Menéndez Pidal s/n, 14004 Córdoba, Spain; miguel.f.talavera@juntadeandalucia.es

* Correspondence: soledadverdejo@gmail.com

Received: 22 September 2020; Accepted: 22 October 2020; Published: 24 October 2020

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 disinfection. 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 disinfections 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
fungal pathogens, in addition to the emergence of more aggressive strains of nematodes.

The presence of dead roots leads to the formation of erithecia (fruiting body structures of the fungus) on dead roots. These structures are important for nematode reproduction as they provide a suitable environment for nematode development. When nematodes emerge from the erithecia, they infect living roots and begin the pathogen cycle.

Nematode parasitism affects a wide range of plants, including cucumbers, melons, and watermelons. Maximum yield losses due to RKN were estimated in 88% for cucumbers, 53% for zucchinis, and 35% for watermelons. The high economic impact of RKN infections is further emphasized by the large market value of affected crops, which represents 5% of the market value received in Southern Spain.

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). 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].

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 cm³ soil for *M. javanica* and 4 J2/100 cm³ 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                                     | All cucurbitis           | Colletotrichium spp.                         | [59]       |
| Suberization and tylosis                   | C. sativus               | FOC                                          | [60]       |
|                                            | C. melo                  | FOM                                          | [61]       |
|                                            | C. lanatus               | Monosporascus cannonballus                   | [25]       |
|                                            | Cucurbita spp.           | Acremonium cucurbitacearum                   | [25]       |
| Enzymes                                    |                           |                                               |            |
| Peroxidases                                | C. sativus               | FORC                                         | [63]       |
|                                            | C. melo                  | Meloidogyne javanica                        | [64]       |
|                                            | C. lanatus               | FOM                                          | [65]       |
|                                            | C. metuliferus           | Meloidogyne incognita                       | [66]       |
|                                            | M. charantia             | Meloidogyne incognita                       | [67]       |
|                                            | R. solani                | Thielaviopsis basicola                      | [69]       |
|                                            | C. melo                  | FOM                                          | [65,71]    |
|                                            | C. lanatus               | FON                                          | [66,72]    |
|                                            | M. charantia             | FOM                                          | [66]       |
| β-1,3-glucanase                            | C. sativus               | Pythium aphanidermatum                      | [73]       |
|                                            | R. solani                | Rhizoctonia solani                          | [70]       |
|                                            | C. lanatus               | FON                                          | [66]       |
|                                            | M. charantia             | Meloidogyne incognita                       | [67]       |
|                                            | Meloidogyne incognita    | [68]                                          |
| Phenylalanine ammonia lyase                | 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]       |
|                                            | R. solani                | Thielaviopsis basicola                      | [69]       |
|                                            | FOM                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
|                                            | FON                      |                                              |            |
| Polyphenol oxidase                         | C. sativus               | FORC                                         | [63]       |
|                                            | M. charantia             | Meloidogyne javanica                        | [64]       |
|                                            | M. charantia             | Meloidogyne javanica                        | [68]       |
|                                            | R. solani                | Thielaviopsis basicola                      | [69]       |
| Lipoxygenase                               | C. sativus               | Rhizoctonia solani                          | [70]       |
| Signal molecules                           |                           |                                               |            |
| Salicylic acid                             | C. sativus               | Rhizoctonia solani                          | [70]       |
|                                            | C. melo                  | Pythium aphanidermatum                      | [76]       |
|                                            | Rhizoctonia solani       |                                              | [77]       |
|                                            | Cucurbita spp.           | Phytophthora capsici                        | [78]       |
|                                            | C. lanatus               | FON                                          | [66]       |
| Jasmonic acid                              | C. sativus               | Rhizoctonia solani                          | [70]       |
|                                            | C. melo                  | FOM                                          | [65]       |
|                                            | Monosporascus cannonballus|                                              | [79]       |
| Ethylene                                   | C. sativus               | Rhizoctonia solani                          | [70]       |
|                                            | C. melo                  | Fusarium solani                             | [70]       |
|                                            | C. melo                  | FOM                                          | [65]       |
| Antimicrobial molecules                     |                           |                                               |            |
| Phytoalexins                               | C. sativus               | Pythium aphanidermatum                      | [80]       |
|                                            |                         |                                              |            |
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 PAL in the presence of watermelon 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., *Micromonaspora* 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. aphanidermatus* [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].

| Defensins | Cysteine-rich peptides with antifungal/bacterial activity | C. melo | *Fusarium oxysporum* FON |
|-----------|--------------------------------------------------------|--------|------------------------|
|           |                                                        |        |                        |

*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).
or the \textit{P. capsici} resistance genes (Crr) in \textit{Cucurbita} spp. [88]. None of the genes presently known confer resistance to all the \textit{formeae speciales} of \textit{F. oxysporum}, but some genes confer specific resistance to each \textit{formeae specialis} in cucumber, melon, and watermelon.

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

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

Information extracted from Cucurbit breeding cooperative gene list [87] and Elkabetz et al., 2016 [96].

\textit{Fusarium oxysporum} f. sp. \textit{cucumerinum} (FOC), \textit{F. oxysporum} f. sp. \textit{melonis} (FOM), \textit{F. oxysporum} f. sp. \textit{radicis-cucumerinum} (FORC), \textit{F. oxysporum} f. sp. \textit{niveum} (FON).

3.2. \textit{Plant-Parasitic Nematodes}

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

\textit{Zucchini} has shown resistance to \textit{M. incognita} but not to \textit{M. javanica} or \textit{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 \textit{M. incognita} giant cells and abnormal growth of the surrounding tissues caused early deterioration of 74% of the \textit{M. incognita} feeding sites before life-cycle completion [101]. Consequently, only 26% of the total \textit{M. incognita} population within the roots reached the egg-laying female stage in contrast to 96% of the \textit{M. javanica} population. The increased frequency of undersized individuals, immature females, and empty galls showed a failure of \textit{M. incognita} to develop. Critical events differentiating the resistant and susceptible response to \textit{M. incognita} and \textit{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 \textit{C. pepo} subsp. \textit{pepo} ‘Murcia MU-CU-16’ × \textit{C. pepo} subsp. \textit{ovifera} ‘Scallop UPV-196’ were evaluated in search for sources of resistance. The nematode differentiated the \textit{C. pepo} genotypes at the subspecies level due to lower egg mass production on the subsp. pepo than ovifera [40]. In addition, \textit{zucchini} ‘Murcia MU-CU-16’ discriminates \textit{M. incognita} from \textit{M. javanica} in terms of egg masses, eggs per gram of root, and RI, 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].

| 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 mi 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 Oumould 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 (fa2.1 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, PALI, PR1, and LOXI 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 ΔFonSIX6 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* x *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* x *C. moschata* 'Strong Tosa' | *C. sativus* 'Adrian' | Meloidogyne sp. | NS           | NS           | Increased | [162]      |
|                             | *C. sativus* 'Athena'        | M. incognita       | Increased    | NS           | Reduced   | [163]      |
|                             | *C. lanatus* 'Fiesta'        | M. incognita       | Increased    | Increased    | Reduced   | [4]        |
|                             | *C. lanatus* 'TriX313'       | M. incognita       | Increased    | NS           |          |            |
| *C. maxima* x *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    | Decreased    | Reduced   | [42]       |
| *C. maxima* x *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). Speciality 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 zucchinis 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* ‘Ojakkoyo’ 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 Shintozu’ differed in their response to FON and *M. incognita* when both pathogens infested the field. Both rootstocks exhibited resistance to Fusarium wilt but ‘Super Shintozu’ 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 Shintozu.’ The yield was greater in grafted than un-grafted watermelon and higher on ‘Robusta’ than ‘Super Shintozu’ 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. bornovanius* [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 nematocidal 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. meusei*, *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 cm³ soil, respectively, but only a 3% loss was recorded in the ‘Sugar baby’-‘Titan’ combination at Pi = 69 juveniles/250 cm³ 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 obtention 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.

Author Contributions: Conceptualization, M.d.C.-G., M.T.-R., and S.V.-L. Investigation, A.A.-D., M.d.C.-G., M.T.-R., and S.V. Writing—original draft preparation, A.A.-D., M.d.C.-G., M.T.-R., and S.V.-L. Writing—review and editing, M.d.C.-G., M.T.-R., and S.V.-L. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the European Regional Development Fund (ERDF) and IFAPA grant number PP.AVA.AVA2019.015.

Acknowledgments: A. Ayala-Doñas thanks INIA for economic support through a pre-doctoral grant (FPI-INIA2016 CFD2016-0199).

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results.
References

1. Food and Agriculture Organization Corporate Statistical Database (FAOSTAT). New Food Balances. Available online: http://www.fao.org/faostat/en/#data/FBS (accessed on 2 December 2019).

2. Greco, N.; Aranda, J.L.; Saporiti, M.; Maccarini, C.; De Tommaso, N.; Myrta, A. Sustainability of European vegetable and strawberry production in relation to fungiation practices in the EU. Acta Hort. 2020, 203–210, doi:10.17660/actahortic.2020.1270.24.

3. Levi, A.; Thies, J.; Ling, K.-S.; Simmons, A.M.; Kousik, C.; Hassell, R. Genetic diversity among Lagenaria siceraria accessions containing resistance to root-knot nematodes, whiteflies, ZYMV or powdery mildew. Plant Genet. Resour. 2009, 7, 216–226, doi:10.1017/s1479262109225354.

4. Thies, J.A.; Ariss, J.J.; Hassell, R.L.; Olson, S.; Kousik, C.S.; Levi, A. Grafting for management of southern root-knot nematode, Meloidogyne incognita, in watermelon. Plant Dis. 2010, 94, 1195–1199, doi:10.1094/pdis-09-09-0640.

5. Liu, B.; Ren, J.; Zhang, Y.; An, J.; Chen, M.; Chen, H.; Xu, C.; Ren, H. A new grafted rootstock against root-knot nematode for cucumber, melon, and watermelon. Agron. Sustain. Dev. 2014, 35, 251–259, doi:10.1007/s13593-014-0234-5.

6. Zheng, Y.; Wu, S.; Bai, Y.; Sun, H.; Jiao, C.; Guo, S.; Zhao, K.; Blanca, J.; Zhang, Z.; Huang, S.; et al. Cucurbit Genomics Database (CuGenDB): A central portal for comparative and functional genomics of cucurbit crops. Nucleic Acids Res. 2018, 47, D1128–D1136, doi:10.1093/nar/gky944.

7. Davis, A.R.; Perkins-Vazie, P.; Sakata, Y.; López-Galarza, S.; Maroto, J.V.; Lee, S.-G.; Huh, Y.-C.; Sun, Z.; Miguel, A.; King, S.R.; et al. Cucurbit Grafting. Crit. Rev. Plant Sci. 2008, 27, 50–74, doi:10.1080/07352680802053940.

8. Louws, F.J.; Rivard, C.L.; Kubota, C. Grafting fruiting vegetables to manage soilborne pathogens, foliar pathogens, arthropods and weeds. Sci. Hortic. 2010, 127, 127–146, doi:10.1016/j.scienta.2010.09.023.

9. Koike, S.T.; Subbarao, K.V.; Davis, R.M.; Turini, T.A. Vegetable Diseases Caused by Soilborne Pathogens: UCANR Publications: Davis, CA, USA, 2003; pp. 1–13.

10. Najafinia, M.; Sharma, P. Cross pathogenicity among isolates of Fusarium oxysporum causing wilt in cucumber and muskmelon. Indian Phytopathol. 2009, 62, 9–13.

11. Chikh-Rouhou, H.; González-Torres, R.; Alvarez, J.M.; Oumouloud, A. Screening and morphological characterization of melons for resistance to Fusarium oxysporum f. sp. melonis race 1.2. HortScience 2010, 45, 1021–1025, doi:10.21273/hortsci.45.7.1021.

12. Perchepied, L.; Pitrat, M. Polygenic inheritance of partial resistance to Fusarium oxysporum f. sp. melonis race 1.2 in melons. Phytopathology 2004, 94, 1331–1336, doi:10.1094/phyto.2004.94.12.1331.

13. Edel-Hermann, V.; LeComte, C. Current status of Fusarium oxysporum formae speciales and races. Phytopathology 2019, 109, 512–530, doi:10.1094/phyto-08-18-0320-rvve.

14. Rezaee, S.; Gharanjik, S.; Mojerdou, S. Identification of Fusarium solani f. sp. ciceribactae races using molecular and morphological approaches. J. Crop Prot. 2018, 7, 161–170.

15. Genetic diversity of Fusarium solani f. sp. cucurbitae the causal agent of crown and root rot of watermelon in Tunisia using ISSR markers. Nov. Res. Microbiol. J. 2019, 3, 271–280, doi:10.21608/nrmj.2019.28113.

16. Deadman, M.; Al-Sadi, A.M.; Al Said, F.; Maawali, Q.A. The use of cucurbit hybrid rootstocks in the management of Pythium-induced damping-off of cucumber seedlings. Acta Hort. 2010, 871, 483–490, doi:10.17660/actahortic.2010.871.67.

17. Mirmajlessi, S.M. Genetic diversity among crown and root rot isolates of Rhizoctonia solani isolated from cucurbits using PCR-based techniques. Afr. J. Agric. Res. 2012, 7, 583–590, doi:10.5897/ajar11.1453.

18. Armengol, J.; Sanz, E.; Martínez-Ferrer, G.; Sales, R.; Bruton, B.D.; García-Jiménez, J. Host range of Acremonium cucurbitacearum, cause of Acremonium collapse of muskmelon. Plant Path. 1998, 47, 29–35, doi:10.1046/j.1365-3059.1998.00199.x.

19. Cohen, R.; Omari, N.; Porat, A.; Edelstein, M. Management of Macrophomina wilt in melons using grafting or fungicide soil application: Pathological, horticultural and economical aspects. Crop Prot. 2012, 35, 58–63, doi:10.1016/j.cropro.2011.12.015.

20. Ambrósio, M.M.D.Q.; Dantas, A.C.A.; Martínez-Perez, E.; Medeiros, A.C.; Nunes, G.H.S.; Picó, B. Screening a variable germplasm collection of Cucumis melo L. for seedling resistance to Macrophomina phaseolina. Euphytica 2015, 206, 287–300, doi:10.1007/s10681-015-1452-x.
21. Shishido, M.; Yoshida, N.; Usami, T.; Shinozaki, T.; Kobayashi, M.; Takeuchi, T. Black root rot of cucurbits caused by *Phomopsis sclerotioides* in Japan and phylogenetic grouping of the pathogen. *J. Gen. Plant Pathol.* **2006**, *72*, 220–227, doi:10.1007/s10327-006-0273-0.

22. De Cara, M.; Fernández-Plaza, M.; Gómez-Vázquez, J. Pathogenic and biological characterization of *Phytophthora capsici* isolates from zucchini and pepper in Southeast Spain. *Span. J. Agric. Res.* **2018**, *16*, e1005, doi:10.5424/sjar/2018162-13129.

23. Pivonia, S.; Cohen, R.; Katan, J.; Kigel, J. Effect of fruit load on the water balance of melon plants infected with *Monosporascus cannonballus*. *Physiol. Mol. Plant Pathol.* **2002**, *60*, 39–49, doi:10.1066/pmpp.2001.0375.

24. De Cara, M.; López, V.; Córdoba, M.C.; Santos, M.; Jordá, C.; Tello, J.C. Association of *Olpidium bornovanus* and melon necrotic spot virus with vine decline of melon in Guatemala. *Plant Dis.* **2008**, *92*, 709–713, doi:10.1094/pdis-92-5-0709.

25. Alfaro-Fernández, A.; Garcia-Luis, A. Colonisation and histological changes in muskmelon and autumn squash tissues infected with *Acremonium cucurbitacearum* or *Monosporascus cannonballus*. *Eur. J. Plant Pathol.* **2009**, *125*, 73–85, doi:10.1007/s10658-009-9460-0.

26. Iglesias, A.; Nuez, F.; Picó, B. A temporal genetic analysis of disease resistance genes: Resistance to melon vine decline derived from *Cucumis melo var. agrestis*. *Plant Breed.* **2000**, *119*, 329–334, doi:10.1046/j.1439-0523.2000.00507.x.

27. Farr, D.F.; Rossman, A.Y. Fungal Databases. Available online: https://nt.ars-grin.gov/fungaldatabases (accessed on 30 July 2020).

28. Zhou, X.G.; Everts, B.D.; Bruton, B.D. Race 3, a new and highly virulent race of *Fusarium oxysporum* f. sp. *niveum* causing Fusarium Wilt in watermelon. *Plant Dis.* **2010**, *94*, 92–98, doi:10.1094/pdis-94-1-0092.

29. Cacciola, S.O.; Gullino, M.L. Emerging and re-emerging fungus and oomycete soil-borne plant diseases in Italy. *Phytopathol. Mediterr.* **2019**, *58*, 451–472, doi:10.14601/phyto-10756.

30. Verdejo-Lucas, S.; Talavera, M. Root-knot nematodes on zucchini (*Cucurbita pepo* subsp. *pepo*): Pathogenicity and management. *Crop Prot.* **2019**, *126*, 104943, doi:10.1016/j.cropro.2019.104943.

31. Talavera, M.; Sayadi, S.; Chirosa-Ríos, M.; Salmerón, T.; Flor-Peregrín, E.; Verdejo-Lucas, S. Perception of the impact of root-knot nematode-induced diseases in horticultural protected crops of south-eastern Spain. *Nematology* **2012**, *14*, 517–527, doi:10.1163/156854112x635850.

32. Barker, K.R. Resistance/tolerance and related concepts/terminology in Plant Nematology. *Plant Dis.* **1993**, *77*, 111–113.

33. Pofu, K.M.; Mashela, P.W.; Mokgalong, N.M. Host-status and host-sensitivity of *Cucumis africanus* and *Cucumis myriocarpus* to *Meloidogyne incognita* race 2 under greenhouse conditions. *Afr. J. Agric. Res.* **2010**, *5*, 1504–1508, doi:10.5897/AJPR10.025.

34. Chandra, P.; Sao, R.; Gautam, S.; Poddar, A. Initial population density and its effect on the pathogenic potential and population growth of the Root knot nematode *Meloidogyne incognita* in four species of cucurbits. *Asian J. Plant Pathol.* **2010**, *4*, 1–15, doi:10.3923/ajppal.2010.1.15.

35. López-Gómez, M.; Verdejo-Lucas, S. Penetration and reproduction of root-knot nematodes on cucurbit species. *Eur. J. Plant Pathol.* **2014**, *138*, 863–871, doi:10.1007/s10658-013-0359-4.

36. Mukhtar, T.; Kayani, M.Z.; Hussain, M.A. Response of selected cucumber cultivars to *Meloidogyne incognita*. *Crop Prot.* **2013**, *44*, 13–17, doi:10.1016/j.cropro.2012.10.015.

37. Diniz, G.M.M.; Candido, W.D.S.; Soares, R.S.; Santos, L.D.S.; Marin, M.V.; Soares, P.L.M.; Braz, L.T. Reaction ofmelon genotypes to *Meloidogyne incognita* and *M. javanica*. *Pesqui. Agropecuária Trop.* **2016**, *46*, 111–115, doi:10.1590/1983-40632016v4639603.

38. López-Gómez, M.; Flor-Peregrín, E.; Talavera, M.; Verdejo-Lucas, S. Suitability of zucchini and cucumber genotypes to populations of *Meloidogyne arenaria*, *M. incognita*, and *M. javanica*. *J. Nematol.* **2015**, *47*, 79–85.

39. Talavera-Rubia, M.; Fernández-Plaza, M.; Verdejo-Lucas, S.; Vela, M.D. Susceptibility y tolerancia del calabacín (*Cucurbita pepo*) a *Meloidogyne incognita* y *M. javanica*. *Phytoma España* **2018**, *295*, 42–46.

40. Verdejo-Lucas, S.; Gómez, P.; Talavera, M. Pathogenicity of *Meloidogyne incognita* and *M. javanica* on recombinant inbred lines from a crossing of *Cucurbita pepo* subsp. *pepo* × *C. pepo* subsp. *ovifera*. *Plant Pathol.* **2019**, *68*, 1225–1232, doi:10.1111/ppa.13025.

41. Desaeger, J.A.; Csinos, A.S. Root-knot nematode management in double-cropped plasticulture vegetables. *J. Nematol.* **2006**, *38*, 59–67.
42. Cohen, R.; Tyutyunik, J.; Fallik, E.; Oka, Y.; Tadmor, Y.; Edelstein, M. Phytopathological evaluation of exotic watermelon germplasm as a basis for rootstock breeding. Sci. Hortic. 2014, 165, 203–210, doi:10.1016/j.scienta.2013.11.007.
43. López-Gómez, M.; Talavera, M.; Verdejo-Lucas, S. Differential reproduction of Meloidogyne incognita and M. javanica in watermelon cultivars and cucurbit rootstocks. Plant Pathol. 2015, 65, 145–153, doi:10.1111/ppa.12394.
44. López-Gómez, M.; Verdejo-Lucas, S. Penetration and post-infection development of root-knot nematodes in watermelon. Spum. J. Agric. Res. 2018, 15, e1010, doi:10.5424/sjar/2017154-11189.
45. Verdejo-Lucas, S.; Talavera, M. Pathogenic potential, parasitic success and host efficiency of Meloidogyne incognita and M. javanica on cucurbitaceous plant genotypes. Eur. J. Plant Pathol. 2018, 153, 1287–1297, doi:10.1007/s10658-018-01642-6.
46. Salata, A.D.C.; Bertolini, E.V.; Magro, F.O.; Cardoso, A.I.; Wilcken, S.R.S. Enxertia e sua influência na produção de pepino e reprodução de Meloidogyne javanica e M. incognita. Hortic. Bras. 2012, 30, 590–594, doi:10.1590/s0102-0536201200400005.
47. Djian-Caporalino, C.; Molinari, S.; Falloix, A.; Ciancio, A.; Fazari, A.; Martue, N.; Ris, N.; Castagnone-Sereno, P. The reproductive potential of the root-knot nematode Meloidogyne incognita is affected by selection for virulence against major resistance genes from tomato and pepper. Eur. J. Plant Pathol. 2011, 131, 431–440, doi:10.1007/s10658-011-9820-4.
48. Edelstein, M.; Oka, Y.; Burger, Y.; Eizenberg, H.; Cohen, R. Variation in the response of cucurbits to Meloidogyne incognita and M. javanica. Isr. J. Plant Sci. 2010, 58, 77–84, doi:10.1560/ijips.58.1.77.
49. Seinhorst, J. The relation between nematode density and damage to plants. Nematology 1965, 11, 137–154, doi:10.1163/187529265x00852.
50. Xing, L.; Westphal, A. Predicting damage of Meloidogyne incognita on watermelon. J. Nematol. 2012, 44, 127–133.
51. López-Gómez, M.; Giné, A.; Vela, M.; Ornati, C.; Sorribas, F.J.; Talavera, M.; Verdejo-Lucas, S. Damage functions and thermal requirements of Meloidogyne javanica and Meloidogyne incognita on watermelon. Ann. Appl. Biol. 2014, 165, 466–473, doi:10.1111/aab.12154.
52. Thies, J.A.; Levi, A. Characterization of watermelon (Citrullus lanatus var. citroides) germplasm for resistance to Root-knot nematodes. HortScience 2007, 42, 1530–1533, doi:10.21273/hortsci.42.7.1530.
53. Anwar, S.A.; McKenry, M.V. Incidence and reproduction of Meloidogyne incognita on vegetable crop genotypes. Pak. J. Zool. 2010, 42, 135–141.
54. Davis, R.F. Effect of Meloidogyne incognita on watermelon yield. Nematropica 2007, 37, 287–293.
55. Seinhorst, J. The relationships between population increase and population density in plant parasitic nematodes. Nematology 1967, 13, 429–442, doi:10.1163/187529267x00670.
56. Gill, U.S.; Lee, S.; Mysore, K.S. Host versus nonhost resistance: Distinct wars with similar arsenals. Phytopathology 2015, 105, 580–587, doi:10.1094/phyto-11-14-0298-rrw.
57. Jones, J.D.G.; Dangl, J.L. The plant immune system. Nat. Cell Biol. 2006, 444, 323–329, doi:10.1038/nature05286.
58. Petit-Houdenet, Y.; Fudal, I. Complex interactions between fungal avirulence genes and their corresponding plant resistance genes and consequences for disease resistance management. Front. Plant Sci. 2017, 8, 1072, doi:10.3389/fpls.2017.01072.
59. Hammerschmidt, R.; Bonnen, A.M.; Bergstrom, G.C.; Baker, K.K. Association of epidermal lignification with nonhost resistance of cucurbits to fungi. Can. J. Bot. 1985, 63, 2393–2398, doi:10.1139/b85-342.
60. Chen, M.; Wang, G.; Wu, D.; Cheng, Y. Histopathological differences between cucumber cultivars with different resistances to Fusarium wilt. J. South China Agric. Univ. Sci. Ed. 2003, 24, 110–112.
61. Mahjoub, M.E.; Le Picard, D.; Moreau, M. Origin of Tyloses in Melon (Cucumis melo L.) in response to a vascular Fusarium. IAWA J. 1994, 5, 307–311, doi:10.1163/22941932-90000417.
62. Miao, C.; Shang, F.; Jiang, J. Cytology study on the Fusarium wilt disease resistance in watermelon. J. Sichuan Univ. 2004, 41, 877–800.
63. Moghbeli, E.; Nemati, H.; Aroiee, H.; Olfati, J.-A. Evaluation of resistance, enzymatic response, and phenolic compounds in roots of F1 cucumber hybrids to Fusarium oxysporum f. sp. radicis-cucumerinum. J. Hortic. Res. 2017, 25, 117–124, doi:10.1515/johr-2017-0012.
64. Sahebani, N.; Hadavi, N.S.; Zade, F.O. The effects of β-amino-butyric acid on resistance of cucumber against root-knot nematode, Meloidogyne javanica. *Acta Physiol. Plant.* **2010**, *33*, 443–450, doi:10.1007/s11738-010-0564-0.

65. Buzi, A.; Chilosi, G.; Magro, P. Induction of resistance in melon seedlings against soil-borne fungal pathogens by gaseous treatments with methyl jasmonate and ethylene. *J. Phytopathol.* **2004**, *152*, 491–497, doi:10.1111/j.1439-0434.2004.00885.x.

66. Mahdy, A.; Abd-El-Mageed, M.; Abd-El-Latif, F.; Diab, M.; Saied, N. Induction of resistance in watermelon plants against Fusarium wilt using chemical inducers and compost under greenhouse conditions. *Egypt. J. Phytopathol.* **2015**, *42*, 1–19, doi:10.21608/ejp.2015.94687.

67. Ye, D.-Y.; Qi, Y.-H.; Cao, S.-F.; Wei, B.-Q.; Zhang, H.-S. Histopathology combined with transcriptome analyses reveals the mechanism of resistance to Meloidogyne incognita in Cucumis melo. *J. Plant Physiol.* **2017**, *212*, 115–124, doi:10.1016/j.jplph.2017.02.002.

68. Tamilselvi, N.; Pugalendhi, L.; Sivakumar, M. Defence responses of cucurbitaceous rootstock trees and bitter gourd scions against root knot nematode Meloidogyne incognita Kofoid and White. *Vegetos Int. J. Plant Res.* **2016**, *29*, 122, doi:10.5958/2229-4473.2016.00111.7.

69. Punja, Z.K. Response of transgenic cucumber and carrot plants expressing different chitinase enzymes to inoculation with fungal pathogens. *Plant Dis.* **1996**, *80*, 999, doi:10.1094/pd-80-0999.

70. Derbalah, A.; Elsharkawy, M.M.; Hamza, A.; El-Saier, A. Resistance induction in cucumber and direct antifungal activity of zirconium oxide nanoparticles against Rhizoctonia solani. *Pestic. Biochem. Physiol.* **2019**, *157*, 230–236, doi:10.1016/j.pestbp.2019.03.018.

71. Zvirin, T.; Herman, R.; Brotman, Y.; Denisov, Y.; Belaousof, E.; Freeman, S.; Perl-Treves, R. Differential colonization and defence responses of resistant and susceptible melon lines infected by *Fusarium oxysporum* race 1·2. *Plant Pathol.* **2010**, *59*, 576–585, doi:10.1111/j.1365-3659.2009.02225.x.

72. Zhang, M.; Xu, J.H.; Liu, G.; Yao, X.F.; Li, P.F.; Yang, X.P. Characterization of the watermelon seedling infection process by *Fusarium oxysporum* f. sp. niveum. *Plant Pathol.* **2015**, *64*, 1076–1084, doi:10.1111/ppa.12355.

73. Chérif, M.; Menzies, J.; Ehret, D.; Bogdanoff, C.; Bélanger, R. Yield of cucumber infected with *Pythium aphanidermatum* when grown with soluble silicon. *HortScience* **1994**, *29*, 896–897, doi:10.21273/hortsci.29.8.896.

74. Guan, W.; Zhao, X.; Hassell, R.; Thies, J. Defense mechanisms involved in disease resistance of grafted vegetables. *HortScience* **2012**, *47*, 164–170, doi:10.21273/hortsci.47.2.164.

75. Chang, P.-F.L.; Hsu, C.-C.; Lin, Y.-H.; Chen, K.-S.; Huang, J.-W.; Liou, T.-D. Histopathology comparison and phenylalanine ammonia lyase (PAL) gene expressions in Fusarium wilt infected watermelons. *Aust. J. Agric. Res.* **2008**, *59*, 1146–1155, doi:10.1071/ar08066.

76. Chen, C.; Bélanger, R.R.; Benhamou, N.; Paulitz, T.C. Role of salicylic acid in systemic resistance induced by *Pseudomonas* spp. against *Pythium aphanidermatum* in cucumber roots. *Eur. J. Plant Pathol.* **1999**, *105*, 477–486, doi:10.1023/A:1008743052784.

77. Mohamed, G.; Amer, S. Application of salicylic acid and some fungicides as seed treatment for controlling damping-off and root rot diseases of squash and cantaloupe plants under field conditions. *J. Plant Prot. Pathol.* **2014**, *5*, 1025–1043, doi:10.21608/jppp.2014.88024.

78. Koné, D.; Csinos, A.; Jackson, K.; Ji, P. Evaluation of systemic acquired resistance inducers for control of *Phytophthora capsici* on squash. *Crop Prot.* **2009**, *28*, 533–538, doi:10.1016/j.cropro.2009.02.005.

79. Aleandri, M.P.; Reda, R.; Tagliavento, V.; Magro, P.; Chilosi, G. Effect of chemical resistance inducers on the control of *Monosporascus* root rot and vine decline of melon. *Phytopathol. Mediterr.* **2010**, *49*, 18–26, doi:10.14601/Phytopathol_Mediterr-3117.

80. Ongena, M.; Daayf, F.; Jacques, P.; Thonart, P.; Benhamou, N.; Paulitz, T.; Bélanger, R.R. Systemic induction of phytoalexins in cucumber in response to treatments with fluorescent pseudomonads. *Plant Pathol.* **2000**, *49*, 523–530, doi:10.1046/j.1365-3059.2000.00468.x.

81. Ntui, V.O.; Thirukkanumaran, G.; Azadi, P.; Khan, R.S.; Nakamura, I.; Mii, M. Stable integration and expression of wasabi defensin gene in “Egusi” melon (*Cucumis sativus* L.) confers resistance to Fusarium wilt and Alternaria leaf spot. *Plant Cell Rep.* **2010**, *29*, 943–954, doi:10.1007/s00299-010-0880-2.

82. Prasannath, K. Plant defense-related enzymes against pathogens: A review. *Agric. J. Agric. Sci.* **2017**, *11*, 38–48, doi:10.4038/agrieast.v11i1.33.
83. Palaniyandi, S.A.; Yang, S.H.; Zhang, L.; Suh, J.-W. Effects of actinobacteria on plant disease suppression and growth promotion. *Appl. Microbiol. Biotechnol.* **2013**, *97*, 9621–9636, doi:10.1007/s00253-013-5206-1.

84. El-Tarabily, K.A. Rhizosphere-competent isolates of streptomycete and non-streptomycete actinomycetes capable of producing cell-wall-degrading enzymes to control *Pythium aphanidermatum* damping-off disease of cucumber. *Can. J. Bot.* **2006**, *84*, 211–222, doi:10.1139/b05-153.

85. Chen, F.; Wang, M.; Zheng, Y.; Luo, J.; Yang, X.; Wang, X. Quantitative changes of plant defense enzymes and phytohormone in biocontrol of cucumber *Fusarium* wilt by *Bacillus subtilis* B579. *World J. Microbiol. Biotechnol.* **2009**, *26*, 675–684, doi:10.1007/s11274-009-0222-0.

86. Segarra, G.; Casanova, E.; Bellido, D.; Odena, M.A.; Oliveira, E.; Trillas, I. Proteome, salicylic acid, and jasmonic acid changes in cucumber plants inoculated with *Trichoderma asperellum* strain T34. *Proteomics* **2007**, *7*, 3943–3952, doi:10.1002/pmic.200700173.

87. Cucurbit Genetics Cooperative Cucurbit Breeding Cooperative Gene List. Available online: http://cuke.hort.ncsu.edu/cgc/cgcgenes/genelists.html (accessed on 30 July 2020).

88. Padley, L.D.; Kabelka, E.A.; Roberts, P.D. Inheritance of resistance to crown rot caused by *Phytophthora capsici* in *Cucurbita*. *Agronomy* **2012**, *4*, 211–213, doi:10.21273/hortsci.44.1.211.

89. Netzer, D. A dominant gene conferring resistance to *Fusarium* wilt in cucumber. *Phytopathology* **1977**, *77*, 525, doi:10.1094/phyto-67-525.

90. Vakalounakis, D.J.; Smardas, K. Genetics of resistance to *Fusarium oxysporum* f. sp. *cucumerinum* races 1 and 2 in cucumber line Wisconsin-2757. *Ann. Appl. Biol.* **1995**, *127*, 457–461, doi:10.1111/j.1444-7721.1995.tb07604.x.

91. Zhang, S.-P.; Miao, H.; Yang, Y.-H.; Xie, B.-Y.; Wang, Y.; Gu, X.-F. A major quantitative trait locus conferring resistance to *fusarium* wilt was detected in cucumber by using recombinant inbred lines. *Mol. Breed.* **2014**, *34*, 1805–1815, doi:10.1007/s11032-014-0140-1.

92. Risser, G. Etude de l’hérédité de la résistance du melon (*Cucumis melo*) aux races 1 et 2 de *Fusarium oxysporum* f. sp. *melonis*. *Ann. L’Amélioration Plantes* **1973**, *23*, 259–263.

93. Oumouloud, A.; El-Ottmani, M.; Chikh-Rouhou, H.; Garcés-Claver, A.; Torres, R.G.; Perl-Treves, R.; Álvarez, J.M. Breeding melon for resistance to *Fusarium* wilt: Recent developments. *Euphytica* **2013**, *192*, 155–169, doi:10.1007/s10681-013-0940-4.

94. Herman, R.; Zvirin, Z.; Kovalski, I.; Freeman, S.; Denisov, Y.; Zuri, G.; Katzir, N.; Perl-Treves, R. Characterization of *Fusarium* race 1.2 resistance in melon and mapping of a major QTL for this trait near a fruit netting locus. *Cucurbitaceae* **2008**, *2008*, 149–156.

95. Oumouloud, A.; Arnedo-Andrés, M.S.; González-Torres, R.; Álvarez, J.M. Inheritance of resistance to *Fusarium oxysporum* f. sp. *melonis* races 0 and 2 in melon accession Tortuga. *Euphytica* **2010**, *176*, 183–189, doi:10.1007/s10681-010-0201-4.

96. Elkabetz, M.; Paris, H.S.; Burger, Y.; Hanan, A.; Cohen, R. Two genes for resistance to *Fusarium oxysporum* f. sp. *radicus-cucumerinum* in melon (*Cucumis melo*, *Cucurbitaceae*). *Sci. Hortic.* **2016**, *201*, 57–60, doi:10.1016/j.scienta.2016.01.029.

97. Netzer, D. Inheritance of resistance in watermelon to race 1 of *Fusarium oxysporum* f. sp. *nicaeum*. *Plant Dis.* **1980**, *64*, 685, doi:10.1094/pd-64-685.

98. Matsumoto, Y.; Miyagi, M. Chromosomal location and mode of inheritance of a gene conferring resistance to *fusarium* wilt in *Cucumis anguria* L. *J. Hortic. Sci. Biotechnol.* **2012**, *87*, 539–544, doi:10.1080/14620316.2012.11512908.

99. Walters, S.A.; Wehner, T.C.; Barker, K.R. NC-42 and NC-43: Root-knot nematode–resistant cucumber germplasm. *HortScience* **1996**, *31*, 1246–1247, doi:10.21273/hortsci.31.7.1246.

100. Walters, S.A.; Wehner, T.C.; Barker, K.R. A Single recessive gene for resistance to the Root-knot nematode (*Meloidogyne javanica*) in *Cucumis sativus* var. *hardwickii*. *J. Hered.* **1997**, *88*, 66–69, doi:10.1093/oxfordjournals.jhered.a023060.

101. Talavera, M.; De Luque, A.P.; López-Gómez, M.; Verdejo-Lucas, S. Differential feeding site development and reproductive fitness of *Meloidogyne incognita* and *M. javanica* on zucchini, a source of resistance to *M. incognita*. *Nematology* **2018**, *20*, 187–199, doi:10.1163/15685411-00003135.

102. Ayala, A. Evaluación de la tolerancia a *Fusarium solani* f. sp. *cucurbitae* y *Phytophthora capsici* en variedades comerciales y conservadas del género *Cucurbita*. In *Libro de Actas del II Congreso de Jóvenes Investigadores de Ciencias Agroalimentarias*; 2019.
103. Ye, D.Y.; Qian, C.T.; Kurowski, C. Identification of a novel source of resistance to the root-knot nematode *Meloidogyne incognita* in *Cucumis*. Russ. J. Nematol. 2012, 20, 45–51.

104. Thies, J.A.; Ariss, J.J.; Hassell, R.L.; Buckner, S.; Levi, A. Accessions of *Citrullus lanatus* var. *citróides* are valuable rootstocks for grafted watermelon in fields infested with Root-knot nematodes. *HortScience* 2015, 50, 4–8. doi:10.21273/hortsici.50.1.4.

105. Expósito, A.; Munera, M.; Giné, A.; López-Gómez, M.; Cáceres, A.; Picó, B.; Gesbert, C.; Medina, V.; Sorribas, F.J. *Cucumis metuliferus* is resistant to root-knot nematode *Mi1.2* gene (a)virulent isolates and a promising melon rootstock. *Plant Pathol.* 2018, 67, 1161–1167, doi:10.1111/ppa.12815.

106. Faske, T.R. Penetration, post-penetration development, and reproduction of *Meloidogyne incognita* on *Cucumis melo* var. *texanus*. *J. Nematol.* 2013, 45, 58–65.

107. Cardin, M.C. Influence of temperature on the relationships of *Meloidogyne hapla* with cucumber roots. *Rev. Nematología* 1979, 2, 169–175.

108. Wehner, T.C.; Walters, S.A.; Barker, K.R. Resistance to Root-knot nematodes in cucumber and horned cucumber. *J. Nematol.* 1991, 23, 611–614.

109. Miller, J.G.; Faske, T.R. Post-penetration response of *Meloidogyne incognita* on *Cucurbita foetidissima* (Buffalo gourd). *Nematropica* 2015, 45, 178–183.

110. Chavez, D.J.; Kabelka, E.A.; Chaparro, J.X. Screening of *Cucurbita moschata* Duchesne Germlasm for crown rot resistance to Floridian isolates of *Phytophthora capsici* Leonian. *HortScience* 2011, 46, 536–540, doi:10.21273/hortsici.46.4.536.

111. Crosby, K.M. Screening *Cucumis melo* L. *agrestis* germplasm for resistance to *Monosporascus cannonballus*. *Subtrop. Plant Sci.* 2001, 53, 24–26.

112. Herman, R.; Perl-Treves, R. Characterization and inheritance of a new source of resistance to *Fusarium oxysporum* f. sp. *melonis* Race 1.2 in *Cucumis melo*. *Plant Dis.* 2007, 91, 1180–1186, doi:10.1094/pdis-91-9-1180.

113. Jo, E.J.; Lee, J.H.; Choi, Y.H.; Kim, J.-C.; Choi, G.J. Development of an efficient method of screening for watermelon plants resistant to *Fusarium oxysporum* f. sp. *niveum*. *Korean J. Hortic. Sci. Technol.* 2015, 33, 409–419, doi:10.7235/hort.2015.14156.

114. Kabelka, E.; Padley, L.; Roberts, P.; Ramos, L.; Martinez, M.; Klassen, W. Resistance to *Phytophthora capsici* within winter squash (*Cucurbita moschata*) derived from a wild *Cucurbita* species. *Proc. Am. Soc. Hortic. Sci.* 2007, 124, 1014.

115. El-Wanis, A.B.D.; Mona, M.; Amin, A.W.; Abdel Rahman, T.G. Evaluation of some cucurbitaceous rootstocks 2-effect of cucumber grafting using some rootstock plants on growth, yield and its relation with root-knot nematode *Meloidogyne incognita* and Fusarium wilt, infection. *Egypt. J. Agric. Res.* 2013, 91, 235–257.

116. Portagrano. Vademécum de Semillas. Available online: http://www.portagrano.net/home/ (accessed on 30 September 2020).

117. Dias, R.D.C.S.; Pico, B.; Espinos, A.; Nuez, F. Resistance to melon vine decline derived from *Cucumis melo* ssp. *agrestis*: Genetic analysis of root structure and root response. *Plant Breed.* 2004, 123, 66–72, doi:10.1046/j.1439-0329.2003.00944.x.

118. Fita, A.; Picó, B.; Dias, R.C.; Nuez, F. ‘Piel de Safo’ Breeding lines tolerant to melon vine decline. *HortScience* 2009, 44, 1458–1460, doi:10.21273/hortsici.44.5.1458.

119. Sousaraei, N.; Ramshini, H.; Lotfi, M.; Sharzei, A. Marker assisted backcrossing for introgression of Fusarium wilt resistance gene into melon. *Euphytica* 2017, 214, 7, doi:10.1007/s10681-017-2080-4.

120. Kantoglu, Y.; Seçer, E.; Tutluer, I.; Kunter, B.; Peskircioglu, H.; Sagel, Z.; Erzurum, K. Improving tolerance to *Fusarium oxysporum* f. sp. *melonis* in melon using tissue culture and mutation techniques. In *Mass Screening Techniques for Selecting Crops Resistant to Disease*; IAEA: Vienna, Austria, 2010; pp. 235–244.

121. Zhang, M.; Yu, T.; Yang, J.; Mao, B.; He, Z. Transformation of glucanase and chitinase genes to watermelon mediated by *Agrobacterium tumefaciens*. J. Fruit Sci. 2006, 3.

122. Zhang, M.; Liu, Q.; Yang, X.; Xu, J.; Liu, G.; Yao, X.; Ren, R.; Xu, J.; Lou, L. CRISPR/Cas9-mediated mutagenesis of Colsk1 in watermelon to confer resistance to *Fusarium oxysporum* f. sp. *niveum*. *Plant Cell Rep.* 2020, 39, 589–595, doi:10.1007/s00299-020-02516-0.

123. Oumouloud, A.; Arnedo-Andres, M.S.; Gonzalez-Torres, R.; Alvarez, J.M. Development of molecular markers linked to the *Fom-1* locus for resistance to Fusarium race 2 in melon. *Euphytica* 2008, 164, 347–356, doi:10.1007/s10681-008-9664-y.
Cucumis melo – Cucumis melo

124. Brotman, Y.; Kovalski, I.; Dogimont, C.; Pitrat, M.; Portnoy, V.; Katzir, N.; Perl-Treves, R. Molecular markers linked to papaya ring spot virus resistance and Fusarium race 2 resistance in melon. *Theor. Appl. Genet.* **2004**, *110*, 337–345, doi:10.1007/s00122-004-1845-z.

125. Devran, Z.; Firat, A.F.; Tör, M.; Mutlu, N.; Elekşioglu, I.H. AFLP and SSRP markers linked to the *mg* gene for root-knot nematode resistance in cucumber. *Sci. Agricul.**2011*, *68*, 115–119, doi:10.1590/s0103-90162011000100017.

126. Tezuka, T.; Waki, K.; Yashiro, K.; Kuzuyu, M.; Ishikawa, T.; Takatsu, Y.; Miyagi, M. Construction of a linkage map and identification of DNA markers linked to Fom-1, a gene conferring resistance to *Fusarium oxysporum* f. sp. *melonis* race 2 in melon. *Euphytica* **2009**, *168*, 177–188, doi:10.1007/s10681-009-9881-z.

127. Baudracco-Arnas, S.; Pitrat, M. A genetic map of melon (*Cucumis melo L.*) with RFLP, RAPD, isozyme, disease resistance and morphological markers. *Theor. Appl. Genet.* **1996**, *93*, 57–64, doi:10.1007/bf0225727.

128. Zheng, X.; Wolff, D.W. Randomly Amplified Polymorphic DNA Markers linked to Fusarium wilt resistance in diverse melons. *HortScience* **2000**, *35*, 716–721, doi:10.21273/hortsici.35.4.716.

129. Zheng, X.; Wolff, D.W.; Baudracco-Arnas, S.; Pitrat, M. Development and utility of cleaved amplified polymorphic sequences (CAPS) and restriction fragment length polymorphisms (RFLPs) linked to the Fom-2 fusarium wilt resistance gene in melon (*Cucumis melo L.*) in China. *Theor. Appl. Genet.* **1999**, *99*, 453–463, doi:10.1007/s001220051257.

130. Wang, Y.-H.; Thomas, C.E.; Dean, R.A. Genetic mapping of a Fusarium wilt resistance gene (Fom-2) in melon (*Cucumis melo L.*). *Mol. Breed.* **2000**, *6*, 379–389, doi:10.1023/a:1009671925793.

131. Burger, Y.; Katzir, N.; Tzuri, G.; Portnoy, V.; Saar, U.; Shriber, S.; Perl-Treves, R.; Cohen, R. Variation in the response of melon genotypes to *Fusarium oxysporum* f. sp. *melonis* race 1 determined by inoculation tests and molecular markers. *Plant Pathol.* **2003**, *52*, 204–211, doi:10.1046/j.1365-3059.2003.00806.x.

132. Yong, X.; Xin-Xing, O.; Hai-Ying, Z.; Guo-Bin, K.; Yong-Jian, W.; Hang, C. Identification of a RAPD marker linked to Fusarium wilt resistant gene in wild watermelon germplasm (*Citrullus lanatus* var. *citroides*). *J. Integr. Plant Biol.* **1999**, *41*.

133. Esteras, C.; Gómez, P.; Monforte, A.J.; Blanca, J.; Vicente-Dolera, N.; Roig, C.; Nuez, F.; Picó, B. High-throughput SNP genotyping in *Cucurbita pepo* for map construction and quantitative trait loci mapping. *BMC Genom.* **2012**, *13*, 80, doi:10.1186/1471-2164-13-80.

134. Branham, S.E.; Levi, A.; Farnham, M.W.; Wechter, W.P. A GBS-SNP-based linkage map and quantitative trait loci (QTL) associated with resistance to *Fusarium oxysporum* f. sp. *niveum* race 2 identified in *Citrullus lanatus* var. *citroides*. *Theor. Appl. Genet.* **2016**, *130*, 319–330, doi:10.1007/s00122-016-2813-0.

135. Meru, G.; McGregor, C. Genotyping by sequencing by SNP discovery and genetic mapping of resistance to race 1 of *Fusarium oxysporum* in watermelon. *Sci. Hortic.* **2016**, *209*, 31–40, doi:10.1016/j.scienta.2016.06.005.

136. Dong, J.; Xu, J.; Xu, X.; Xu, Q.; Chen, X.-H. Inheritance and quantitative trait locus mapping of Fusarium wilt resistance in cucumber. *Front. Plant Sci.* **2019**, *10*, 10, doi:10.3389/fpls.2019.01425.

137. Brotman, Y.; Normantovich, M.; Goldenberg, Z.; Zvirin, Z.; Kovalski, I.; Stovbun, N.; Doniger, T.; Bolger, M.E.; Troadeac, C.; Bendahmane, A.; et al. Dual resistance of melon to *Fusarium oxysporum* races 0 and 2 and to papaya ring-spot virus is controlled by a pair of head-to-head-oriented NB-LRR genes of unusual architecture. *Mol. Plant Genet.* **2013**, *6*, 235–238, doi:10.1093/mp/sss121.

138. Morata, J.; Puigdomènech, P. Variability among Cucurbitaceae species (melon, cucumber and watermelon) in a genomic region containing a cluster of NBS-LRR genes. *BMC Genom.* **2017**, *18*, 1–7, doi:10.1186/s12864-017-3529-5.

139. García-Mas, J.; Benjak, A.; Sanseverino, W.; Bourgeois, M.; Mir, G.; González, V.M.; Hénaff, E.; Câmara, F.; Cozzuto, L.; Lowy, E.; et al. The genome of melon (*Cucumis melo L.*) (*Proc. Natl. Acad. Sci. USA* **2012**, *109*, 11872–11877, doi:10.1073/pnas.1205415109).

140. Guo, S.; Zhang, J.; Sun, H.; Salse, J.; Lucas, W.J.; Zhang, H.; Zheng, Y.; Mao, L.; Ren, Y.; Wang, Z.; et al. The draft genome of watermelon (*Citrullus lanatus*) and resequencing of 20 diverse accessions. *Nat. Genet.* **2012**, *45*, 51–58, doi:10.1038/ng.2470.

141. Joobeur, T.; King, J.J.; Nolin, S.J.; Thomas, C.E.; Dean, R.A. The fusarium wilt resistance locus *Fom-2* of melon contains a single resistance gene with complex features. *Plant J.* **2004**, *39*, 283–297, doi:10.1111/j.1365-313x.2004.02134.x.

142. Roig, C.; Fita, A.; Rios, G.; Hammond, J.P.; Nuez, F.; Picó, B. Root transcriptional responses of two melon genotypes with contrasting resistance to *Monosporascus cannonballus* (Pollack et Uecker) infection. *BMC Genom.* **2012**, *13*, 601, doi:10.1186/1471-2164-13-601.
Xu, X.; Wang, R.; Chao, J.; Lin, Y.; Jin, Q.; He, X.; Luo, S.; Wu, T. The expression patterns of Cucumis sativus WRKY (CsWRKY) family under the condition of inoculation with Phytophthora melonis in disease resistant and susceptible cucumber cultivars. *Can. J. Plant Sci.* 2015, 95, 1121–1131, doi:10.4141/cjps-2014-403.

Zhang, D.; Meng, K.X.; Hao, Y.H.; Fan, H.Y.; Cui, N.; Wang, S.S.; Song, T.F. Comparative proteomic analysis of cucumber roots infected by Fusarium oxysporum f. sp. cucumerium Owen. *Physiol. Mol. Plant Pathol.* 2016, 96, 77–84, doi:10.1016/j.pmpp.2016.09.002.

Robb, J.; Castroverde, C.D.M.; Nazar, R.N. *Defense Genes in Tomato*; Nova Science Publishers: Hauppauge, NY, USA, 2010; ISBN 9781616688875.

Narusaka, M.; Kubo, Y.; Hatakeyama, K.; Imamura, J.; Ezura, H.; Nanasato, Y.; Tabei, Y.; Takano, Y.; Shirasu, K.; Narusaka, Y. Interfamily transfer of dual NB-LRR genes confers resistance to multiple Pathogens. *PLoS ONE* 2013, 8, e55954, doi:10.1371/journal.pone.0055954.

Ye, D.; Jiang, Y.; Wang, C.; Roberts, P.A. Expression analysis of microRNAs and their target genes in Cucumis melo L. infected by the root-knot nematode Meloidogyne incognita. *Physiol. Mol. Plant Pathol.* 2020, 111, 101491, doi:10.1016/j.pmpp.2020.101491.

Pathirana, R. Plant mutation breeding in agriculture. *CAB Rev. Perspect. Agric. Veter. Sci. Nutr. Nat. Resour.* 2011, 6, 6, doi:10.1079/pavsnr20116032.

Niu, X.; Zhao, X.; Ling, K.-S.; Levi, A.; Sun, Y.; Fan, M. The ForSil6 gene acts as an avirulence effector in the Fusarium oxysporum f. sp. niveum-watermelon pathosystem. *Sci. Rep.* 2016, 6, 28146, doi:10.1038/srep28146.

Nieto, C.; Piron, F.; Dalmais, M.; Marco, C.F.; Moriones, E.; Gómez-Guillamón, M.L.; Truniger, V.; Gómez, P.; García-Mas, J.; Aranda, M.; et al. EcoTILLING for the identification of allelic variants of melon elF4E, a factor that controls virus susceptibility. *BMC Plant Biol.* 2007, 7, 34, doi:10.1186/1471-2229-7-34.

Vicente-Dólara, N.; Troadec, C.; Moya, M.; Del Río-Celestino, M.; Pomares-Viciana, T.; Bendahmañe, A.; Picó, B.; Román, B.; Gómez, P. First TILLING Platform in Cucurbita pepo: A new mutant resource for gene function and crop improvement. *PLoS ONE* 2014, 9, e112743, doi:10.1371/journal.pone.0112743.

Fraenkel, R.; Kovalski, I.; Troadec, C.; Bendahmañe, A.; Perl-Trevés, R. Development and evaluation of a cucumber TILLING population. *BMC Res. Notes* 2014, 7, 846, doi:10.1186/1756-0500-7-846.

Gonzalez, M.; Xu, M.; Esteras, C.; Roig, C.; Monforte, A.J.; Troadeç, C.; Pujol, M.; Nuez, F.; Bendahmañe, A.; García-Mas, J.; et al. Towards a TILLING platform for functional genomics in Piel de Sapo melons. *BMC Res. Notes* 2011, 4, 289, doi:10.1186/1756-0500-4-289.

Schmidt, S.M.; Lukasiewicz, J.; Farrer, R.A.; Van Dam, P.; Bertoldo, C.; Rep, M. Comparative genomics of Fusarium oxysporum f. sp. melonis reveals the secreted protein recognized by the Font-2 resistance gene in melon. *New Phytol.* 2015, 209, 307–18, doi:10.1111/nph.13584.

Chandrasekaran, J.; Brumin, M.; Wolf, D.; Leibman, D.; Klap, C.; Pearlsman, M.; Sherman, A.; Arazil, T.; Gal-On, A. Development of broad virus resistance in non-transgenic cucumber using CRISPR/Cas9 technology. *Mol. Plant Pathol.* 2016, 17, 1140–1153, doi:10.1111/mpp.12375.

Ali, Z.; Zaidi, S.S.-E.-A.; Tashkandi, M.; Mahfouz, M.M. A Simplified Method to Engineer CRISPR/Cas9-Mediated Geminivirus Resistance in Plants. In *Advanced Structural Safety Studies*; Springer Science and Business Media LLC: Berlin, Germany, 2019; Volume 2028, pp. 167–183.

Giné, A.; López-Gómez, M.; Vela, M.D.; Ornat, C.; Talavera, M.; Verdejo-Lucas, S.; Sorribas, F.J. Thermal requirements and population dynamics of root-knot nematodes on cucumber and yield losses under protected cultivation. *Plant Pathol.* 2014, 63, 1446–1453, doi:10.1111/ppa.12217.

Rostami, F.; Alaee, H.; Reza, H.K.; Abad, A.B. Controlling the root and stem rot of cucumber, caused by Phytophthora aphanidermatum, using resistance cultivars and grafting onto the cucurbit rootstocks. *Azarian J. Agric.* 2015, 2, 19–24.

Yamaguchi, T.; Iwadate, Y. Adaptability of several cucurbit plants for use as rootstocks to prevent cucumber black root rot caused by Phytophthora slerotioides. *Annu. Rep. Soc. Plant Prot. North Japan* 2009, 2009, 96–101, doi:10.11455/kitanohon.2009.60_96.

Pavlou, G.C.; Vakalounakis, D.J.; Ligoxigakis, E.K. Control of root and stem rot of cucumber, caused by Fusarium oxysporum f. sp. radicis-cucumerinum, by grafting onto resistant rootstocks. *Plant Dis.* 2002, 86, 379–382; doi:10.1094/pdis.2002.86.4.379.

Amin, A.W.; El-Wanis, A. Protecting cucumber against root-knot nematode, Meloidogyne incognita using grafting onto resistant cucurbit rootstocks and interplanted Tagetes spp. as an alternative to Cadusafos nematicide under protected plasticulture conditions. *Middle East J. Agric. Res.* 2014, 3, 167–175.
162. Ban, S.G.; Žanić, K.; Dumnicic, G.; Raspudic, E.; Selak, G.V.; Ban, D. Growth and yield of grafted cucumbers in soil infested with root-knot nematodes. *Chil. J. Agric. Res.* 2014, 74, 29–34, doi:10.4067/s0718-58392014000100005.

163. Kokalis-Burelle, N.; Butler, D.M.; Hong, J.C.; Bausher, M.G.; McCollum, G.; Rosskopf, E.N. Grafting and Paladin Pic-21 for nemate and weed management in vegetable production. *J. Nematol.* 2016, 48, 231–240, doi:10.21307/jofnem-2017-031.

164. Thies, J.A.; Levi, A.; Ariss, J.J.; Hassell, R.L. RKVL-318, a Root-knot nematode-resistant watermelon line as rootstock for grafted watermelon. *HortScience* 2015, 50, 141–142, doi:10.21273/hortsci.50.1.141.

165. Giné, A.; González, C.; Serrano, L.; Sorribas, F.J. Population dynamics of *Meloidogyne incognita* on cucumber grafted onto the *Cucurbita* hybrid RS841 or ungrafted and yield losses under protected cultivation. *Eur. J. Plant Pathol.* 2017, 148, 795–805, doi:10.1007/s10658-016-1135-z.

166. Sigüenza, C.; Schochow, M.; Turini, T.; Ploeg, A. Use of *Cucumis metuliferus* as a rootstock for melon to manage *Meloidogyne incognita*. *J. Nematol.* 2005, 37, 276–280.

167. Guan, W.; Zhao, X.; Dickson, D.W.; Mendes, M.L.; Thies, J. Root-knot nematode resistance, yield, and fruit quality of specialty melons grafted onto *Cucumis metuliferus*. *HortScience* 2014, 49, 1046–1051, doi:10.21273/hortsci.49.8.1046.

168. Nisini, P.T.; Colla, G.; Granati, E.; Temperini, O.; Crinò, P.; Saccardo, F. Rootstock resistance to Fusarium wilt and effect on fruit yield and quality of two muskmelon cultivars. *Sci. Hortic.* 2002, 93, 281–288, doi:10.1016/s0304-4238(01)00335-1.

169. Crinò, P.; Bianco, C.L.; Rouphael, Y.; Colla, G.; Saccardo, F.; Paratore, A. Evaluation of rootstock resistance to Fusarium wilt and gummy stem blight and effect on yield and quality of a grafted ‘Inodorus’ Melon. *HortScience* 2007, 42, 521–525, doi:10.21273/hortsci.42.3.521.

170. Castro, G.; Perpiñá, G.; Esteras, C.; Armengol, J.; Picó, B.; Pérez-De-Castro, A. Resistance in melon to *Monosporascus cannonballus* and *M. eutypoides* : Fungal pathogens associated with Monosporascus root rot and vine decline. *Ann. Appl. Biol.* 2020, 177, 101–111, doi:10.1111/aab.12590.

171. Kim, D.; Ferris, H. Relationship between crop losses and initial population densities of *Meloidogyne arenaria* in Winter-Grown Oriental Melon in Korea. *J. Nematol.* 2002, 34, 43–49.

172. Vela, M.D.; Giné, A.; Lópe-Gómez, M.; Sorribas, F.J.; Ornat, C.; Verdejo-Lucas, S.; Talavera, M. Thermal time requirements of root-knot nematodes on zucchini-squash and population dynamics with associated yield losses on spring and autumn cropping cycles. *Eur. J. Plant Pathol.* 2014, 140, 481–490, doi:10.1007/s10658-014-0482-x.

173. Yetişir, H.; Sari, N.; Yücel, S. Rootstock resistance to Fusarium wilt and effect on watermelon fruit yield and quality. *Phytoparasit.* 2003, 31, 163–169, doi:10.1007/bf02980786.

174. Miguel, A.; Maroto, J.; Bautista, A.S.; Baixauli, C.; Cebolla, V.; Pascual, B.; Lopez, S.; Guardiola, J. The grafting of triploid watermelon is an advantageous alternative to soil fumigation by methyl bromide for control of Fusarium wilt. *Sci. Hortic.* 2004, 103, 9–17, doi:10.1016/j.scienta.2004.04.007.

175. Kousik, C.S.; Donahoo, R.S.; Hassell, R. Resistance in watermelon rootstocks to crown rot caused by *Pythophthora capsici*. *Crop Prot.* 2012, 39, 18–25, doi:10.1016/j.cropro.2012.04.004.

176. Armengol, J.; José, C.M.; Moya, M.J.; Sales, R.; Vicent, A.; García-Jiménez, J. *Fusarium solani* f. sp. *cucurbitae* race 1, a potential pathogen of grafted watermelon production in Spain. *EPPO Bull.* 2000, 30, 179–183, doi:10.1111/j.1365-2338.2000.tb00875.x.

177. Keinath, A.P.; Wechter, W.P.; Rutter, W.B.; Agudelo, P.A. Cucurbit rootstocks resistant to *Fusarium oxysporum* f. sp. *niveum* remain resistant when coinfected by *Meloidogyne incognita* in the field. *Plant Dis.* 2019, 103, 1383–1390, doi:10.1094/pdis-10-18-1869-re.

178. Wechter, W.P.; Kousik, C.; McMillan, M.; Levi, A. Identification of resistance to *Fusarium oxysporum* f. sp. *niveum* race 2 in *Citrullus lanatus* var. citroides plant introductions. *HortScience* 2012, 47, 334–338, doi:10.21273/hortsci.47.3.334.

179. García-Mendivil, H.A.; Munera, M.; Giné, A.; Escudero, N.; Picó, M.B.; Gisbert, C.; Sorribas, F.J. Response of two *Citrullus ananas* accessions to isolates of three species of *Meloidogyne* and their graft compatibility with watermelon. *Crop Prot.* 2019, 119, 208–213, doi:10.1016/j.cropro.2019.02.005.

180. Álvarez-Hernández, J.C.; Castellanos-Ramos, J.Z.; Aguirre-Mancilla, C.L.; Huitrón-Ramírez, M.V.; Camacho-Ferre, F. Influence of rootstocks on Fusarium wilt, nematode infestation, yield and fruit quality in watermelon production. *Ciência Agrotecnológica* 2015, 39, 323–330, doi:10.1590/s1413-70542015000400002.
181. García-López, F.A.; González-Eguiarte, D.R.; Rodríguez-Macias, R.; Zarazúa-Villaseñor, P.; Huitrón-Ramírez, M.V. Watermelon production with rootstocks in soils infested with the necrotic melon spot virus. *Rev. Mex. Ciencias Agrícolas* 2018, 9, 577–587.

182. Huitrón, M.; Rodríguez, N.; Diaz, M.; Camacho, F. Effect of different rootstocks on the production and quality of watermelon cv. reina de corazones. *Acta Hortic.* 2008, 797, 437–442, doi:10.17660/actahortic.2008.797.63.

183. Pofu, K.M.; Mashela, P.W.; Mphosi, M.S. Management of *Meloidogyne incognita* in nematode-susceptible watermelon cultivars using nematode-resistant *Cucumis africanus* and *Cucumis myriocarpus* rootstocks. *Afr. J. Biotechnol.* 2011, 10, 8790–8793, doi:10.5897/ajb10.1252.

184. Pofu, K.; Mashela, P.; de Waele, D. Survival, flowering and productivity of watermelon (*Citrullus lanatus*) cultivar in inter-generic grafting on nematode resistant *Cucumis* seedling rootstock in *Meloidogyne*-infested field. *Int. J. Agric. Biol.* 2012, 14, 1421–1222.

185. Mashela, P.W.; Shimelis, H.A.; Mudau, F.N. Comparison of the efficacy of ground wild cucumber fruits, Aldicarb and Fenamiphos on suppression of *Meloidogyne incognita* in tomato. *J. Phytopathol.* 2008, 156, 264–267, doi:10.1111/j.1439-0434.2007.01353.x.

186. Matsumoto, Y.; Ogawara, T.; Miyagi, M.; Watanabe, N.; Kuboyama, T. Response of wild *Cucumis* species to inoculation with *Fusarium oxysporum* f. sp. *melonis* Race 1,2y. *J. Jpn. Soc. Hortic. Sci.* 2011, 80, 414–419, doi:10.2503/jjshs1.80.414.

187. Pofu, K.; Mashela, P.; Oelofse, D. Nematode resistance in bitter gourd to *Meloidogyne incognita*. *Acta Agric. Scand. Sect. B Plant Soil Sci.* 2014, 65, 1–5, doi:10.1080/09064710.2014.955876.

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