Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 16 April 2021 doi:10.20944/preprints202104.0444.v1

Breeding for Root-Knot Nematode Resistance in Eggplant: Progress and Prospects

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Abstract

Eggplant is a functional food owing to its anti-diabetic, anti-inflammatory, and cardio-protective properties. Root-knot nematodes (RKN) are a threat to the successful production of eggplant. RKN infestation manifests as root damage, stunted development, and structural deformations of the plant. RKN infestation can be managed using a variety of management techniques like soil amendments and chemical treatments. Breeding for nematode tolerance is critical for high yields and stable results. As a result, breeding approaches are the most efficient and cost-effective nematode management methods. Furthermore, with advances in breeding technology and genomics assistance, it is becoming more feasible and straightforward. As a result, we've compiled a list of the most recent breeding developments for *Meloidogyne spp*. resistance in eggplant. We hope this information will serve as an important resource for the eggplant breeders.

Keywords: Eggplant; Galls; Meloidogyne; Root-knot; Nematodes

Introduction

Eggplants are known to be abundant in minerals (Mg, P, Cu, K, Mn, Zn, Fe), vitamins (Vit. C, K, B6, B3, B1), dietary fiber, protein, anti-oxidants, and some phytochemicals with scavenging activities (Butnariu and Butu, 2015; Li, 2008), which render them highly beneficial for human health due to their anti-diabetic, anti-obesity, anti-inflammatory, anticarcinogenic and cardio-protective properties (Naeem and Ugur, 2019). However, various pathogens such as fungi, bacteria, viruses, and nematodes have become a major concern since they invade the eggplant, and subsequently cause significant yield losses. One among them, root-knot nematodes (RKN), recognized as significant crop pests worldwide, are obligate pathogens of plant roots' vascular tissues in eggplant (Caillaud et al., 2008). The most common signs of RKN infestation include root lesions, reduced plant development, and severe deformations (Castagnone-Sereno et al., 2013; Ibrahim et al., 2019). The contaminated plant has a smaller root system with fewer feeder roots which suggests that nematode infection is associated with extensive galling and root injury (Collange et al., 2011; Molinari, 2011). Despite these facts, RKN can be controlled using a wide range of management methods, which include resistant crops, solarization, seed rotation, chemical and biological regulation (Ibrahim et al., 2019). Out of these, biological management is recognized as a long-term approach that is environmentally sustainable and significantly efficient (Abd-Elgawad, 2016; Abd-Elgawad and Askary, 2020). This approach prevents the pests from acquiring tolerance. Keeping this in view, several microbial pathogens have been formulated into nematode-fighting agents.

The RKN *Meloidogyne spp*., infestation in eggplant leads to stunting and chlorosis, along with decreased water intake and nutrient transfer in contaminated plants (Di Vito et al., 1986; Kirwa, 2020; Robab, 2011). *Meloidogyne spp*., are among the most harmful plant nematodes in the world (Ralmi et al., 2016; López Gómez, 2015; Onkendi, 2012). In places where temperate RKN species predominate, increasing global warming may favor the expansion and proliferation of tropical RKN species also (García Mendívil, 2019; Phani et al., 2021). This reality highlights the importance of concentrating research efforts on developing and controlling tropical RKN species. The primary technique of controlling this nematode species is to use synthetic nematicides but the overuse of these agrochemicals has been found to be associated with increased risks to human health, animals, trees, and beneficial soil fauna (Dhananjayan et al., 2020; Stirling, 2014) and this necessitates the conception of reliable, secure, and low-cost alternative management strategies.

Isozymes, the morphology of selected characters, biochemical processes, and host differential tests are some of the most popular methods for identifying RKN (Blok and Powers, 2009; Carneiro et al., 2017). RKN identification and differentiation with malate dehydrogenase (MDH) is found to be very efficient (Archidona-Yuste et al., 2018; Santos, 2018). Furthermore, mitochondrial haplotypes, used to classify certain *Meloidogyne*, are tropical organisms fully compatible with EST research (Janssen et al., 2016; Khanal, 2014). Morphological identification of *Meloidogyne spp*., to some extent, is time-consuming and complex. Despite this fact, female perineal patterns are one of the most widely used methods for morphological identification of RKNs (Adam et al., 2007). However, for closely associated *Meloidogyne spp*., the procedure may be inconclusive since populations from the same group may differ significantly. To obtain high yields and maintain stable performance, breeding for nematode resistance is vital. Therefore, the most effective and most economical methods for controlling nematodes are genetic means. Moreover, with advancements in breeding technology and aid from genomics, it is getting more straightforward and feasible (Kaushik, 2020, 2019; Kaushik et al., 2020; Matsuo et al., 2012; Saini and Kaushik, 2019; Sinha et al., 2019). However, as shown by a review of the literature, most of the research has been focused on tomato and pepper. Therefore, here we have compiled the updates on the advancements in breeding for *Meloidogyne spp.* resistance in eggplant

Life cycle of nematode species affecting eggplant

RKNs require a suitable host plant to complete their life cycle. In general, nematodes emerge from the nests as second-stage juveniles (J2) (Hunt et al., 2005). After hatching, the infective J2 enters the root and invades the elongation zone, lateral roots, and surrounding areas of the pre-infected tissues (Ravichandra, 2014). To establish a feeding position inside the roots, J2 migrates through the intercellular space to the vascular cylinder (Palomares-Rius et al., 2017). Finally, J2 begins maturation by shedding the third and fourth molts (Wang'ombe, 2019) and, once established, maturing into adult females or males. Males abandon the root, while sedentary females prefer to feed on it (Ralmi et al., 2016). The galling of tissues in contaminated root systems along with the annihilation of the plant development system, defense mechanism, and metabolism are caused by the accretion of giant cells (Ralmi et al., 2016). Adolescents that have been contaminated become sedentary (Nguyen, 2016) and develop a "sausage" look as their size increases. J2 then molts three times to reach adulthood (Figure 1). *M. arenaria, M. incognita*, and *M. javanica*, all tropical insects, reproduce parthenogenetically (Castagnone-Sereno, 2006; Koutsovoulos et al.,

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2019). The sedentary adult female, have a pear-shaped body with a gelatinous matrix added to the rear end (Nguyen, 2016), tends to feed from the giant cells and lay up to 300-500 eggs in the gelatinous mass. However, juveniles become males under undesirable conditions such as high nematode intensity, food scarcity, or stressed plants.

Meloidogyne spp. is, basically, a poikilothermic organism whose life cycle and length are influenced by its environment (Trudgill et al., 2005). Nematode development generally takes place between 10 and 32˚C (Dávila-Negrón and Dickson, 2013). *Meloidogyne spp*., for example, has been shown to take 600 to 700 cumulative degree-days at a base temperature of 10 °C to complete its tomato life cycle (Giné Blasco, 2016; Maleita, 2011), for example, optimum temperatures of 25-30˚C and 32-34˚C were observed in Australian *M. javanica* (Hallmann and Meressa, 2018). Moreover, in the absence of a host, temperature affects nematode survival: the optimum temperature for egg and juvenile survival is between 5 and 10˚C (Wang and McSorley, 2008).

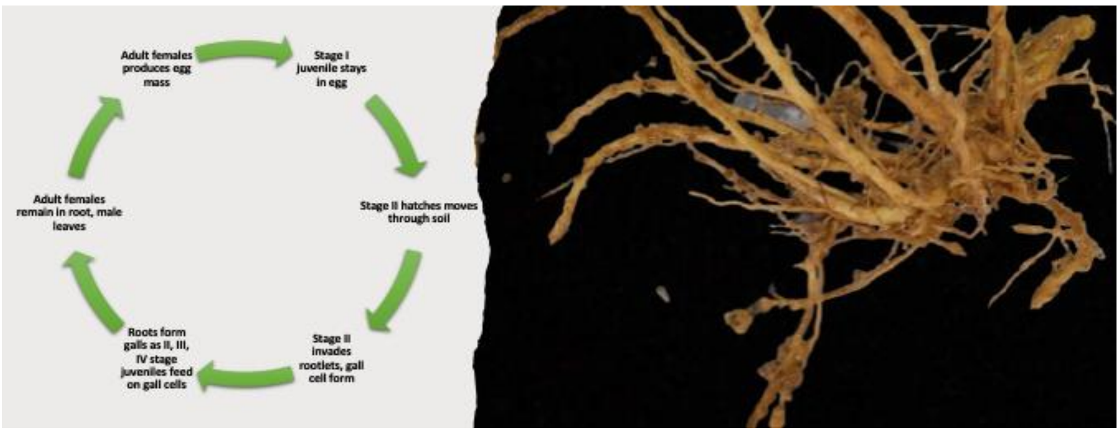

Figure 1. Stages in the life cycle of *Meloidogyne spp.* and galls formed on the roots.

In recent years, the intensive agriculture adopted to feed a growing population with inadequate land resources has increased the soil-borne diseases and pests tremendously. According to a conservative estimation, RKNs could result in a 16.67 percent reduction in eggplant yield in India, resulting in a monetary loss of approximately $23 million per year. It has been reported that RKN has a major impact on two of the world's most widely cultivated crop families: *cucurbit* and *solanaceous* crops (García Mendívil, 2019; López-Gómez and Verdejo-Lucas, 2014). Being one of the most harmful soil-borne pathogens for *solanaceous* crops, RKN causes maximum yield losses in pepper, eggplant, and tomato (Khan et al., 2021). The involvement of RKNs in crop damage may go undetected (e.g., Fusarium spp.) (Mai and Abawi, 1987; San-Blas et al., 2020, p.). Root galling prevents the plant from absorbing nutrients and water, causing leaf chlorosis, stunting, and wilting (Bernard et al., 2017), particularly, in hot climates. Moreover, infection with the RKN renders plants more vulnerable to other diseases also and stunts their growth and yield (Abd-Elgawad, 2021; Khan, 2015). Extreme attacks may cause plants to die. Furthermore, nematode-induced water stress influences tomato fruit quality (Atkinson et al., 2011).

Impact, Yield Loss and Feeding Habit

As nematode secretions invade a plant cell, they get associated with cytoplasmic receptors, causing a sequence of proteomic modifications in the infected cell (Escobar et al., 2011). The appearance of numerous organelles, ribosomes, and mitochondria in transformed cells indicates that they are metabolically active. Further, the cell wall's different invaginations tend to increase the touching area between the cell and the rest of the vascular tissues, leading to the increased nutritional flux to the giant cell (Johansson, 2015) (Figure 1) . To estimate the damage caused by nematode infection, Zeck index assigns a score of 0 to 10 to root system harm, with 0 indicating a completely healthy root system (no galls) and 10 indicating plant and root death (Giné et al., 2016). Parasitism affects the morphology and productivity of roots adversely by disturbing the vascular structure, resulting in reduced water intake and nutrient transfer and, finally, photosynthesis inhibition. As a consequence, the infected eggplants develop nutrient deficiency symptoms such as leaf yellowing/chlorosis, poor response to appropriate soil moisture, and premature wilting (Abd-Elgawad, 2021; Khan, 2015). Galls on roots (root-knot), necrosis of roots (root-lesion), or a subtle stubby-appearance are all major consequences of RKN injury on eggplant. In other words, when plants are infiltrated and infected by RKNs, the intact root structure gets reduced to a small number of strikingly RKN-galled roots and the vascular system of the roots becomes extremely disorganized (Sitaramaiah and Pathak, 1993; Tordable et al., 2010). Like other PPNs, it is also characterized by stunted plants and reduced growth parameters, which ultimately leads to severe death of plant parts (Phani et al., 2021; Zvenyika, 2019). In response to nematode secretions, plants undergo many physiological and biochemical modifications to kill the pathogens. Slow responses involve the development of phytoalexins, a hypersensitive response in rapidly dying host cells, and a reduced necrosis consistent with plant resistance (Ayala-Doñas et al., 2020; Zinovieva, 2014). After the detection of a pathogen assault, reactive oxygen intermediates (ROIs) and nitric oxide (NO) are generated in a rapid reaction (Abbasi et al., 2014). Moreover, plants that have been contaminated with RKNs are found to be more vulnerable to noxious weeds.

Indeed, decline in eggplant yield and growth restrictions have been rightly attributed to nematode population density, host suitability, as well as biological and ecological factors. RKNs of the genus *Meloidogyne*, in particular, exhibit a parasitic procedure that is somewhat different from that of their entomopathogenic counterparts (Kaloshian and Teixeira, 2019; Sommer and Streit, 2011). On the other hand, plants are confined to an immune system more similar to the insect humoral system than the cellular system in dealing with this invasion since they lack the specialized cell types needed for a cellular response (Whitten and Coates, 2017). Although the specific programs that moderate RKN resistance remain unknown, progress has been made in understanding how such plants may benefit with their immune systems against nematode parasites (Kennedy and Harnett, 2013). Resistance genes (R genes), such as Mi 1.2 in tomato plants (Barbary et al., 2015; El-Sappah et al., 2019), which encrypts a member of the leucine-rich nucleotide-binding repeat gene family, and the hypersensitive response (Sato et al., 2019), which seems to be a commonly used mechanism for limiting RKN feeding capacities, appear to play a crucial role in RKN resistance (Kenney and Eleftherianos, 2016). Faize and Faize, (2018) discovered that application of the SA analog benzothiadiazole (BTH) to tomato plants exogenously reduced gall formation, which was attributed to cell-wall stiffening induced by enhanced H_2O_2 synthesis, lignin aggregation, and peroxidase activity in reaction to BTH treatment. Although increasing Meloidogyne tolerance in crop plants can be advantageous to the agricultural sector as a whole, there are still substantial gaps in our understanding of the plant immune processes that can confer this resistance (Wubben et al., 2015, 2008).

Resistance in the Cultivated and Wild Sources

Numerous abiotic and biotic stresses, especially RKNs, pose a significant threat to eggplant production. Because of wide host range for *Meloidogyne spp*., crop rotation is less efficient, and chemical nematodes have negative side effects (Abawi and Widmer, 2000; Nusbaum and Ferris, 1973). Although many wild relatives of eggplant are found to be immune to RKNs (Boiteux and Charchar, 1996), study on RKN tolerance is restricted due to the cross-incompatibility issue between wild *Solanum* species and *S. melongena*. The use of eggplant interspecific hybrids, generated by the crosses between the cultivated *S. melongena* and its wild ancestor *S. incanum* (Prohens et al., 2012), or with *S. aethiopicum L. Kumba* (Prohens et al., 2013), was proposed as a technique for increasing eggplant yield, or developing new, more robust eggplant rootstocks that could enhance its yield and ripeness without compromising produce quality. *S. incanum* and *S. aethiopicum*, both have been discovered in the same location and both the interspecific hybrids stand a good chance of success. Furthermore, tolerance and immunity to *F. oxysporum f. sp. melongena* have been found in *R. solanacearum* products (Namisy et al., 2019). *S. incanum* develops in dry climates, indicating that it exhibits drought-tolerance, which is a desired characteristic of inter-specific hybrids (Rana et al., 2012; Singh, 2017). Further, Gisbert et al. (2006) discovered that *S. melongena* and *S. aethiopicum* are amenable to in vitro culture (Gisbert et al., 2011; Plazas et al., 2016), which may be beneficial to produce the desired results. Generally, micropropagation is used to spread interspecific hybrids (Bhojwani and Dantu, 2013). The transplant has been grafted with tomato rootstocks, however, plant death, after transplanting, may be caused due to incompatibility with tomato rootstocks. This shows that, amid increased nematode resistance, *S. aethiopicum* is susceptible to nematodes (Ofori, 2015). Therefore, nematode resistance accessions after a thorough examination of the intermediated galling index (GI) values in eggplant accessions are needed for nematode resistance (Gisbert et al., 2011). The appearance of variants produced from the *S. melongena* varieties suggests that these materials are of good quality. Following this, the use of highly promising materials to develop new eggplant cultivars or rootstocks as sources of variety of nematode resistance has been accelerated.

S. aculeatissimum is another wild relative of eggplant with many attractive characteristics, such as tolerance to soil-borne diseases including *verticillium* wilt and RKNs (Bletsos and Olympios, 2008; Zhou et al., 2016). The active hybridization of *S. aculeatissimum* and *S. melongena*, allows for the use of R genes from *S. aculeatissimum*. However, the range of genetic tolerance and genetic properties are distinct. For instance, the previous Mi-1 gene discovered in tomatoes is temperature-sensitive, for the Mi-1-mediated tolerance is weakened at soil temperatures above 28°C (Sahu et al., 2012) but the Mi-1 gene provides resistance to *Macrosiphum euphorbiae* (de Ilarduya et al., 2004, p. 1). However, whether the gene SacMi is vulnerable to high temperature deserves more research (Zhou et al., 2018), it was not expressed differently in wilt-treated and control samples of *Verticillium*. Therefore, whether the SacMi gene still resists other plant pathogens requires additional study. This research aims to study the role of root-knot R genes in *S. aculeatissimum* and its potential presence in responses to *M. incognita* disease. With the growing usage of greenhouses for eggplant production, the concerns regarding RKNs are getting extremely serious (Li et al., 2020), and developing disease-resistant cultivars becomes an efficient and necessary way to combat associated diseases. Yang et al. (2014) concluded that in *S. torvum*, the whole disease tolerance phase is amplified, consequently improving plant defense mechanisms and resistance survival as compared to tomato and potato. After a certain number of R gene exposures, the same plant species' nematode resistance in susceptible cultivars can incur a

 doi:10.20944/preprints202104.0444.v1

fitness cost (García-Mendívil and Sorribas, 2019). Surprisingly, despite not being chosen for virulence, the nematode's infective and reproductive health deteriorated after two years of extended cultivation (Jung and Wyss, 1999; Stirling and Stanton, 1997). It is critical to investigate the causes of this health-loss and the long-term viability of this characteristic.

Classical Breeding Techniques to Modern Tools

Repetitive R-gene cultivation leads to the selection of virulent nematodes (Expósito et al., 2019). Further, only a few R-genes have been introgressed into commercial *solanaceous* cultivars; Me1, Me3, and N in pepper, and Mi1.2 in tomato but none have been introgressed into *cucurbits* (García Mendívil, 2019). Some approaches proposed to avoid RKN virulence selection or to reduce the degree of virulence and crop yield losses include resilient and susceptible crops in rotation (Chitambo, 2019), or the use of crops of two distinct resistant plant species, or separate R-genes in a pyramid (Djian-Caporalino et al., 2014; McDowell and Woffenden, 2003). Transgenic approaches and RNA interference (RNAi) is also used in the nematode management (Fuller et al., 2008; Gheysen and Vanholme, 2007) that can be used in conjunction with extremely dangerous, less precise chemical-based PPN management techniques. However, even though target transcripts possess a higher degree of sequence survival, an off-target impact on a large variety of rhizosphere species cannot be ruled out if the dsRNA molecule is improperly designed. In this regard, the parasite ability of *M. incognita* in adzuki bean and tomato was significantly reduced using an in vivo and in vitro RNAi approach (Chaudhary et al., 2019a, 2019b). In terms of biosafety, effectors are found to be an outstanding candidate for host-induced gene silencing (HIGS) since they neglect the substantial homology with non-PPN nematodes. Furthermore, the HIGS impact was found to be significant in T2 and T3 cases, suggesting that the progeny plants did not lose resistance (Akther, 2019). However, other PPN effector gene analyses through HIGS support the partial resistance to nematodes observed in our sample.

A combinatorial HIGS utilizing *M. incognita* serine and cysteine protease genes in tomatoes was investigated. However, the degree of nematode resistance could not be improved in that study by utilizing a dual build against a single gene cassette. Further, it has been reported that it is nearly impossible to attain total nematode resistance (Van Esse et al., 2020). In *M. incognita*, the Mi-msp-1 HIGS impact is thought to be universal, spreading across the nematode body after picking up dsRNA/siRNA molecules through the stylet orifice (Joshi et al., 2020; Somvanshi et al., 2020). Furthermore, the RNAi effect was sustained until nematode maturity, suggesting that *M. incognita* offspring with Mi-msp-1 could be formed (Nguyen, 2016). RKNs digest large biomolecules quickly through the type of orifice, allowing for one or both alternatives. HIGS is a common method for increasing plant tolerance to pests and pathogens (Ghag, 2017). Some RNAi-based genetically modified crops, such as DuPont's Plenish R high-oleic acid soybean (Mall et al., 2018) and Monsanto's SmartStax Pro to eradicate western corn earworm (Ludwick et al., 2017), have recently been approved for commercialization. HIGS also ensures that dsRNA/siRNA molecules generated by the host plants are continuously spread to biotrophic pathogens such as PPNs (Essigmann et al., 2012; Jain et al., 2018).

Advancement in the genomics can be applied to the RKN control in eggplant. In this direction, silencing Mi-msp-20, on the other side, culminated in 409 transcripts being differentially regulated in *M. incognita* J2s compared to 29 in Mi-msp-1 silenced J2s (Somvanshi et al., 2020). A fascinating discovery was that silenced Mi-msp-1 and Mi-msp-20 nematodes shared 5.9% of

the up-regulated transcripts, suggesting that there is no crosstalk between the two effectors. However, on the other hand, they did not share any of the down-regulated transcripts. Both genes have also been shown to interfere with other cell-wall degrading enzymes (CWDEs) (Haegeman et al., 2013; Jones et al., 2013). In eggplants, Mi-msp-1 HIGS decreased root galling, the number of eggs per egg mass by 36.08–41.20%, and the nematode multiplication factor by 62.37–70.62 % (Chaudhary et al., 2019a; Somvanshi et al., 2020).

Conclusions

Every year, PPNs produce considerable damage to the agriculture industry, and this issue has mostly gone unaddressed. Using the evidence, the opportunity to apply this collaboration to large-scale field conditions has emerged, theoretically alleviating one of the most important problems of the agricultural industry. Eggplant is vulnerable to exposure to RKN; if it is not protected, yield losses up to 30% are typical. Breeding technologies are determined to be advantageous by experimentation and scientific means, and they settled on implementation as the preferred method. Thanks to emerging biotechnologies, resistance breeding is becoming easier. Though recombination gives us new solutions, it also serves as a vehicle for recognizing pathogen vulnerability and interaction.

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