



Grafting vegetable crops to manage plant-parasitic nematodes: a review

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Abstract

Vegetables constitute 12% of world agricultural produce. Solanaceous and cucurbitaceous crops constitute the major share of vegetable production, but their productivity is greatly impaired by plant-parasitic nematodes, among which root-knot nematodes pose the greatest threat. Due to climate change, water scarcity, shrinking of arable land, and ill effect of pesticides, a major shift in world agriculture is taking place toward sustainability, including organic and protected farming of high-value vegetable crops year-round. Grafting offers a sustainable alternative to conventional and transgenic breeding for nematode resistance. The technique can potentially reduce the phytonematode damage relying on several factors. These include *R* gene-mediated plant responses, efficient cross talk of defensive genes, alteration of plant metabolism and nutrient mobility, changes in plant vigor and physiological attributes, and modification of rhizosphere microbial community. Additionally, epigenetic factors also determine the success of graft union between the scion and rootstock. Grafting should also be included as a tool in integrated nematode management practices. Studies on identifying potential rootstocks and using grafted vegetable crops to manage nematode incidence are exhaustive but scattered. Here, we review the current status of vegetable grafting for nematode management using resistant rootstocks in both open-field condition and greenhouses. This is the first review, which compiles and summarizes the information on managing nematodes using grafted vegetables. We conclude the review with futuristic research perspectives of grafting that may aid in improving vegetable productivity in a sustainable manner.

Keywords Nematode resistance · *R* gene · Rootstock · Scion · Molecular and epigenetic changes · Protected agriculture

Introduction

Vegetables constitute about 12% of the world annual agricultural produce (9 billion tons), including watermelon, cucumber, eggplant, and tomato, with average annual productions of 117, 80, 54, and 42 million tons, respectively (FAOSTAT 2020). Nowadays, due to modernization of cultivation techniques and advancement in transport and

post-harvest processing, the vegetables are not only available on a seasonal basis in local markets but also year-round, in different parts of the world. Considering their nutritional value, consumption of vegetables has dramatically increased over the past few decades necessitating advanced production techniques. In order to cope with the changing climate, limited arable land, and water scarcity, these crops are often increasingly grown under protected structures including tunnels and greenhouses. Global trends indicate that the majority of greenhouse-grown vegetables are grafted (Bie et al. 2017). While adopting intensive farming strategies for yield maximization to meet the demand, pest and disease attacks also pose critical threats to growers, under both field and greenhouse conditions (Capinera 2020; Phani et al. 2021).

Among the major pests causing serious economic losses to the vegetables, plant-parasitic nematodes (PPNs) account for around 11% yield losses in these crops. Losses are reported in vegetables, such as bitter melon (4–48%), cucumber (25–88%), melon (14–65%), pumpkin (27%), watermelon (10–37%), sponge gourd (15%), eggplant (17–43%),

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pepper (19–70%), tomato (20–85%), okra (20–90%), lettuce (10–64%), and onion and garlic (60–80%), that suffer heavily due to PPN damage (Olthof et al. 1974; Sasser and Freckman 1987; Sturhan and Brzeski 1991; Viaene and Abawi 1996; Ali 1997; Kim and Ferris 2002; Anwar and McKenry, 2012; Gine et al. 2014; Lopez-Gomez et al., 2014; Lopes-Caitar et al. 2019). The extent damage is largely dependent on the PPN's initial soil population density (P_i), as the final density at crop harvest is proportional to P_i (Seinhorst 1970). The relationship between crop growth, yield, and P_i is derived by Seinhorst's damage function model that may be used to forecast the level of expected yield loss (Sorribas et al. 2020). Typically, PPNs attack the roots (few species infect aboveground parts), resulting in attenuated quality and quantity of produce due to reduced water and nutrient uptakes. Minute body size, non-specific damage symptoms, and lack of farmers' awareness eventually may lead to a huge population buildup of PPNs in soil, which ultimately become un-manageable under open-field and/or protected conditions (Jones et al. 2013; Phani et al. 2021).

In spite of heavy losses incurred by PPNs, limited management options are available to mitigate these pests. Identifying the existing or potentially harmful PPN species is essential for successful vegetable cultivation. Tracking the movement and distribution of the nematode species and checking their introduction (by quarantine, clean cultivation) provide a first-hand protection against PPNs. Unlike the availability of insecticides, fungicides, or bactericides, very few nematicides are present in the global market, and most of them have been introduced very recently. The fumigants were phased out due to environmental concerns, and PPN management is still predominantly practiced by adopting the conventional techniques (such as crop rotation, soil solarization, flooding, organic amendment, biocontrol, resistant breeding) including novel nematicides, viz., fluensulfone, fluazaindolizine, thiazafen, fluopyram, and ethanedinitrile claimed to be target-specific and environment-benign (Kearn et al. 2014; Slomczynska et al. 2014; Faske and Hurd 2015; Lahm et al. 2017; Dutta et al. 2019; Douda et al. 2021). However, many nematicides are not recommended for all crops as per their label claims. The conventional strategies (as above), though effective, cannot be advocated irrespective of cropping system, agroclimatic condition, and socioeconomic condition of the farmers (Dutta et al. 2019). Under the prevalence of such therapeutic bottlenecks, exploitation of host resistance by means of graftage proves to be an effective alternative for PPN management and can serve as an excellent mean to induce pest resistance (King et al. 2008).

Grafting refers to the practice of deliberate joining of plant parts, where the resultant combined parts attain physical union and grow as a single composite plant (Lee and Oda 2003; Martínez-Ballesta et al. 2010). The vigorous plant part replacing the root system is called rootstock

or stock, and the upper portion of economic interest is called scion (Martínez-Ballesta et al. 2010). The majority of cucurbitaceous (watermelon, cucumber, and melons) and solanaceous (tomato, eggplant, and pepper) crops are routinely grafted by multinational seed companies and commercial seedling producers (Thies 2021; <https://avrdc.org/seed/improved-lines/rootstock/>). Currently, around 20–40% of the world tomato production comes from graftages. In Japan and Korea, grafted watermelons and cucumbers individually share about 90% and 75% of the total cropped area, respectively. In Netherlands and the USA, 100% of the soil-less tomato production utilizes grafted transplants. Mexico imports grafted vegetable seedlings from Canada. Additionally, semi- or fully automated grafting robots are being used commercially in few countries such as Japan, Korea, Spain, and Netherlands (Pardo-Alonso et al. 2019). Furthermore, farmers in China (1500 commercial nurseries) and the USA are rapidly adopting vegetable grafting as a profitable business. According to a conserved estimate, a grafted tomato seedling costs around US \$ 0.4–1.2 in the USA, Japan, and Korea, whereas the same plant may cost around € 0.6–1.2 in Spain and other EU countries (Spanò et al. 2020). All these facts and figures indicate the rising trend of acceptance and increase in international trading of the grafted vegetables (Bie et al. 2017). Normally, the woody perennials are grafted for dwarfing, ease of propagation, and sturdiness, whereas grafting in herbaceous plants aims to increase productivity and curb the effects of abiotic and biotic stresses (Sigüenza et al. 2005; Yin et al. 2012). Further, grafting protects vegetables from soil-borne pests and pathogens (Ioannou 2001; Bletsos et al. 2003; Davis et al. 2008). This technique also intensifies tolerance against salinity, water logging, and temperature fluctuations (Ahn et al. 1999; Rivero et al. 2003a,b; Estan et al. 2005; Venema et al. 2008; Abdelmageed and Gruda 2009).

Major plant-parasitic nematodes damaging vegetables and the factors favoring them

Root-knot nematodes (RKN, *Meloidogyne* spp.) are the major threat to vegetable production worldwide (Collange et al. 2011). Typically, RKNs develop giant cells (GCs) that help funneling the plant metabolic products to the developing nematode as a continuous source of nourishment (Jones et al. 2013). The endoparasite feeds by inducing the formation of specialized cells leading to the development of root galls that become visible upon uprooting the plants. The common RKN species attacking vegetables include *M. incognita*, *M. javanica*, *M. arenaria*, *M. hapla*, *M. chitwoodi*, *M. enterolobii* (syn. *M. mayaguensis*), and *M. floridensis* across different agroclimatic zones in many countries (Sikora and Fernandez 2005; Collange et al.

2011). RKNs are distributed in the tropical, subtropical, and temperate regions and cause an average of 10% economic losses in vegetables (Koenning et al. 1999; Collange et al. 2011). However, yield losses may reach over 30% depending on the attacking species, population density level, environmental conduciveness, and host plant susceptibility (Sikora and Fernandez 2005; Ornat and Sorribas 2008). Lamberti (1979) reported 50–60% losses in eggplant and tomato by RKN, whereas around 70–90% losses were measured by Alam and Jairajpuri (1990) in those crops. Estimation of maximum yield losses in vegetables under open-field and protected conditions showed around 88% losses in cucumber, 65% in melon, 37% in watermelon, and 60% in tomato (Ploeg and Phillips 2001; Sorribas et al. 2005; Talavera et al. 2009; Gine et al. 2014). Studies have shown that RKN may cause damage at a very low threshold population density. For example, Moosavi (2015) estimated the threshold population to be 1.8 eggs and infective juveniles g^{-1} soil in bell pepper, according to the Seinhorst's model. However, the damaging threshold may vary according to the crop cultivars (*cv/cvs*), nematode species, and prevailing agroclimatic conditions (Viaene and Abawi 1996; Gugino et al. 2006; Subbotin et al. 2021).

Apart from the RKNs, other PPNs may also cause considerable damage to vegetables. The reniform nematode *Rotylenchulus reniformis* infects vegetables including okra, cabbage, sweet potato, alfalfa, cucumber, tomato, squash, radish, eggplant, and melon (Robinson et al. 1997; Sikora and Fernandez 2005; Stetina et al. 2014). The lesion nematode species *Pratylenchus brachyurus*, *P. barkati*, *P. dasi*, *P. coffeae*, *P. delattrei*, *P. loosi*, *P. singhi*, *P. thornei*, and *P. zae* attack a large number of vegetables causing stunting, wilting, and necrotic lesions in roots, with yield losses that may reach up to 59% (Olthof and Potter 1973; Sikora and Fernandez 2005). The false root-knot nematodes *Nacobbus aberrans*, *N. bolivianus*, and *N. dorsalis* may reduce the yield of cabbage, turnip, sweet pepper, chili, squash, tomato, and cucumber under varied agronomic conditions. In tomato, the yield losses may vary from 12–83% (Cristóbal et al. 2006; Cabrera-Hidalgo et al. 2019). Additionally, some species within the genera *Helicotylenchus*, *Tylenchorhynchus*, *Hoplolaimus*, *Paratylenchus*, *Hemicycliophora*, *Hemicriconemoides*, *Ditylenchus*, *Belonolaimus*, *Xiphinema*, *Longidorus*, *Trichodorus*, and *Paratrichodorus* also attack solanaceous and cucurbitaceous vegetables in different parts of the world (Sikora and Fernandez 2005; Jones et al. 2013; Crow 2020; Phani et al. 2021). Apart from a direct damage, PPN-induced wounds predispose the plants to soil fungi and bacteria allowing the development of disease complexes that further worsen the situation (Rao et al. 2015).

The extent of PPN damage in vegetables largely depends on the adopted farming systems, as well as on environmental

and climatic factors, host type, and bio-physico-chemical properties of soil (Moura and Franzener 2017; Tileubayeva et al. 2021). The complex interactions between nematode communities and soil types are correlated with external factors such as temperature, humidity, and precipitation. Their effects determine the survival, parasitism, pathogenicity, and reproductive potential of the PPN species. Intensive cultivation of vegetables in greenhouses or protected conditions also spikes the risk of PPN damage together with other pests and pathogens (Phani et al. 2021). Several high-value vegetables are in fact cultivated under protected structures to meet the year-round demand, avoiding natural vagaries and climatic risks. However, the accidental PPN introduction through infested planting materials, farm instruments, and irrigation water in such structures always proves to be fatal. Once introduced, favorable temperature and humidity, continuous monocropping, higher host plant densities, and supra-optimal use of agronomic inputs rapidly build up the PPN numbers making the infested structures unsuitable for vegetable cultivation (Phani et al. 2021). The factors can also be correlated with the increase in soilless cropping (using hydroponics or substrates other than soil) that substantially reduces the risk of PPN damage.

Resistance grafting against root-knot nematodes

Notably, all vegetable graftages (in eggplant, chili, cucumber, tomato, melon, squash, and sweet pepper) aim at mitigating the sedentary endoparasitic *Meloidogyne* spp. No rootstock has been developed to counteract the damage of other endo-, semiendo-, or ectoparasitic PPN species. A detailed account of resistant grafting performed in the vegetables aiming to achieve resistance/tolerance against RKNs is provided in Table 1.

Vegetable grafting to manage crop pests has emerged as a priority research area lately (Goldschmidt 2014). However, the information about plant defense mechanisms against RKN in grafted plants is limited. The literature data are mostly concentrated toward other soil-borne pathogens and viruses, as the plant breeders do not consider grafting for nematode resistance as a focal point of their activity (Coyne et al. 2018). Nevertheless, the research findings can be extrapolated to comprehend the scenario in the case of nematodes. The primary level of pest/disease control in the grafted plants is achieved by pest/pathogen avoidance, mostly because of the resistance characterizing the rootstock (King et al. 2008). A few resistance genes (known as *R* genes) were identified mostly from wild relatives, cloned, and transferred to the cultivated plants to achieve effective resistance response against PPN (Ali et al. 2017). Grafting can successfully impart resistance from the wild hosts

Table 1 A list of grafted vegetable crops that conferred resistance/tolerance to plant-parasitic nematodes

Crop	Nematode species	Significant findings	Reference
Eggplant	<i>M. incognita</i>	Reduced galling for susceptible scion <i>Solanum melongena</i> cv Senryo 2 grafted onto <i>S. sisymbriifolium</i> ; <i>S. sisymbriifolium</i> appeared to be promising rootstock for eggplant and tomato; high resistance of <i>S. torvum</i> and <i>S. toxicarium</i> rootstocks top-grafted with susceptible scions (in greenhouse)	Ali et al. (1992)
Eggplant	<i>M. incognita</i>	Resistance of susceptible scion <i>cv</i> s Sufala, Singnath and Kazia upon grafting onto <i>Solanum torvum</i> and <i>S. sisymbriifolium</i> (in field)	Rahman et al. (2002)
Eggplant, tomato	<i>M. incognita</i>	<i>Solanum torvum</i> , <i>S. aethiopicum</i> , <i>S. macrocarpon</i> and eggplant accessions VI046103 (EG195) and VI045276 (EG203) recommended by AVRDC show resistance against nematodes and fungal or bacterial pathogens, when used as rootstocks with various eggplant and tomato scions (in screenhouse)	Black et al. (2003); Keatinge et al. (2014); Nyaku and Amisshah (2018)
Eggplant	<i>Meloidogyne</i> spp.	Avoidance of nematode damage by grafting <i>S. melongena</i> onto <i>S. integrifolium</i> rootstocks (in field and greenhouse)	Lee and Oda (2003)
Eggplant	<i>M. incognita</i>	Grafting of <i>S. melongena</i> <i>cv</i> s Pala and Faselis onto <i>S. torvum</i> rootstock protected plants from nematode damage (in field)	Çürtük et al. (2009)
Eggplant	<i>M. incognita</i>	<i>S. melongena</i> cv Cristal grafted onto <i>S. torvum</i> cv Brutus reduced nematode populations to non-damaging levels in two seasons (in field)	García-Mendivil and Sorribas (2019)
Eggplant	<i>M. incognita</i>	Grafting of <i>S. melongena</i> on its wild relative <i>S. palinacanthum</i> rootstock reduced nematode reproduction and population densities (in field and greenhouse)	Murata et al. (2022)
Tomato	<i>M. incognita</i>	Cross-grafted plants of susceptible <i>S. lycopersicum</i> cv Black and resistant <i>S. lycopersicum</i> cv Anaf evaluated for nematode gall development and phosphate metabolism; higher accumulation of phosphates on galled roots after exogenous application	Ishibashi and Shimizu (1970)
Tomato	<i>M. incognita</i>	Resistance of <i>S. lycopersicum</i> <i>cv</i> s Momotaro and Kyoury-okubeiju grafted onto <i>S. sisymbriifolium</i> , <i>S. torvum</i> and <i>S. toxicarium</i> rootstocks were evaluated; resistance to nematode persisted for cv Kyouryokubeiju grafted onto all three species	Matsuzoe et al. (1993)
Tomato	<i>Meloidogyne</i> spp.	Use of resistant rootstock cv Brigeor F1 along with soil solarization was effective against nematodes and also <i>Verticillium</i> spp. and <i>Pyrenochaeta lycopersici</i> (in field)	Ioannou (2001)
Tomato	<i>M. arenaria</i>	Tomato <i>cv</i> s Capita, Vigomax and Beaufort showed resistance against nematode infection; grafting of cv Vanessa on selected rootstocks also increased yield	Augustin et al. (2002)

Table 1 (continued)

Crop	Nematode species	Significant findings	Reference
Tomato	<i>M. incognita</i>	Susceptible tomato cultivar Blitz grafted onto cv Beaufort rootstock showed reduced damage by tolerance; rootstock cv Hypeel45 prevented both nematode damage and population buildup (in greenhouse)	Lopez-Perez et al. (2006)
Tomato	<i>M. javanica</i>	Rootstocks with the <i>Mi</i> resistance gene were evaluated for nematode resistance; cvs PG76, Gladiator and MKT-410 responded as highly resistant; relative resistance levels of rootstocks Brigeor, 42,851, 43,965, Big Power and He-Man (in field)	Cortada et al. (2008)
Tomato	<i>M. javanica</i>	Susceptible cv Durinta grafted onto <i>Mi</i> -resistant rootstock SC 6301 and was compared to <i>Mi</i> -resistant cv Monika; grafting provided intermediate resistance response (in plastic house)	Verdejo-Lucas and Sorribas (2008)
Tomato	<i>M. incognita</i> , <i>M. javanica</i> , <i>M. arenaria</i>	Rootstock cvs PG76 (<i>S. lycopersicum</i> × <i>Solanum</i> sp.), Brigeor (<i>S. lycopersicum</i> × <i>S. habrochaites</i>), Beaufort and Maxifort assessed for nematode resistance; cv PG76 showed high resistance and cv Brigeor showed high to moderate resistance (in greenhouse)	Cortada et al. (2009)
Tomato	<i>M. javanica</i>	Durability of resistance mediated by <i>Mi</i> gene in rootstock cvs PG76 (<i>S. lycopersicum</i> × <i>Solanum</i> sp.), Brigeor (<i>S. lycopersicum</i> × <i>S. habrochaites</i>), Monika (<i>S. lycopersicum</i> × <i>S. habrochaites</i>), Monika (<i>S. lycopersicum</i>) and Durinta (<i>S. lycopersicum</i>) was measured for three consecutive years; cvs Brigeor and Monika retained intermediate resistance levels for total period; cv PG76 became susceptible at third cropping cycle (in field)	Verdejo-Lucas et al. (2009)
Tomato	<i>M. incognita</i>	Grafting onto cv Beaufort reduced root galling and nematode damage under organic agriculture system (in greenhouse)	Kaskavalci et al. (2009)
Tomato	<i>M. incognita</i>	Grafting onto rootstock cvs Big Power, Beaufort and Maxifort reduced nematode galling and infection; also effective against fungus <i>Sclerotium rolfsii</i> (in field)	Rivard et al. (2010)
Tomato	<i>M. incognita</i>	Grafting of susceptible scion cv Florida 47 onto cvs TX301, Multifort and Aloha rootstocks showed similar nematode development in soil after two consecutive years (in field)	Kokalis-Burelle and Roskopf (2011); Kokalis-Burelle et al. (2016)
Tomato	<i>Meloidogyne</i> sp.	Reduced nematode damage and galling for susceptible heirloom tomato cultivars Brandywine and Flamme grafted onto hybrid rootstock cv Multifort and Survivor (in field)	Barrett et al. (2012a)

Table 1 (continued)

Crop	Nematode species	Significant findings	Reference
Tomato	<i>M. incognita</i>	Resistance for nematode damage using cvs Big Beef, Celebrity and Jetsetter as rootstocks for susceptible cvs Tropimech and Power as scions (in field and plant-house)	Owusu et al. (2016)
Tomato	<i>M. incognita</i> , <i>M. javanica</i>	Grafting onto resistant rootstock of <i>S. sisymbriifolium</i> reduced root galling (in plastic tunnel)	Baidya et al. (2017)
Tomato	<i>Meloidogyne</i> spp.	The success of <i>S. lycopersicum</i> cv Pectomech grafting onto <i>Mi</i> gene containing <i>S. macrocarpon</i> and <i>S. aethiopicum</i> was higher (93 and 94%) than Pectomech/ <i>S. lycopersicum</i> 'Mongal F1' (0%) and Pectomech/ <i>S. lycopersicum</i> 'Samrudhi' grafts (0%)	Agyeman et al. (2019)
Tomato, melon	<i>Meloidogyne</i> spp.	Evaluation of susceptible tomato grafted onto cv Alligator, and melon grafted onto cv <i>C. meluliferus</i> accession BGV1135 rootstocks, and vice versa; nematode damage was significantly reduced (in greenhouse)	Expósito et al. (2020)
Cucumber	<i>Meloidogyne</i> spp.	Use of Bur cucumber (<i>Sicyos angulatus</i>) cv Andong as rootstock for cucumber provides nematode tolerance, but reduced yield (in field)	Ko (1999)
Cucumber	<i>Meloidogyne</i> spp.	Grafting of cv Palmera onto <i>Fusarium</i> wilt-resistant <i>C. maxima</i> × <i>C. moschata</i> seedlings provided nematode control (in field and greenhouse)	Giannakou and Karpouzas (2003)
Cucumber	<i>Meloidogyne</i> spp.	Grafting of cucumber onto Bottle gourd, Calabash gourd, <i>Lagenaria siceraria</i> , <i>Cucurbita</i> rootstocks pumpkin (<i>C. moschata</i>), figleaf gourd, interspecific hybrids rootstocks Shintosa, Ercole Nun 6001, Ferro RZ F1, Super Shintosa (<i>C. maxima</i> × <i>C. moschata</i>), Balsam pear <i>Momordica charantia</i> and Horned cucumber by using tongue approach grafting provides resistance and tolerance against nematode damage (in greenhouse)	El-Eslamboly and Deabes (2014)
Cucumber	Plant-parasitic nematodes	Grafted onto Shintoza or Camel (both <i>C. maxima</i> × <i>C. moschata</i>) rootstocks provided significant reduction in nematode damage (in greenhouse)	Echevarria et al. (2004)
Cucumber	<i>M. incognita</i>	Grafting onto wax melon (<i>Benincasa hispida</i>) and <i>C. maxima</i> × <i>C. moschata</i> Ercole hybrid 6001 provided efficient nematode control of improved plant vigor (in plastic house)	Amin and Mona (2014)
Cucumber	<i>Meloidogyne</i> spp.	Grafting of cv Adrian onto rootstocks of <i>Lagenaria siceraria</i> cvs Emphasis, S-1 and Gourd; <i>C. maxima</i> × <i>C. moschata</i> cvs Strong Tosa and RS 841 improved; and <i>C. pepo</i> cv Romanesco Zucchini reduced nematode damage (in greenhouse)	Goreta Ban et al. (2014)

Table 1 (continued)

Crop	Nematode species	Significant findings	Reference
Melon	<i>M. incognita</i>	Intergeneric grafting of susceptible cv Durango onto <i>C. metuliferus</i> resulted good performance under high nematode densities (in field)	Di Vito et al. (1983); Pofu et al. (2012)
Melon	<i>M. incognita</i>	Grafting onto <i>C. metuliferus</i> and <i>C. moschata</i> rootstocks were evaluated for nematode infestation; <i>C. moschata</i> did not provide resistance to susceptible scion (in greenhouse)	Sigüenza et al. (2005)
Melon	<i>Meloidogyne</i> spp.	Use of interspecific <i>Cucumis</i> hybrids UPV-FA (<i>C. ficifolius</i> × <i>C. anguria</i>) and UPV-FMy (<i>C. ficifolius</i> × <i>C. myriocarpus</i>) as rootstocks provided nematode resistance (in greenhouse)	Cáceres et al. (2017)
Melon	<i>M. incognita</i> , <i>M. arenaria</i> , <i>M. javanica</i>	Grafting onto <i>C. metuliferus</i> accession BGV1135 did not affect fruit quality traits and conferred nematode resistance with poorly developed giant cells and necrotic lesion formation around feeding nematodes	Expósito et al. (2018)
Watermelon	<i>M. incognita</i>	Grafting of cv Reina de Corazones onto cvs Shintoza F1, RS841 F1 (<i>C. maxima</i> × <i>C. moschata</i>), <i>C. moschata</i> and <i>Citrullus lanatus</i> var <i>citroides</i> rootstocks were evaluated for nematode damage; <i>C. lanatus</i> var <i>citroides</i> showed minimum parasitism (in field)	Huitrón-Ramírez et al. (2009)
Watermelon	<i>M. incognita</i>	Grafting of cvs Fiesta (diploid seeded) and Tri-X 313 (triploid seedless) onto bottle gourd (<i>Lagenaria siceraria</i>), squash (<i>C. moschata</i> × <i>C. maxima</i>) hybrid, wild watermelon (<i>C. lanatus</i> var. <i>citroides</i>) rootstocks were evaluated for nematode resistance; <i>C. lanatus</i> var. <i>citroides</i> identified as potential resistant rootstock (in field)	Thies et al. (2010)
Watermelon	<i>M. incognita</i>	Grafting of susceptible cvs Congo and Charleston Gray onto <i>Cucumis myriocarpus</i> and <i>C. africanus</i> rootstocks reduced nematode reproduction (in greenhouse)	Pofu et al. (2011)
Watermelon	<i>M. incognita</i>	Grafting of susceptible cv TriX Palomar onto cvs Emphasis (lagenaria-type), and StrongTosa (interspecific squash hybrid) showed no differences in nematode numbers and galling (in field)	Kokalis-Burelle and Roskopf (2011); Kokalis-Burelle et al. (2016)
Watermelon	<i>M. incognita</i>	Grafting onto hybrid of <i>C. lanatus</i> cv Robusta and <i>C. maxima</i> × <i>C. moschata</i> cv Super Shintoza rootstocks were evaluated; <i>C. lanatus</i> cv Robusta showed significant reduction in nematode damage; also reduced <i>Fusarium</i> wilt incidence (in field)	Álvarez-Hernández et al. (2015)
Muskmelon	<i>M. incognita</i>	Grafting of susceptible cv Athena onto <i>Cucumis metuliferus</i> and cv Tetsukabuto (<i>C. maxima</i> × <i>C. moschata</i>) were evaluated; only <i>C. metuliferus</i> rootstock reduced galling (in field)	Kokalis-Burelle and Roskopf (2011); Kokalis-Burelle et al. (2016)

Table 1 (continued)

Crop	Nematode species	Significant findings	Reference
Net melon	<i>M. incognita</i>	Graft compatibility was evaluated with <i>Benincasa hispidia</i> , <i>Luffa cylindrica</i> , pumpkin, squash, watermelon, melon and cucumber rootstocks; few melon, pumpkin and watermelon cultivars including <i>L. cylindrica</i> showed nematode resistance (in greenhouse)	Galatti et al. (2013)
Cucumber, melon, watermelon	<i>Meloidogyne</i> spp.	Use of African horned cucumber (<i>Cucumis metuliferus</i>) cv NHR1 as rootstock for watermelon and cucumber provides good nematode tolerance	Igarashi et al. (1987)
Cucumber, melon, watermelon	<i>M. incognita</i>	<i>Cucumis pistulatus</i> was found as a suitable rootstock for nematode and <i>Fusarium</i> wilt (in greenhouse)	Liu et al. (2015)
Cucurbits	<i>Meloidogyne</i> spp.	Watermelon rootstock <i>C. amarus</i> cv Strongback provided nematode resistance (in field)	Kembla et al. (2019); Keinath et al. (2019)
Pepper	<i>M. incognita</i> , <i>M. javanica</i>	<i>Capsicum annuum</i> , <i>C. baccatum</i> , <i>C. chinense</i> , <i>C. chacoense</i> and <i>C. frutescens</i> genotypes were evaluated for nematode resistance; <i>C. annuum</i> AR-96023 and <i>C. frutescens</i> accessions as rootstocks showed moderate and relatively high resistance against nematodes (in greenhouse)	Oka et al. (2004)
Pepper	<i>M. incognita</i>	Grafting onto rootstocks Graffito and Gc 1002 gave tolerance to <i>Phytophthora capsici</i> , but were susceptible to RKN (in field and greenhouse)	Morra and Bilotto (2006)
Pepper	<i>M. incognita</i>	Grafting of scion cv Aristotle onto several rootstocks were evaluated for RKN resistance; cvs Charleston Hot, Carolina Wonder, Charleston Belle, Mississippi Nemaheart and Carolina Cayenne showed consistent resistance to galling (in greenhouse)	Kokalis-Burelle et al. (2009)
Pepper	<i>M. incognita</i>	Grafting susceptible cultivars onto cvs Robusto FI and Snooker FI rootstocks reduced nematode damage (in plastic tunnel)	Mándoki and Péntzes (2012)
Sweet pepper	<i>M. incognita</i>	Grafting onto rootstock cv Atlante reduced nematode damage, and also found to be effective as alternative to methyl bromide (in greenhouse)	Ros et al. (2006)
Okra	<i>M. incognita</i> , <i>M. enterolobii</i>	Grafting of cv Colhe Bem IAC onto resistant rootstocks of cotton (cvs PRO 277, IAC 29–233, PR 136, IAC 24 and IAC 03–979), and vinagreira (<i>Hibiscus sabdariffa</i>) reduced nematode damage (in greenhouse)	Vinícius-Marin et al. (2017)

averting the difficulties faced in the hybridization of cytologically diverse plant genera (Cook 2004). *R* genes reported from tomato (*Mi1-9*, *Hero A*), potato (*Gpa2*, *H1*, *Gro1-4*, *Rmc1*, *Mh*), pepper (*Me1-7*, *Mech1-2*), and eggplant (an unidentified gene in *S. torvum*) are available in plant genotypes with a potential for being used as rootstocks (Fuller et al. 2008; Barbary et al. 2015; El-Sappah et al. 2019). Notably, *R* genes are constitutively expressed and encode surveillance proteins that detect specific effector molecules from the nematodes directly or indirectly, and initiate defense responses (Milligan et al. 1998). A few of them have been utilized to generate homo- and hetero-grafted vegetables, tested for nematode resistance (Thies et al. 2010; Rivard et al. 2010; Barrett et al. 2012a,b; Guan et al. 2014; Kunwar et al. 2017; Liu et al. 2015; Kokalis-Burelle et al. 2016; Owusu et al. 2016; Expósito et al. 2020). However, most *R* genes are yet underexplored. For example, even though more than 20 *R* genes for RKN resistance were collectively identified from wild tomato and pepper accessions, only two of them are widely available in commercial cvs, i.e., *Mi-1.2* in tomato and *N* in pepper (Barbary et al. 2015; El-Sappah et al. 2019). This may be due to the changes observed in gene expression patterns from one grafting experiment to another. As grafting interactions are complex (Tsballa et al. 2021), it is preferable to employ such molecular techniques on a case-by-case basis (Abd-Elgawad 2022). Although wild crop relatives are often selected as resistant rootstocks, integrating the desirable traits with resistance to multiple diseases (horizontal resistance) is challenging (Mudge et al. 2009; Louws et al. 2010). Besides, *R* gene-mediated vertical resistance often leads to large and differential effects on the pathogens (Hammond-Kosack and Jones 1997). A number of tomato rootstocks (PG76, Gladiator, MKT-410, Brigeor, Big Power, He-Man, Beaufort, and Maxifort) with *Mi* gene (showing resistance against *M. incognita*, *M. javanica*, *M. arenaria*, and *M. luci*) were introgressed into agronomically superior tomato cvs to minimize the RKN damage (Cao et al. 2005; Cortada et al. 2008). However, at constant high soil temperature (> 28 °C), *Mi* gene is not expressed, allowing the nematodes to parasitize the host plants. In an isolated study, the heat-induced breakdown of *Mi-1* resistance in tomato cv Amelia was restored when heat stress was lifted (de Carvalho et al. 2015). Despite the fact that a number of heat stable *Mi* genes (e.g., *Mi-2*, *Mi-3*, *Mi-4*, *Mi-5*, *Mi-6*, *Mi-9* and *Mi-HT*) were identified from different tomato rootstocks (El-Sappah et al. 2019), the level of resistance/tolerance of commercially available rootstocks and their potential grafting partners (agronomically superior cvs) need to be evaluated in local environments, prior grafting. Furthermore, different scion–rootstock combinations presumably elicit a shift in the root microbiome affecting the incidence of plant growth-promoting rhizobacteria and of endophytic fungi (Poudel et al. 2019). Microbial communities in the rootstock

rhizosphere may alter the root exudate profile, micronutrient uptake, and induce hormone synthesis, which in turn impart plant resistance to soil-borne pathogens and abiotic stresses (Garbeva et al., 2008; Roupael et al. 2018; Cardarelli et al. 2020). Disease suppressiveness in the grafted plants can be equally attributed by induced systemic resistance of the scion. A number of induced defense mechanisms including antioxidant enzymes (SOD, CAT, APX) and non-enzymatic antioxidants (ascorbate, carotenoid, glutathione, tocopherol) were identified that scavenge the reactive oxygen species (ROS) (Guan et al. 2012; Cohen et al. 2017). An effect of phytohormone (abscisic acid, gibberellin, auxin, cytokinin, jasmonate, salicylate, ethylene, and brassinosteroid are transported via xylem sap)-mediated defenses in fostering plants' tolerance has also been reported (Albacete et al. 2015). Additionally, greater vigor of plants (Cohen et al. 2005) and efficient mobilization of plant nutrients (Savvas et al. 2010) might also be effective against the nematodes.

The genetic background for selecting RKN-resistant rootstocks is fairly wide in tomato because many closely related *Solanum* spp. can be used for grafting (King et al. 2010). Successful intergeneric tomato grafting was also achieved with rootstocks of Goji berry (*Lyceum chinense*) and tobacco (*Nicotiana tabacum* cv Samsun and *N. rustica* cv Hasankeyf) (Huang et al. 2015; Iseri et al. 2015). However, both were used for abiotic stress tolerance. Under biotic stresses, tomato grafting largely aimed at managing bacterial wilt or brown root rot (Black et al. 2003; King et al. 2010). Nevertheless, the RKN damage may extend up to 56% under open-field and greenhouse conditions (Expósito et al. 2020). Though several nematode resistance genes have been reported in wild tomato plants, only few of them (most commonly the *Mi-1.2* gene) could be successfully introgressed into commercial cvs (Barbary et al. 2015; Ali et al. 2017). In developing countries, eggplant rootstocks commonly used for tomato grafting include *Solanum torvum*, *S. sisymbriifolium*, *S. macrocarpon*, and *S. aethiopicum* (Gisbert et al. 2011). Studies with other rootstocks, such as Big Beef, Celebrity, Jetsetter (Owusu et al. 2016), Anchor T, Arnold, Estamino, Multifort, RT-04-105-T, and RT-04-106-T (Roskopf et al. 2017) showed promising RKN resistance with concomitant control of *Verticillium* and *Fusarium* wilt, *Sclerotium* blight, bacterial wilt (caused by *Ralstonia solanacearum*), and Tomato Mosaic virus. The other notable rootstocks include Beaufort, Maxifort, Hypeel45, Big Power, Brigeor, He-Man, Survivor, RST-104–106-T, PG76, BHN-998, and BHN-1054 (Thies 2021). In high tunnel tomato productions in Florida, root galling was substantially reduced by up to 88%, with a decline in soil nematode populations recorded when using these rootstocks (Thies 2021).

The rootstocks differ in the magnitude of nematode resistance and tolerance depending on genes, scion species,

nematode population pressure, and environmental conditions. For example, Rivard et al. (2010) studied the response of tomato rootstocks Big Power, Beaufort, and Maxifort to a natural RKN infestation and found significant differences in root galling and nematode densities among rootstocks. Similar observations were also recorded by Lopez-Perez et al. (2006), as the yields of resistant rootstocks were satisfactory, despite differences seen in galling. Management of multiple soil-borne pathogens was also achieved using the rootstock BHN-998 which significantly reduced both *R. solanacearum* and *M. incognita* in field-grown tomato (Kunwar et al. 2017). Additionally, grafting of tree tomato (Tamarillo, *Solanum betaceum*) onto potato tree (*Solanum macranthum*) conferred adequate resistance against *M. incognita* (Jamison 2020).

In other crops, such as eggplant, grafting primarily aims at controlling RKNs along with wilting caused by bacteria, *Fusarium*, and *Verticillium* spp. (King et al. 2010). Although a number of wild eggplant genotypes were reported to be RKN resistant, such resistance is not universal and may vary with RKN populations of different geographic origins. For example, Tzortzakakis et al. (2006) reported that few eggplant accessions of *S. aethiopicum*, *S. gilo*, *S. macrocarpon*, and *S. torvum* did not show resistance against local populations of *M. incognita* and *M. javanica* in Greece. Intriguingly, the parasitic and reproductive fitness of *M. incognita* subpopulations (obtained from *S. torvum* cv Brutus roots) was dramatically reduced when inoculated in susceptible *S. melongena* cv Cristal (García-Mendivil and Sorribas 2019). Sargin and Devran (2021) reported a few *S. torvum* rootstocks (cvs Hawk and Boğaç) to be resistant to both *Mi-1.2*-avirulent and *Mi-1.2*-virulent isolates of *M. incognita*, *M. javanica*, and *M. luci*. *Solanum torvum* was also found to be resistant to an avirulent pathotype (A2-O) of *M. arenaria* (Sato et al. 2021). The Asian Vegetable Research and Development Center (AVRDC) reported some eggplant accessions, namely VI046103 (EG195), VI034845 (TS03), VI046104 (EG219), and VI046101 (EG190), to be highly resistant to RKNs and tolerant versus bacterial and *Fusarium* wilts, and flooding (source: <https://avrdc.org/seed/improved-lines/rootstock>). In a recent study, *S. melongena* grafted onto its wild relative *S. palinacanthum* (rootstock) significantly reduced the reproduction of *M. incognita* in pot soil (Murata et al. 2022). In view of this, tomato is used as a popular interspecific rootstock for eggplant scions for being at a better position for genetic improvements (for biotic and abiotic stress tolerance) than eggplant (Khah 2005; King et al. 2010).

In pepper, grafting primarily aims at controlling RKNs along with *Phytophthora* blight, bacterial blight, and leaf curl virus (King et al. 2010). Although pepper is not commercially grafted very often, successful grafts have been achieved using other solanaceous rootstocks to improve

disease resistance. Apart from accessions such as VI064659 (PP0237 7502), VI037556 (PBC535), and VI014995 (PI201232), recommended as resistant to RKN by AVRDC, several other rootstocks confer resistance to *M. incognita*, *M. javanica*, *M. arenaria*, and *M. chitwoodi* due to the presence of the *R* genes *Me1*, *Me3*, *Me7*, and *Mech1* (Oka et al. 2004; Djian-Caporalino et al. 2007; Kokalis-Burelle et al. 2009). Pepper cvs provided with the *N* gene (mediating resistance to RKN) were found to be effective as rootstocks against *M. incognita*, *M. arenaria*, and *M. javanica* (Guan et al. 2012). Although *Me1* and *Me3* genes remain active even at 42 °C, a partial loss of resistance to *Meloidogyne* spp. was documented at > 28 °C in bell pepper cvs harboring the *N* gene. Notably, *N* and *Me3* resistance-breaking populations have been documented in *M. incognita* infecting pepper (Barbary et al. 2015).

Resistance grafting serves as a promising tool for RKN management also in cucurbitaceous vegetables, where yield losses due to RKN may reach up to 88% (Verdejo-Lucas and Talavera 2019). Watermelon is commonly grafted onto the rootstocks of bottle gourd, interspecific hybrids of *Cucurbita maxima* and *C. moschata*, and wild watermelon (*Citrullus amarus*) (Davis et al. 2008; Thies et al. 2016). Tolerance to RKN is also achieved with proliferated root system (owing to the vigorous rooting of bottle gourd and interspecific *Cucurbita* hybrids), although the rootstocks are genetically susceptible to the nematode (Giannakou and Karpouzas 2003). Melons are commonly grafted onto *Cucurbita* spp., bottle gourd (*Lagenaria siceraria*), *Cucumis melo* rootstocks, and also luffa (*Luffa cylindrica*) and wax gourd (*Benincasa hispida*) (King et al. 2010). Self-grafting onto melons may reduce some compatibility problems, but the limited availability of disease-resistant melon germplasm poses a major obstacle.

As compared to watermelon and melon, cucumber can be successfully grafted onto a variety of genetic bases including *Cucumis* spp., *Cucurbita* spp., *Cucurbita* interspecific hybrids, bottle gourd, wax gourd, luffa, and figleaf gourd (*Cucurbita ficifolia*) (Sakata et al. 2007). Use of *Cucumis pustulatus* (Liu et al. 2015) and *Cucumis metuliferus* (Sigüenza et al. 2005) rootstocks for watermelon, melon, and cucumber scions provides promising protection against *M. incognita*. However, grafting onto *C. metuliferus* may carry some disadvantages such as weak temperature tolerance and lower yields (Davis et al. 2008). Two *C. metuliferus* accessions (BGV11135 and BGV10762) were found to be resistant to *Mi-1.2*-avirulent *M. arenaria*, *M. incognita*, and *M. javanica* isolates (Expósito et al. 2018). In an USDA-ARS field trial, seedless watermelon cvs Citation, Fascination, Melody, grafted onto the resistant *C. amarus* rootstock, showed significantly lower root galling and *M. incognita* reproduction, than plants grafted onto wild tinda (*Praecitrullus fistulosis*), bottle gourd cv Emphasis, and

squash *cv* Strong Tosa. Subsequently, three resistant rootstocks (RKVL-301, RKVL-316, and RKVL-318) were recommended for nematode-infested fields, and RKVL-318 was released by USDA-ARS for commercial use (Thies 2021). Additionally, a number of *C. lanatus* wild accessions exhibited moderate resistance to *M. arenaria* race 1 in the greenhouse (Thies 2021).

Successful grafting for nematode resistance: a case study

In India, adoption of grafting technique to improve vegetable production is slowly making its progress. Vegetable grafting was initiated at ICAR—Indian Institute of Vegetable Research (IIVR, Varanasi) from 2013 onward to select the best rootstocks for RKN resistance, soil-borne diseases, and waterlogging tolerance. Successful field trials of Pomato (tomato scion grafted on potato rootstock) and Brimato (both eggplant and tomato grafted on an eggplant rootstock) during 2020–2021 resulted in the initiation of their commercial production (ICAR newsletter; <https://icar.org.in/>). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Hyderabad) assisted more than 400 farmers and stakeholders in Andhra Pradesh to obtain 30–50% higher yields in grafted vegetables, compared to the non-grafted traditional varieties (ICRISAT happenings newsletter; <https://www.icrisat.org/>).

To identify the potential RKN-resistant rootstocks, a number of eggplant germplasm accessions were procured from IIVR and screened in the greenhouse, in pots. Four- to five-day-old seedlings, obtained from surface sterilized seeds, were transferred to plug trays containing equal mixture of sterilized soil and soilrite. After 15 days, individual plants were transferred to a 500-ml plastic pot containing soil and soilrite. The plants were challenged against a threshold population of infective *M. incognita* second-stage juveniles (J2s) (Pokharel 2011). Briefly, 500 freshly hatched J2s (collected from the egg masses of *M. incognita* race 1 maintained in *Solanum lycopersicum cv* Pusa Ruby in the greenhouse) were inoculated in the rhizosphere by pipetting in 3–4 holes. After 75 days, plants were harvested, roots were washed free of soil, and different nematode parasitism parameters including number of galls, egg masses, and eggs per egg mass were measured. Among the screened germplasms, *S. torvum* accession IC111056 exhibited greatest resistance, with lowest galling index (GI), equal to 1 (based on the 0–5 GI scale depicted by Taylor and Sasser 1978) and lowest multiplication factor (MF) ratio (indicative of nematode reproductive success in a host plant; Dutta et al. 2015). Next, in order to generate interspecific grafts, high yielding susceptible tomato (*S. lycopersicum cv*s Kashi Aman and Kashi Vishesh) were used as scions (Fig. 1).

Grafting was performed using the splice grafting method, with 5–7 mm, 45° angle slanting cuts in both the scion and rootstock (rootstock and scion stem diameters = 2 mm each) when *S. torvum* seedlings were 25–30 days old and tomato varieties were 22–25 days old. For post graft healing, seedlings were kept in controlled environment (relative humidity: 65%, temperature: 28 °C, 16:8 h light/dark photoperiod; light level: 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for initial one week followed by partial shade for another week. The grafted plants were supplied with nutrient solutions containing N, P, and K, and any unwanted shoot growth in the graft union was removed. Production of roots by the scion was not observed. Approximately 15 days after grafting operation, plants were transplanted to 500 ml pots in the greenhouse. Survival rate of the grafted plant was determined at this stage. After another 15 days, the plants were inoculated with RKN J2s as above. At 75 days after inoculation, the plants were harvested, fruit yield was determined, and different infection parameters per root system were assessed. Self-grafted Kashi Aman and Kashi Vishesh served as controls. RKN-resistant eggplant (*S. melongena cv* Hisar Lalit) was used as positive control. A survival rate of 92% and 90% ($n = 50$) was recorded with Kashi Aman/*S. torvum* and Kashi Vishesh/*S. torvum* scion-rootstock combinations, respectively. The grafted plants exhibited greater nematode resistance with least galling on roots (GI = 1) and least MF ratio (a significant 96% decline in MF ratio was documented in interspecies grafts compared to the self-grafted control, $P < 0.01$; Table 2). Lower GI and MF ratio also indicated a lower number of gravid females leading to a lower RKN population pressure in the soil. In accordance, significantly greater ($P < 0.0001$) fruit yield was documented in the interspecies grafts compared to their self-grafted counterparts (Table 2).

Molecular and epigenetic changes in grafted plants: determinants of grafting success

Grafting triggers systemic signals via cross talk involving genes related to hormone signaling, metabolic processes, activity of transcription factors, and physiological responses (Sidorova et al. 2021). The scion and rootstock share a unified vascular connection that becomes a single plant entity. At early grafting stages, phytohormones such as auxin, cytokinin, ethylene, jasmonic acid, and gibberellin aid in establishing the vascular connection (by promoting wound healing) in chimeric plants. The re-establishment of a grafted plant commences with vigorous cell division at the graft union followed by formation of the callus bridge, ending with the differentiation of new vascular tissues from callus cells leading to the secondary xylem and phloem tissue generation (Martínez-Ballesta et al. 2010). By involving genetic components, grafting results in migration of chromatin from

cell to cell via plasmodesmata or through vascular bundles, thereby allowing scion-rootstock communication (Wang et al. 2017). The plasmodesmatal connection is established among the adhering cells in order to facilitate transport of molecules and cell-to-cell communication between rootstock and scion (Bartusch and Melnyk 2020; Tsaballa et al. 2021). Fuentes et al. (2014) found direct transfer of nuclear genome between the scion and rootstock. Plastid genes were found to move for short distances across the graft union, indicating an opportunity for grafting to pursue horizontal gene transfer (Wang et al. 2017). Additionally, protein molecules and messenger RNAs (mRNAs) also show long-distance transportation through graft union that acts as regulatory signals or produce functional proteins in the targeted organs (Wang et al. 2017). In view of this, grafting may also serve as an easy vegetative propagation technique, to overcome the difficulties of sexual incompatibility between two species.

A global transcriptome profiling of *S. torvum* attacked by *M. incognita* revealed that plant-derived sesquiterpenoids and chitinase could be the major effectors of the rootstock nematode resistance (Bagnaresi et al. 2013). Transcriptomic analysis of *S. torvum* parasitized by *M. arenaria* (avirulent population A2-O) revealed the early induction of plant genes, such as fatty acid desaturase and sesquiterpene synthase, as an early line of defense from invading nematodes. Avirulent RKN infection also induced lignin and suberin accumulation in the root tip, indicating cell wall

reinforcements to restrict nematode invasion and migration (Sato et al. 2021). RNAseq analysis of *C. metuliferus* parasitized by *M. incognita* showed the upregulated expression of phenylalanine ammonia lyase, peroxidase, salicylate, jasmonate, and WRKY transcription factors (Ye et al. 2017).

Histopathology studies showed that accession BGV11135 of the *M. incognita*-resistant melon rootstock *C. metuliferus* although harbored (at 15 days after nematode inoculation) greater number of GC in the vascular cylinder. However, the GCs were smaller, less voluminous with fewer nuclei (occasionally devoid of cytoplasm) when compared with the susceptible *C. melo cv* Paloma. This indicates that the feeding cells play a greater role in arresting nematode development in grafted plants by modulating the root metabolic activity available for nematode feeding (Expósito et al. 2018, 2020). Similarly, undernourished and degenerated GCs were observed in *M. incognita*-resistant tomato *cv* Monika when compared with susceptible tomato *cv* Durinta (Expósito et al. 2020). Ye et al. (2017) reported poorly developed GC in *M. incognita*-resistant *C. metuliferus* accession PI482443 with multiple vacuoles and necrotic lesions around the nematode head, characteristic of a cell death response mediated by a hypersensitive reaction (HR). Additionally, greater accumulation of enzymes related to the phenylpropanoid biosynthesis pathway, and of transcripts from pathogenesis-related (PR) proteins, genes involved in lignification of cell wall (as structural barrier), with ROS production, etc., was

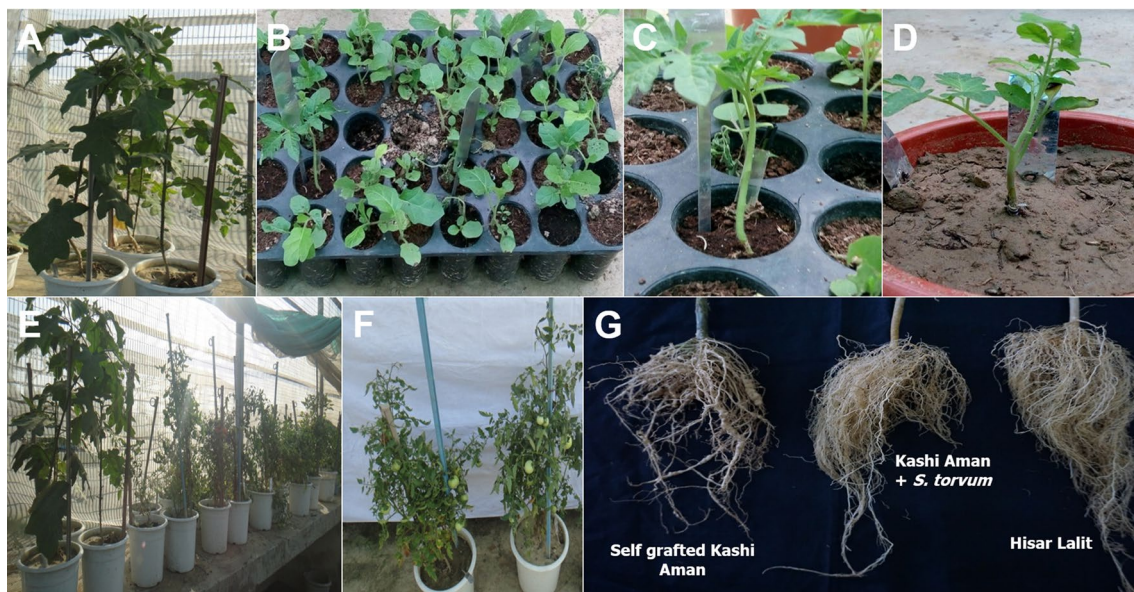


Fig. 1 Production of interspecific graft Brimato (tomato grafted onto eggplant rootstock) for nematode resistance at ICAR-IIVR, Varanasi. Maintenance of *S. torvum* germplasm (IC111056) at institute greenhouse as rootstock (A). Progeny plants of *S. torvum* at 2–3 leaf stage prior grafting (B). Splice or side grafted *S. lycopersicum* cvs Kashi Aman and Kashi Vishesh as scion onto *S. torvum* rootstock at 15 days

after grafting (C). Pot transplantation of grafted plant (D). Maintenance of the grafted plants in greenhouse (E). Fruiting in grafted plants (F). Nematode resistance analysis in grafted plants (G). Negligible gall numbers observed in interspecific graft (Kashi Aman/*S. torvum*) and resistant check (Hisar Lalit), compared to greater number of galls in self-grafted Kashi Aman root system

Table 2 Nematode resistance analysis of interspecific grafts. Self-grafted tomato cultivars Kashi Vishesh and Kashi Aman were used as controls (IC: infected control, HC: healthy control), and Hisar Lalit as resistant check. The experiment was repeated three times, with five

replicates per treatment. Data were analyzed using one-way ANOVA. Different letters (within the identical parameter) indicate significant difference at $P < 0.01$, Tukey's HSD test

Treatments	Grafting success (%)	Gall index (0–5 scale)*	Egg masses	Eggs per egg mass	MF ratio ^ψ	Fruit yield per plant (Kg)
<i>S. torvum</i>	NA	1.0	5.5 ± 0.9 ^d	212.6 ± 6.5 ^c	2.34 ^d	NA
Hisar Lalit	NA	1.0	4.8 ± 0.8 ^d	221.4 ± 6.9 ^c	2.13 ^d	1.41 ± 0.10 ^c
Kashi Vishesh IC	NA	5.0	122.5 ± 5.0 ^a	405.6 ± 9.2 ^a	99.37 ^a	0.72 ± 0.09 ^e
Kashi Vishesh HC	NA	NA	NA	NA	NA	1.57 ± 0.12 ^b
Kashi Aman IC	NA	5.0	119.6 ± 4.8 ^a	399.8 ± 8.9 ^a	95.63 ^b	0.89 ± 0.08 ^d
Kashi Aman HC	NA	NA	NA	NA	NA	1.61 ± 0.11 ^b
Kashi Vishesh + <i>S. torvum</i>	92	1.0	7.8 ± 1.2 ^b	252.0 ± 6.0 ^b	3.93 ^c	1.92 ± 0.15 ^a
Kashi Aman + <i>S. torvum</i>	90	1.0	6.5 ± 0.9 ^c	248.6 ± 7.5 ^b	3.23 ^c	1.96 ± 0.16 ^a

*Gall Index: 0=no galls, 1=1–2 galls/root system, 2=3–10 galls/root system, 3=11–30 galls/root system, 4=31–100 galls/root system, 5= > 100 galls/root system (Taylor and Sasser 1978). NA: not applicable

^ψNematode multiplication factor (MF) ratio=[(number of egg mass × number of eggs per egg mass) ÷ nematode inoculum level] (Dutta et al. 2015)

documented (Ye et al. 2017). A similar defense response was demonstrated in *Mi-1.2*-expressing tomato rootstocks (Walters et al. 2006; Williamson and Roberts 2009).

Although the phytohormone-mediated physiological alterations involved during the rootstock–scion interactions are widely explored (Aloni et al. 2010; Martínez-Ballesta et al. 2010), the trafficking of molecular information exchange between grafted partners is yet an underexplored territory. Genetic information, in the form of DNA or plastids, was shown to be horizontally transferred among rootstock and scion (Stegemann et al. 2012). Nevertheless, the RNA molecules, trafficked between grafted partners via phloem tissue and plasmodesmata, have considerable implications toward the fate of a grafting success. A number of mobile RNA molecules such as messenger RNA (mRNA) and small RNA (sRNA) including micro RNA (miRNA) were identified that alter plant development and physiology. For example, micro-grafting experiments showed that miR399, miR156, miR172, and miR395 move from scion to rootstock (Tsaballa et al. 2021). Different classes of sRNAs such as 22, 23, and 24 nucleotide (nt) small-interfering RNAs (siRNAs), generated by the enzymatic cleavage of RNaseIII or Dicer (DCL)-like proteins, were found to be mobile in the grafted plants. Among them, 24-nt siRNAs (generated by DCL3) were demonstrated as the predominant causal factor of epigenetic changes in grafted *Arabidopsis* plants. These siRNAs caused de novo methylation of transposable elements (TEs) and repetitive DNAs by RNA-directed DNA methylation (RdDM) process, leading to transcriptional gene silencing (TGS) in grafted plants (Molnar et al. 2010; Melnyk et al. 2011; Lewsey et al. 2016). Down-regulated expression of fatty acid desaturase (*FAD7*) gene

was documented in non-transgenic grafted tomato scions when grafted to a transgenic tomato rootstock with silenced *FAD7* gene (Nakamura et al. 2015). Mobility of sRNAs within grafted plants has immense practical significance. Notably, virus resistance trait (mediated by RNAi-based gene silencing) was transmitted from rootstock to scion in tomato, and grafting was found to enhance such trait (Spanò et al. 2015).

The epigenetic mechanisms in plants involve DNA methylation (addition of a CH₃ group to DNA cytosines for production of 5-methylcytosine in CG/CHG/CHH background), histone modification, and non-coding RNA-induced action (21–24-nt sRNAs targeting homologous gene transcripts to either cleave them or inhibit their translation), all resulting in the activation or suppression of plant genes (Dalakouras and Vlachostergios 2021). Using methylation-specific amplified marker (MSAP) analysis and bisulfite sequencing (BS) of methylated loci, heritable cytosine methylation alterations were detected in interspecies grafting of solanaceous vegetables (Wu et al. 2013). Similar epigenetic changes were documented in interspecies grafting of cucurbitaceous vegetables (Avramidou et al. 2015; Xanthopoulou et al. 2019). Significant changes in the global DNA methylation were also observed in the interspecies grafting of brassicaceous crops. However, few changes were retained over five subsequent generations of grafted plants (Cao et al. 2016). Differential DNA methylation patterns and miRNA expression in cucumber grafted onto a pumpkin rootstock have been linked with the plant adaptation to salt stress (Li et al. 2016). However, the direct role of miRNAs in grafted plants adaptation to stress (whether biotic or abiotic) is yet to be determined.

A number of differentially expressed genes (DEGs) including stress response and plant development were identified from the transcriptomic profile of watermelon scions grafted on bottle gourd and vice versa. Additionally, more than 400 mobile mRNAs (moved from rootstock to scion) were detected in both the heterografts compared to homografted controls (Garcia-Lozano et al. 2020). A transcriptomic insight of tomato scion grafted onto potato rootstock revealed thousands of DEGs and most of these appeared to be involved in the plant resistance to biotic and abiotic stresses (Song et al. 2016; Zhang et al. 2019). It is assumed that developmental features of grafted vegetables can be significantly influenced by stress-inducing conditions (Wei et al. 2019). Mobile epigenetic signals have vast implications in routinely grafted solanaceous and cucurbitaceous vegetables because grafting per se affects the expression of genes involved in different functions such as flower development, transcription factor, hormonal pathway, and biotic/abiotic stress response, in scion as well as rootstock (Kumari et al. 2015). The gene expression changes caused by grafting can positively or negatively impact the phenotypic characteristics of the grafted plant (Tsaballa et al. 2021). The interaction between the grafted partners has specific transcriptome signatures and epigenetic marks, which often lead to complete re-programming of gene expression. With the advent of high-throughput next-generation sequencing technologies and greater availability of reference genome sequences, it is becoming plausible to investigate in detail the molecular interaction between grafted partners, including the trafficking of genetic information in grafted plants, and their epigenome plasticity. As the epigenetic diversity may act as a novel source of phenotypic variability, mapping epigenetic marks and identifying epigenetic targets in the plant genome may provide crucial information to crop breeders who are constantly engaged in developing new, environmentally sustainable varieties. A deeper understanding of the environmental adaptation of grafted plants in the face of different biotic and abiotic stresses would be an invaluable input in that direction.

Evidence of epigenetic changes due to PPN infestation in grafted solanaceous and cucurbitaceous vegetables is scant to date (Wu et al. 2013; Avramidou et al. 2015). Cerruti et al. (2018) reported long-distance transfer of 24-nt sRNAs from rootstock to scion involving changes in DNA methylation in grafted eggplants. Hetero-grafting of a double haploid eggplant line onto *S. torvum* significantly increased plant vigor and RKN resistance. Further, whole-genome sequencing and transcriptome sequencing were performed to assess whether the changes in (cytosine) methylation affects the observed phenotypic differences. The results revealed down-regulated trends of expressed genes in the hetero-grafted events.

Applicability of grafting as a tool of integrated nematode management

Various nematode management tactics such as removal of crop residues, deep summer plowing, regular cleaning of farm instruments, and use of nematode-free planting material can significantly help curtailing the nematode population load on vegetables. Periodic removal of weeds (either mechanically or by herbicide spraying) is also advised because a number of weeds, belonging to families Amaranthaceae, Chenopodiaceae, Compositae, Malvaceae, Poaceae, and Polygonaceae, act as excellent hosts for nematode perpetuation in vegetable farming (Rich et al. 2009; Khan et al. 2014). Rotation of susceptible vegetables with tolerant or resistant *cvs*, use of trap and/or antagonistic crops, and biofumigation by incorporating chopped brassicaceous and non-brassicaceous plant biomass may elicit a strong biocidal effect on PPN populations (Dutta et al. 2019). Integration of such cultural and physical methods with grafting can have an additive effect toward limiting PPN density levels in soil, below their economic impact threshold. For example, Ros et al. (2018) found additive reduction of *M. incognita* infestation in grafted chili (a susceptible *cv* grafted onto resistant rootstock *cv* Atlante) when grafting was combined with biosolarization.

The combinations of grafted and non-grafted crops can also help increasing the vegetable ecosystem resilience. In order to diversify the selective pressures on RKN populations, extensive use of the rootstocks containing the same *R* gene must be avoided. Selection of virulent *M. incognita* populations resistant to the *Mi-1.2* gene was considerably reduced when ungrafted melon and tomato crops were rotated with their grafted counterparts (susceptible tomato *cv* Durinta grafted onto resistant rootstock *cv* Aligator; susceptible melon *cv* Paloma grafted onto *C. metuliferus cv* BGV11135) (Expósito et al. 2019). It was suggested that inclusion of more resistant crops, alternating with susceptible ones, would increase the time elapsed between two crops with identical *R* genes, preventing virulence selection in RKN populations.

Soil solarization (by using single- or double-layered transparent polyethylene sheets) in moistened soil or nursery beds during hot summer months can significantly suppress soil-borne pathogens and PPN, increasing (by 5–10 °C) the soil temperature (Wang and McSorley 2008). This also results in soil suppressiveness by microbial shifts (Katan and Gamliel 2014). In the Mediterranean region, grafting is often combined with soil solarization as a non-chemical alternative, where an intensive monocropping is common in the greenhouses (Moncada et al. 2013). In this line, Ioannou (2001) obtained higher yields (20.2 kg plant⁻¹) and better protection against *M. incognita* when

soil solarization was combined with grafting in tomato (onto rootstock Brigeor F₁), when compared to both methods used alone (grafting: 16.1 kg plant⁻¹; solarization: 14.1 kg plant⁻¹). Similar results were obtained by Yilmaz et al. (2011) when integrating solarization with grafting in cucumber (Maximus F₁ + Bergama F₁) that significantly reduced RKN damage and increased yields.

Enrichment of soil with exogenously applied organic amendments (including farmyard manure, vermicompost, green manure, oilseed cakes, defatted cakes) can significantly suppress PPN populations by stimulating the resident, antagonistic microbial communities. This leads to improved soil nutrient status, which in turn benefits plant vigor that impart tolerance to PPN, also releasing high concentrations of nematicidal compounds during decomposition and/or increasing anaerobic conditions (Pulavarty et al. 2021). Therefore, prior to transplanting of grafted plants, soil enrichment with organic amendments may provide added benefits sustaining the vegetable productivity.

New tactics such as low-risk chemical ‘SPK’ (a non-fumigant, unique formulation of organic acids) and anaerobic soil disinfection (ASD) appeared successful in managing PPN populations in multiple raised-bed vegetable production systems in Florida. SPK poses minimal risks to the environment and its applicators. ASD uses combined principles of solarization, organic amendments to stimulate microbial activity and soil saturation to create anaerobic condition in soil (Kokalis-Burelle et al. 2014).

Fungal biocontrol agents such as *Arthrobotrys*, *Catenaria*, *Dactylellina*, *Hirsutella*, *Pochonia*, *Purpureocillium*, *Trichoderma*, *Glomus*, and bacterial biocontrol agents such as *Pasteuria*, *Pseudomonas*, and *Bacillus* spp. have been effectively exploited for nematode management in vegetable cropping systems (Forghani and Hajihassani 2020). Inundative application of the biocontrol agents in nursery or greenhouses prior transplanting of grafted rootstocks may confer synergistic effect toward nematode management. Additionally, grafted plants act as soil environment conditioners that modulate the microbial communities in the rhizosphere. In grafted tomato, pepper, and eggplant, it has been shown that selection of suitable rootstocks can enhance soil-borne disease resistance by improving the plants ability to recruit microbial antagonists releasing antimicrobial molecules, and activate the systemic plant immune responses (Cardarelli et al. 2020). In an isolated study, Pham et al. (2020) demonstrated that the combination of grafting *Coffea canephora* scion onto *C. liberica* rootstock with mycorrhizal symbiosis additively improved viability of young Robusta seedlings and significantly decreased the populations of PPN such as *Pratylenchus coffeae* and *M. incognita*. Similarly, the combination of grafting and mycorrhization significantly improved the growth of tomato and reduced the population of the false root-knot nematode *N. aberrans* (Garita et al.

2019). In order to limit the selection of virulent nematode populations and thereby enhancing the resistance durability, tomato cv Monika harboring the *Mi-1.2* resistance gene was primed with *Trichoderma asperellum* (strain T34) and *T. harzianum* (T22). Intriguingly, both *Trichoderma* formulations induced resistance to *M. incognita*, the resistance conferred by *Mi-1.2* and that induced by strain T34 being additive in nature (Pocurull et al. 2020).

Minimal use of novel target-specific nematicides can provide sufficient control of nematodes in greenhouses and open-fields although it is not considered as an ‘environment-benign’ alternative (Desaeger et al. 2020; Phani et al. 2021). In this direction, Thies et al. (2016) found that nematicidal treatment significantly reduced the *M. incognita* damage in grafted watermelon, but the effect varied according to the plant genotypes. Resistance breakdown in high soil temperature and repeated planting of resistant rootstocks can give rise to virulent RKN races, due to the selection pressure (Noling 2019). Landi et al. (2018) showed that the combination of grafting (nematode susceptible *S. lycopersicum* cv Ikram scion grafted onto resistant *S. lycopersicum* cv Armstrong rootstock; resistance lost at soil temperature above 28 °C) and soil applications of fosthiazate, abamectin, and oxamyl synergistically controlled *M. incognita* in tomato. A meta-analysis (including 159 publications from 126 geographic locations, 202 rootstocks and 1023 experimental treatments) indicated that grafted tomato plants (mostly with Maxifort rootstock) maintain high fruit yields in pathogen-infested fields with the minimal use of pesticides, including fumigants (Grieneisen et al. 2018).

In order to achieve best results, focus must be given to the integration of multiple strategies, since the earliest crop growth phase. Sanitation, avoidance, and prevention of PPN infestation act as the first line of defense in nursery crops (Crow and Dunn 2005). High nematode populations in nursery beds lead to poor root development and weak seedlings that cannot establish upon transplanting. Such situation also predisposes the plants to secondary pathogens and simultaneous spread of PPN in larger areas. Use of grafted seedlings with adequate precautions to avoid nematodes will effectively minimize the chance of initial crop damage. For example, Morra and Bilotto (2006) revealed solarization to be a cheap soil treatment alternative that can effectively curb RKN damage, using grafted pepper in biennial rotation. Continuous use of resistant rootstocks should be avoided to halt the development of resistance-breaking populations (Verdejo-Lucas et al. 2009; Landi et al. 2018). Chemotherapeutics can be used as an alternative (Crow and Dunn 2005) when preventive measures fail to provide sufficient nematode control. Oka et al. (2012) found that chemical nematicides (alone or in combination) act best at early crop growth stages, but may even remain effective when applied at intermediate crop growth phases (Desaeger

et al. 2020). Biological control, though advocated, does not always provide satisfactory control under all types of socio-agroecological conditions (Crow and Dunn 2005). In order to achieve sustainable nematode management, appropriate biocontrol tactics should be chosen and/or developed that can be integrated with grafting.

Conclusion and future prospects

Under the ongoing changing climate scenario, incidence of pests and pathogens is rapidly changing, posing an unprecedented threat to the global food security. Among them, PPNs cause sufficient yield losses in vegetables under both open-field and protected conditions. Considering the continued thrust toward sustainable agriculture with minimal chemical pesticide usage, grafting appears as an economically effective alternative to other management techniques, minimizing the PPN damage. As an alternative to classical breeding, intra- or interspecies grafting offers viable alternatives to select and introduce desirable disease resistance trait in cultivated vegetables. In addition, grafting is an amenable technique that synchronizes well with the current trend of shifting agriculture and horticulture to indoor farming. Though a number of nematode-resistant rootstocks and grafts were developed for solanaceous and cucurbitaceous crops, a long way is still ahead for their successful commercialization and hassle-free availability. Research needs to be directed toward monitoring of PPN populations and their dynamics that may change by the frequent introduction of grafted vegetables via intensive farming. This may simultaneously alter the soil microbiome community and lead to development of new nematode biotypes in response to selective pressures. It is also possible that certain diseases and pests other than PPN, affecting the scion, may become prevalent. As a precautionary measure, rotation of rootstocks among different species, if possible, must be sought. Last but not the least, new information on epigenetic factors in grafted plants may be gained through transcriptome analyses, deep sequencing, and functional studies. The future exploitation of resistant rootstocks will surely depend on several factors including the local environment, scion genotypes, target PPN species, and population pressure of nematodes in the intended cropping sites.

Author contributions

VP and TKD had idea for the article; VP, TKD, and MGT performed the literature search and data analysis; VP, TKD, and MGT drafted the first version; and TKD and VP drafted the final version and critically revised the manuscript.

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