

Nematode problems in sugarcane and sugar beet and their sustainable management

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Introduction

Sugarcane, *Saccharum officinarum* L., is largely used to produce sugar and other related products in the world. The global sugar production was 166.18 million metric tons in 2020–21 which was obtained by processing 182 million metric tons cane (Statista 2020–21). The processing of 1 tons of cane yields 100 kg sugar, 40 kg molasses, and 10 L ethanol (Singh et al., 2021). The major sugarcane-producing countries are Brazil, India, China, Thailand, Russia, United States, Mexico, Pakistan, and Australia (Prasad & Shivay, 2020). Besides the use of sugarcane as a sweetener, sugar is also used to produce vine, 72–75-L vine per 100 kg sugar (total fermentable sugars), and other products (Singh et al., 2021). One ton molasses may produce 220–250 L ethanol (Singh et al., 2021). In addition to sugar, jaggery or Gur is produced from sugarcane which contains around 50% sucrose, 20% invert sugars, and 20% moisture. The remaining 10% contains other insoluble material such as wood ash, fibers, and other sweetening products of cane sugar. The waste of cane is bagasse (fiber) which is used in making various products.

The sugar beet industry began in Prussia in 1747 with the discovery of sugar in the roots of fodder beets, followed by breeding to develop commercial sugar beet (*Beta vulgaris*) varieties. Commercial sugar beets are white and have the shape of an inverted cone. The amount of sugar in the root ranges from 12% to 20% (Steele, 1984). In addition to sugar extracted from

the taproot, all parts of the plant are utilized to produce a wide range of products that include animal feed, pharmaceuticals, plastics, textiles, and ethanol. Around 136–160 kg sugar can be obtained from 1 ton of sugar beets. Sugar provides approximately 90% of the value of the crop, with by-products contributing an additional 10% of the value of the sugar (FAO, 1999). There is increasing interest in using sugar beets for the production of ethanol for use as a biofuel. This is a reality in the European Union (Flach et al., 2020; Marso et al., 2019; Voegelé, 2019, 2020), and production economics have been evaluated in the United States (Haankuku et al., 2015). The European Union and Russia grow sugar beets, while Africa, China, and the United States grow both sugarcane and sugar beets. In 2019, sugar beet production in the European Union was 194,460,403 tons; in Asia it was 41,507,477 tons; in the United States it was 28,225,847 tons, and in Africa it was 14,304,253 tons (Soare et al., 2021).

Sugarcane is cultivated in heavy soil with adequate moisture. The perennial nature (ratooning) and extensive root system make the crop an ideal habitat for survival of different soil-borne pests and pathogens, especially nematodes. Plant nematodes constitute an important group of pests in sugarcane root zone (Stirling et al., 2011), and have been estimated to cause approximately 15% reduction in cane production (Sasser & Freckman, 1987). Nematodes attack mainly the sugarcane root system and inflict a decline of approximately 15-ton cane/ha/year (Cadet & Spaul, 2003). Blair and Stirling (2007) estimated the monetary loss of around AU\$82 million to the Australian sugar industry annually due to nematode infestation. In India, around 10%–40% yield loss to sugarcane has been estimated depending on the nematode species and its population density (Haidar & Dutta, 2004). The crop losses may rise further when other soil-borne pathogens occur along with nematode and cause disease complexes (Khan, 1993).

Sugar beet is grown as an annual crop, and is cultivated mainly in temperate zones close to processing facilities. Nematodes primarily attack the fibrous roots originating from the taproot but can also be found on the tap root itself. Plant stems and leaves can be parasitized by *Ditylenchus dipsaci*, which is known as the stem and bulb nematode (Steele, 1984).

The nematode infestation in sugarcane was first observed in 1885, when *Meloidogyne javanica* (= *Heterodera javanica*) was recorded infesting the crop in Java (Treub, 1885). Within 12 years of this report, two most important nematodes, *Pratylenchus penetrans* (Soltwedel (1888) and *Radopholus similis* as *Tylenchus similis* (Cobb, 1893), were discovered attacking sugarcane. Barber (1919) reported nematode infestation in sugarcane in India, when he noticed malformation in sugarcane roots attributing “eelworms” (root-knot nematode). Sugarcane harbors large number of plant nematodes, and over all, the widest nematode diversity has been recorded in sugarcane in comparison to any other crop, evidenced by infestation with nematodes from 310 species belonging to 48 genera (Cadet & Spaul, 2005). Siddiqi (1959, 1960, 1961, 1964) and Siddiqi (1961) reported several plant nematodes, viz., *Meloidogyne javanica*, *Xiphinema brevicaudatum*, *Trichodorus acudatum*, *Criconema brevicaudatum*, *Tylenchorhynchus elegans*, and *Hemicriconemoides cocophilus* from sugarcane fields in India.

Sugar beet has been reported to host 65 species of nematodes belonging to 27 genera. In 1859, on sugar beet, Schacht found *Heterodera schachtii*, now known as sugar beet nematode, attacking plants in Germany (Schacht, 1859a, 1859b). Frequent planting of sugar beet resulted in rapid spread of the nematode, producing severe yield losses. “Rüben-müdigkeit” or “Beet weariness” resulted in the closing of more than 20 sugar beet factories in Germany in 1876. In 1885, root-knot nematode (*Meloidogyne* sp.) was reported infesting sugar beet in Germany, and

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in 1911, it was found in the United States (Bessey, 1911). In 1900, *Ditylenchus dipsaci* was found to be causing problems in England, Germany, and the Netherlands (Weischer & Steudel, 1972). In 1956, the false root-knot nematode, *Nacobbus aberrans*, was found on sugar beets in the United States (Thorne & Schuster, 1956). *Trichodorus* sp. and *Paratrichodorus* sp. (stubby-root nematodes) and *Longidorus* sp. (needle nematodes) were recorded infesting beet in England and in the Netherlands (Whitehead et al., 1970) and also in Sweden and Denmark (Andersson, 2018). In the 1970s, *Heterodera trifolii*, which is a race of the clover cyst nematode, caused problems in the Netherlands on sugar beet (Steele, 1984). It was first named as *Heterodera trifolii* f.sp. “*betae*” but was later described by Wouts et al. (2001) as *Heterodera betae*.

During the last four decades, numerous nematode species have been described from sugarcane soils; among them, the commonly occurring species are *Meloidogyne*, *Pratylenchus*, *Rotylenchulus*, *Helicotylenchus*, *Belonolaimus*, *Tylenchorhynchus*, *Heterodera*, *Radopholus*, *Rotylenchus*, *Paratylenchus*, *Hoplolaimus*, *Scutellonema*, *Criconema*, *Criconemoides*, *Hemicriconemoides*, *Macroposthonia*, *Hemicycliophora*, *Caloosia*, *Boleodorus*, *Trophurus*, *Tylenchus*, *Ditylenchus*, *Dolicodorus*, *Neopsilenchus*, *Filenchus*, *Aphelenchoides*, *Aphelenchus*, *Xiphinema*, *Longidorus*, *Trichodorus*, and *Paralongidorus* (Sankranarayana, 2010). However, some genera such as *Pratylenchus*, *Hoplolaimus*, *Tylenchorhynchus*, *Meloidogyne*, and *Helicotylenchus* have shown predominance in sugarcane fields, hence deserve detailed coverage in the present chapter.

Sugar beet is a host to the following 27 genera of plant parasitic nematodes (Ferris, 2022): *Atetylenchus*, *Belonolaimus*, *Criconema*, *Ditylenchus*, *Helicotylenchus*, *Hemicycliophora*, *Heterodera*, *Hexatylus*, *Hoplolaimus*, *Longidorus*, *Meloidogyne*, *Merlinius*, *Nacobbus*, *Paralongidorus*, *Paratrichodorus*, *Paratylenchus*, *Pratylenchus*, *Quinisulcius*, *Radopholus*, *Rotylenchus*, *Rotylenchulus*, *Tylenchorhynchus*, *Scutellonema*, *Scutylenchus*, *Trichodorus*, *Tylenchorhynchus*, and *Xiphinema*. The most important genera that will be covered in detail are *Heterodera*, *Meloidogyne*, *Pratylenchus*, *Nacobbus*, *Ditylenchus*, and *Trichodorus/Paratrichodorus* (Gray, 1986). Important nematodes infesting sugarcane and sugar beet are discussed under:

Lesion nematode, *Pratylenchus* species

Pratylenchus spp. commonly known as lesion nematodes predominantly occur in sugarcane fields and cause significant crop loss in most of the major cane producing countries especially Australia (Blair et al., 1999a, 1999b), Brazil (Moura et al., 1999), Egypt (Moussa et al., 2002), and India (Sundararaj & Mehta, 1991a, 1991b). Over 20 species of *Pratylenchus* have been reported from sugarcane fields, the *P. zae* being of most economic significance and wide spread in distribution (Cadet & Spaul, 2005). *P. parazeae* was isolated from *Saccharum sinensis* fields causing considerable damage to the crop in China (Wang et al., 2015). In addition, *P. brachyurus*, *P. coffeae*, *P. delattrei*, *P. goodeyi*, and *P. pratensis* have also been encountered at high population densities in sugarcane farms (Onapitan & Amasu, 1982; Spaul, 1981).

Pratylenchus spp. has a worldwide distribution and is the most frequently found nematode in sugar beet fields in many regions (De Zinger, 2016; Ebrahimi et al., 2004; Rubilar & Aballay, 2006; Smiley et al., 2014). Four species viz., *P. thornei*, *P. neglectus*, *P. crenatus*, and *P. penetrans* have been reported from sugar beet fields. More seldom, *Pratylenchus fallax* is found (De Zinger, 2016).

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Symptoms

The aboveground symptoms caused by lesion nematodes in sugarcane resemble to poor soil (nutrition deficiency) symptoms such as stunted plant growth and leaf yellowing. However, unlike nutrition deficiency, these symptoms appear in patches of plant distributed irregularly all over the field (Khan & Jairajpuri, 2010).

On underground parts, the nematode incites characteristic necrotic lesions especially on lateral roots. *Pratylenchus zaei* causes red colored lesions within the root cortex. The lesions are gradually intensified leading to formation of large and extensive necrotic lesions. The necrotic part of the root turns dark brown to black in color (Harris, 1974). The root mass is greatly reduced, shoot becomes shorter, and leaves show yellowing. However, Onapitan and Amasu (1982) reported that *P. brachyurus* does not suppress shoot and root growth, although the species causes damage to the vascular system as well as root cortex. However, at high population densities, the *Pratylenchus* spp. may extensively destroy the root system of sugarcane (Holtzmann, 1964). The larvae of *P. zaei* penetrate at the root tip and cause brown lesions at the site of entry but nematodes may also be found in areas without any detectable lesions (Sundararaj & Mehta, 1992). The necrosis of roots and significant reduction in the root mass occurs due to severe infection of *P. zaei*. Infected lateral roots show reddish brown to black necrotic lesions (Fig. 1A and B). The nematode penetration into a cell leads to disintegration of constituents of the cell as well as the nucleus. The nematode larvae can be seen feeding on the vascular tissue but endodermal cells are usually not attacked.

Pratylenchus spp. rarely cause any aboveground symptoms in sugar beet. On the underground parts of sugar beet, the lesion nematodes cause a characteristic forking of the main root which develops numerous lateral roots. Sugar beet is regarded as a poor host to *Pratylenchus* spp. (De Zinger, 2016) (Fig. 2).

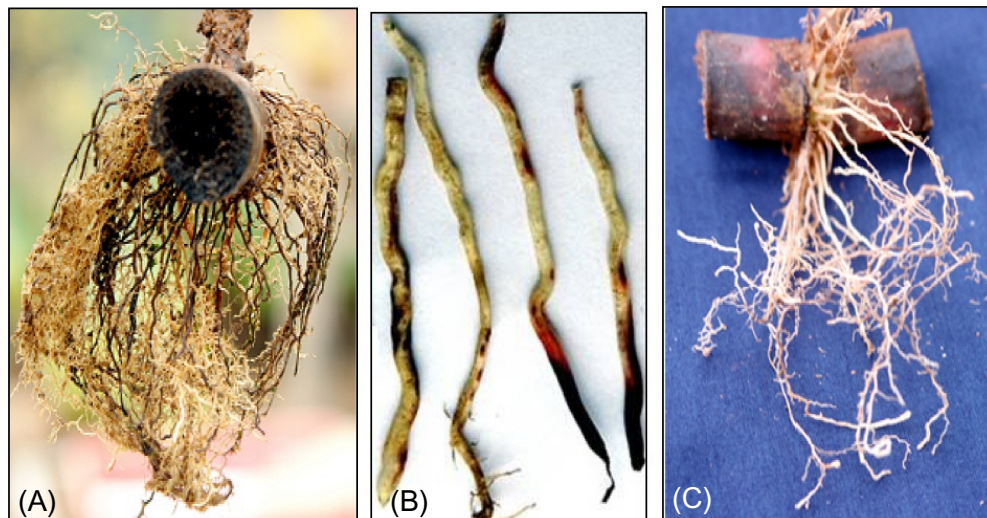


FIG. 1 Sugarcane roots infected with *Pratylenchus zaei* show root necrosis (A and B), and root galls caused by *Meloidogyne javanica* (C). Source C: Sankranarayana, C. (2010). NASI, India.

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Pratylenchus spp., especially *P. zae*, is of economic significance in several major sugarcane-producing countries such as Australia (Blair et al., 1999a), Panama (Pinochet, 1987), South Africa (Cadet & Spaull, 1985), Brazil (De Moura et al., 1999), Mauritius (Williams, 1960), and United States (Birchfield, 1984). A few studies conducted on the economic threshold of different *Pratylenchus* spp. on sugarcane indicate that an initial population of 10 nematodes/100 cc soil may inflict economic damage to sugarcane crop (Sundararaj & Mehta, 1992). Stirling and Blair (2000) suggested that 100 larvae of *Pratylenchus* spp. per 200 g soil at planting and 250 larvae/200 g soil at mid-session caused significant damage to sugarcane in Australia. In sugar beet, the excessive growth of lateral roots can lead to yield losses during harvest as root pieces are lost during lifting and cleaning.

Interaction with other pathogens

Root-lesion nematodes have been frequently found synergizing root-rot causing fungi leading to disease complexes of economic significance (Evans & Joshi, 2016). Cohabitation of lesion nematode and *Pythium* spp. resulted to severe leaf chlorosis and root-rot in sugarcane (Srinivasan, 1958). Singh (1960) reported the occurrence of *Pratylenchus zae* along with *Pythium aphanidermatum*, *Cephalosporium*, and *Fusarium* caused a disease complex in sugarcane. Santo and Holtzmann (1970) demonstrated synergistic interaction between *Pratylenchus zae* and *Pythium graminicola* on sugarcane. However, the nematode population in the presence of the fungus was reduced. *Pratylenchus* spp. have also been found associated with wilt disease complex (Patel et al., 1988). It has been found that *Pratylenchus zae* and *Hoplolaimus indicus* may act as predisposing agents for the *Fusarium* wilt development in sugarcane (Mehta et al., 1994a, 1994b). Spaull and Baily (1993) investigated the possible interaction of



FIG. 2 Sugar beet infected by *Pratylenchus thornei* showing numerous lateral roots. Photo: Åsa Olsson Nyström.

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Pratylenchus, *Meloidogyne*, *Paratrichodorus*, and *Xiphinema* with *Clavibacterium xyli*. It was found that in both the first crop and the first ratoon crops, the severity of the bacterial disease and nematode population was increased, but effect on the yield of cane and sucrose was additive.

Root-knot nematode, *Meloidogyne* species

Of the plant parasitic nematodes, *Meloidogyne* spp. are among the most economically important nematodes attacking a large number of agricultural crops (Eisenback & Triantaphyllou, 1991; Khan, 2008; Jones et al., 2013). Occurrence of root-knot nematodes has been commonly observed in sugarcane fields (Mehta, 1992). The predominant species of *Meloidogyne* in several sugarcane growing areas of the world are *M. javanica*, *M. incognita*, and *M. arenaria* (Cadet & Spaull, 2005; Dinardo, 2001; Mehta, 1986; Moussa et al., 2002). Seven others species, *M. acrita*, *M. arenaria*, *M. hispanica*, *M. kikuyensis*, *M. thamesi*, *M. enterolobii*, and *M. ethiopica*, have also been reported from cane fields. *M. enterolobii* was recorded in sugarcane fields in Brazil, but in experimental plots, the species proved as nonpathogenic to sugarcane cultivars (Da Silva et al., 2012). However, *M. ethiopica* was found to be highly pathogenic on the variety RB72454, showing a 60% reduction in plant height with a reproduction factor of 16.6 (Bellé et al., 2017).

The species within *Meloidogyne* are very diverse in temperature requirements. The predominant species attacking sugar beet in temperate regions such as northern Europe and northwestern United States are *M. hapla*, *M. naasi*, *M. chitwoodi*, and *M. fallax*. These species are able to survive temperatures below -10°C . In contrast, *M. javanica* and *M. arenaria* cannot survive temperatures below -10°C for longer periods of time (Moens et al., 2009). In the southern regions of United States, the predominating species attacking sugar beet are *M. incognita* and *M. javanica* (Weiland & Yu, 2003). In the tropical and subtropical regions, sugar beet is attacked by *M. javanica*, *M. incognita*, and *M. arenaria*.

Symptoms

Meloidogyne spp. cause nondiscernable symptoms on the aboveground parts of sugarcane. The symptoms generally resemble to nutrition deficiency (Khan & Jairajpuri, 2010). Plants show stunted growth, sparse foliage, and yellowish leaves. Plants show these symptoms in the patches, which are irregularly distributed all over the field (Mehta, 1992). High populations of the nematode occur in the soil of these patches, and the roots of such plants show numerous galls of varying sizes (Rao, 1961). The plants may also show leaf rolling and chlorosis and the foliage appears mildly wilted. The nematode infection may lead to formation of lesser number of tillers as well as slender cane (Salawu, 1986). The symptoms become more discernable on ratoon crops, especially yellowing of foliage due to gradual build of the nematode population. On the underground parts, the root galls (knots) are the most obvious

symptoms of the nematode infestation (Mehta, 1992). The galls are small bead-like and frequently terminal as seen in graminaceous crops (Fig. 1C). The galls in sugarcane are not much fleshy and appear as elongated nodules generally at the root tip or just below it, and infected thicker roots are often curved. Due to invasion of apical meristem, the elongation and terminal growth of roots are inhibited. As a result, lateral proliferation of roots takes place and the root system becomes shallow. This subsequently leads to impairment of absorption of water and nutrients, which manifests as a chlorosis and mild wilting of foliage. The unexperienced farmers may overlook nematode infestation in sugarcane due to smaller size of galls. Hence, the disease may be confirmed on the dicot weeds growing in the field, on which bigger and easily recognized galls are formed.

When the sugar beet roots are infected by root knot nematodes early in the growing season, many plants die which results in severe yield losses (Weiland & Yu, 2003). The plants also grow slowly and cannot compete with weeds. In a study by Griffin et al. (1982), the tolerance limit in sugar beet to *Meloidogyne chitwoodi* and *Meloidogyne hapla* was 2.8 and 0.6 eggs and juveniles per cm³ soil, respectively. In comparison between the two species, *Meloidogyne hapla* was found to reproduce better on sugar beet than *Meloidogyne chitwoodi* and is thus considered to be a better host (Griffin et al., 1982). Sugar beet is also a good host to *Meloidogyne naasi*, but in trials in Germany, the damage was very low (Thomas, 2000) (Fig. 3).

Interaction with other pathogens

Sugarcane being a ratoon crops with massive root system coupled with adequate moisture collectively offers conducive conditions for aggregation and colonization of different kinds of pathogens which may interact and affect each other positively or negatively. The pathogenicity of *Meloidogyne* and other pathogens may be influenced under their cohabitation in sugarcane root zone (Khan & Sharma, 2020). The concomitant inoculation with *Curvularia lunata* and *M. javanica* interacted synergistically and caused greater suppressive effects on sugarcane in comparison to their individual effects (Khurana & Singh, 1971). Apt and Koike (1962a) also observed synergistic interaction on the growth of sugarcane seedlings grown in the soil of inoculated concomitantly with *Pythium graminicola* and *M. incognita*. In another study, inoculation with *M. incognita* and *Fusarium moniliforme* significantly enhanced the fungal infection (Portales, 1990). However, additive interaction between *M. incognita* and *Leifsonia xyli* subsp. *xyli* was recorded which led to severe ratoon stunting disease (Regis & de Moura, 1989; Spaul & Baily, 1993).

Lance nematodes, *Hoplolaimus* species

Hoplolaimus spp., commonly known as lance nematode for its lance like lip region, are one of the predominant nematode genus occurring in sugarcane cropping systems (Mehta & Somasekhar, 1998a). *Hoplolaimus coronatus* (= *Hoplolaimus galeatus*) was first reported from

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FIG. 3 Sugar beet field severely infested with *Meloidogyne hapla* (A) and an infect root system showing galls (B). Photo: Åsa Olsson Nyström.

sugarcane rhizosphere in Hawaii (Cobb, 1923). Seven species of *Hoplolaimus* have been reported from sugarcane fields in different major cane-growing countries (Sankranarayana, 2010). In India, *Hoplolaimus indicus* and *H. seinhorstii* have been found to be distributed in many sugarcane-growing zones (Singh, 1967).

Symptoms

General symptoms of *Hoplolaimus* infestation in sugarcane appear as restricted normal growth of shoot and root. *Hoplolaimus* species are migratory endoparasites in sugarcane roots, and their feeding leads to necrosis of cortical cells which appear as reddish black lesions on young lateral roots. *Hoplolaimus indicus* and *H. columbus* cause necrosis to cortical cells and may restrict normal growth and development of roots (Misra & Singh, 1976). Purple red necrotic lesions may appear on the roots invaded by *H. indicus*, and in severe infestations, the lesions may girdle the root.

Hoplolaimus spp., especially *H. indicus* and *H. columbus*, are migratory endoparasites and feed on endodermis and phloem parenchyma. Males and females remain vermiform throughout the life. Sexual dimorphism is present in the head region (Khan, 2008). Females possess didelphic amphidelphic ovaries. Reproduction is amphimictic; females do not deposit eggs without mating. Eggs in soil take about 8 days to hatch giving rise to a second stage juveniles (Siddiqui, 2005). First moulting occurs within the egg. Young adult larvae of both the sexes penetrate roots. Root exudates seem to help the nematode in locating the roots for penetration feeding (Badri & Vivanco, 2009). Fully developed females feed for at least 3 days before they start laying eggs inside the roots. A single female on average may lay 14 eggs in 4 days. The eggs inside the roots hatch in 3–4 days. One generation from egg to egg completes in a month.

The adults penetrate up to stellar region and feed on phloem parenchyma. In endodermis, the injury is mostly confined to 2–4 cells in all the directions (Haque & Khan, 2021). Due to migration and feeding of the nematode, cavities are formed mostly in cortex pointing towards

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stele. These cavities are called feeding cavities in which the nematode lay eggs (Misra & Singh, 1976). Cells of the cavities have thickened walls and are devoid of cytoplasm. The cellular elements are disorganized and eventually the cells die. The nematodes do not feed on xylem but their activities result in extensive damage to this tissue. Tylosis is also reported to occur in damaged xylem cells. The cells in the cavities lose turgidity; vascular elements are distorted as a result roots become flaccid. Due to death and decay of cavity cells, purple necrotic lesions appear on the root surface.

Spiral nematodes, *Helicotylenchus* species

Helicotylenchus spp., commonly known as spiral nematodes for its spiral body shape, occur in large numbers in sugarcane root zone. Numerous species of *Helicotylenchus* (around 30) are reported to infest sugarcane in different countries (Mehta, 1992), the most common species being *Helicotylenchus dihystra*, *H. erythrinae*, *H. mucronatus*, *H. multincinctus*, and *H. retusus* (Misra & Singh, 1976). Among these, *H. dihystra* has been found to be a predominant species causing severe damage to sugarcane in South Africa (Willers & Mdluli, 1995), India (Darekar et al., 1990), Brazil (Agudelo & Volcy, 1998), and Nigeria (Fademi et al., 1997). *H. multincinctus* also attacks sugarcane (Jonathan et al., 1999).

Symptoms

Spiral nematodes feed ectoparasitically, semiendoparasitically, or endoparasitically on the root cortex causing distortion and collapse of the cells (Brawthwaite, 1980). Both shoots and roots of the nematode-infected plants become stunted (Saeed et al., 1989). The primary root becomes blunt and malformed with fewer lateral roots (Rao & Swarup, 1975). The nematode feeding results in the formation of brownish red lesions or a general discoloration of roots. Severe root rotting may occur due to synergistic interaction with *Pythium* spp. (Apt & Koike, 1962b). *Pythium graminicola* is found to be associated with *Helicotylenchus nannus* causing root rot disease complex (Khan, 1993). The concomitant inoculation with *Fusarium moniliforme* and *Helicotylenchus indicus* also caused extensive rotting to sugarcane roots (Nath et al., 1976).

Helicotylenchus spp. are generally migratory endoparasites of root cortex where all stages can be found (Khan, 2008). Males and females of *Helicotylenchus* spp. remain vermiform throughout life. Females bear didelphic amphidelphic ovary. Reproduction in *Helicotylenchus* spp. is amphimictic as well as parthenogenic (Siddiqui, 2005). The larvae and adult penetrate epidermis of the root. The females and probably males directly feed on parenchymatous cells. Within four days of start of penetrations, the nematodes are usually wholly within the cortex to a depth of 4–6 cells. The head of each nematode is usually oriented parallel to the long axis of the root, but posterior portion is curved or spiral usually occupying several adjoining cells. The nematodes feed on the cytoplasm of cortical cells in the root, and the damaged cells show contracted cytoplasm, distorted or ruptured walls, and enlarged nucleus. The damaged cells are often discolored and become necrotic. Nematode completes life cycle from penetration to egg lying within a month.

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Burrowing nematode, *Radopholus similis*

Radopholus similis is an important nematode pest of sugarcane causing the decline in many crops including sugarcane in tropical and subtropical regions (Ambrogioni, 1995). The nematode has been reported to infest sugarcane in a number of countries and states like Australia, Cuba, Florida, Hawaii, India, Java, Louisiana, Mauritius, and Philippines (Williams, 1969).

Symptoms

The burrowing nematode invades lateral roots and burrow cavities in the root cortex (Geetha & Koshy, 1995). The invaded lateral roots show reddish brown diffused lesions. The nematode larvae enter through young sugarcane roots and endoparasitically feed in the cortex (Mehta, 1986). Upon entering the roots, larvae occupy an intracellular position in the cortex and feed on the cytoplasm of parenchymatous cells around. The cells are destroyed; as a result, cavities in the cortex are formed. These cavities coalesce and expand due to continuous nematode feeding. As a result, tunnels are formed laterally toward the endodermis (Khan, 2008). The cavities and tunnels appear as reddish-brown lesions through the cortex. Extensive cavities are formed within 3–4 weeks. The cavities crack with raised margins. Eventually, the root system may be reduced to a few short stubs. Reduction in the feeder roots was the most significant effect on the plant. A minimum population of 100 nematodes per plant was found to be the damage threshold level for *Radopholus similis* on sugarcane (Sankranarayana, 2010). A population of 1000 nematodes per plant may cause significantly decline.

The burrowing nematode, *Radopholus similis*, is a migratory endoparasite of underground parts and feeds on cortical cells. The sexual dimorphism can be seen in adult males being somewhat degenerated (Siddiqui, 2005). Females possess didelphic amphidelphic ovaries. All the stages of males and females are found in the soil as well as in the root cortex. The larvae invade healthy succulent feeder roots and penetrate at any point. After penetration, the nematode moves through the intercellular spaces, laying eggs on the way at several points. The females lay eggs at 2–4 eggs/day for about 7–8 days. The first moulting takes place within the egg. The second stage larvae undergo rest of the three moults inside the host tissue or in the soil, if present outside the root to become adults. Males do not feed. Reproduction is parthenogenetic and females lay eggs without matting. The life cycle (egg to egg) completes in 3–4 weeks, and eggs take 8–10 days to hatch.

Stubby root nematodes, *Trichodorus* spp. and *Paratrichodorus* spp.

Damage to sugar beet by stubby root nematodes was first observed in United Kingdom in the parish Docking (Gratwick, 1992). The damage was seen as patches in the field with small stunted plants suffering from nutrient deficiencies beside larger plants. Stubby root

nematodes are found on all major continents in the world (Winfield & Cooke, 1975). Sugar beets are infested predominantly on coarse soils as stubby root nematodes are rather large and are favored by the greater pore size. There are two main genera, *Trichodorus* spp. and *Paratrichodorus* spp. The main species infesting sugar beet are *Trichodorus primitivus*, *Paratrichodorus teres*, *Paratrichodorus christie*, and *Paratrichodorus pachydermus*. *Paratrichodorus allius* has also been associated with sugar beet roots in a survey of the family Trichodoridae in Chile (Aballay & Eriksson, 2006).

Symptoms

Stubby root nematodes are migratory ectoparasites of underground parts of sugar beet. Damage on sugar beet during the seedling stage is most common in years with low temperatures and high rainfall. Aboveground symptoms are unevenly sized plants often in patches in the field. Typical underground symptoms are short and stubby lateral roots as a result of the nematodes feeding on epidermal cells behind the zone of root elongation (Shurtleff & Avere, 2000). The feeding results in poor growth of the seedlings, and eventually, the root system becomes severely forked with numerous lateral roots.

Stem and bulb nematode, *Ditylenchus dipsaci*

Ditylenchus dipsaci has a worldwide distribution and attacks both wild and cultivated plants. Host races exist, some of which are polyphagous whereas others have limited host ranges (IPPC, 2016; Storelli et al., 2021a, 2021b). The stem and bulb nematode are a serious plant parasitic nematode on sugar beet in many countries in Europe, e.g., France, Germany, and Switzerland (Storelli et al., 2021a, 2021b).

Symptoms

Ditylenchus dipsaci is a migratory endoparasite that may survive long periods in the soil as desiccated fourth-stage juvenile clumps of individuals, the so-called “nematode wool” (IPPC, 2016). The nematodes enter plants through stomata and wounds (Storelli et al., 2020). *Ditylenchus dipsaci* may reproduce rapidly under favorable conditions with as many as six generations per year (Storelli et al., 2020). Consequently, low initial densities may cause severe yield losses in sugar beet. Typical early symptoms on sugar beet are swollen hypocotyls and distorted cotyledons (Hillnhütter et al., 2011). Later in the growing season, rots in the crown may occur as a consequence of secondary infections by soil-borne fungi such as *Rhizoctonia solani* and *Verticillium albo-atrum*.

When *Ditylenchus dipsaci* occurs together with *Rhizoctonia solani*, synergistic damage has been observed on sugar beet (Hillnhütter et al., 2011).

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Sugar beet cyst nematode, *Heterodera schachtii* and *Heterodera betae*

Sugar beet cyst nematodes (BCN) occur in all major growing areas for sugar beet (Moens et al., 2018). There are two species of *Heterodera* infecting sugar beet, *H. schachtii* and *H. betae* (Wouts et al., 2001), the white and yellow beet cyst nematode, respectively. During cyst development, *H. betae* passes through a yellow phase. *H. betae* has been recorded from Netherlands, Sweden, Germany, Switzerland, and Italy (Wouts et al., 2001). Due to the higher temperature requirement for *H. betae* compared to *H. schachtii*, it is often found on sandy soils. Sometimes, both species occur in mixed populations.

Symptoms

Aboveground symptoms are wilting plants despite adequate soil moisture. The plants also suffer from nutrient deficiencies and show various degree of yellow chlorosis on the leaves. The nematodes often occur in patches in the field resulting in poor growing of plants and many weeds. On the roots, an excessive amount of extra small roots is formed, giving the main root a “bearded” appearance. On these roots, small white females can be seen (Fig. 4). As they mature and die, they turn light brown and eventually fall off the roots and survive in the soil for several years where they are able to infect new plants. Each cyst contains several hundred eggs and juveniles. The hatching of second-stage juveniles from the cysts is stimulated by a host but some spontaneous hatching also occurs. The temperature range for hatching and infection in *H. betae* is narrower than for *H. schachtii* (Wouts et al., 2001). The life cycle takes 4–6 weeks and several generations can be completed in one year (Moens et al., 2018). *Heterodera schachtii* is a parasite on members of the families Chenopodiaceae and Brassicaceae (Handoo & Subbotin, 2018). Besides sugar beet, oil seed rape, cabbage, and spinach are good hosts of *H. schachtii*. In addition, many weeds, e.g., *Chenopodium album*, are also susceptible to the nematode. The host range for *H. betae* includes members of the families Brassicaceae, Chenopodiaceae, Polygonaceae, Fabaceae, and Caryophyllaceae (Wouts et al., 2001).



FIG. 4 Sugar beet root with white female cysts of *Heterodera schachtii* on the lateral roots. Photo: Åsa Olsson Nyström.

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False root-knot nematode, *Nacobbus aberrans*

Nacobbus aberrans, known as the false root-knot nematode, attacks the roots of sugar beet. The common name is derived from root gall symptoms that can be confused with those caused by the root-knot nematode *Meloidogyne* sp. in the family Heteroderidae. However, morphologically *Nacobbus* sp. are more similar to lesion nematodes and so are in the family Pratylenchidae (Gray, 1986).

Symptoms

Stunting and chlorosis are typical aboveground symptoms of false root-knot nematode. Belowground, the nematodes cause galling similar to that of root-knot nematode. Males, young females, and the juvenile stage are motile. They damage roots as they move intercellularly through the cortex. Young females are long and slender and migrate from the cortex to a position near the vascular cylinder. Adult females are sedentary endoparasites. Unlike root-knot, there are no striations in the perineal region. Eggs are deposited in a gelatinous matrix outside the body of the female. Females become sedentary, and as they mature to adults, galls develop. Females produce an egg sac that extends to the outside of the root surface. The life cycle takes about 45 days at 25°C. In addition to sugar beet, hosts include broccoli, cabbage, carrot, cucumber, lettuce, pea, pumpkin, radish, rutabaga, spinach, tomato, and turnip (Ferris, 2021). Nonhost rotation crops include alfalfa, potato, and grain. Weed hosts that must be controlled during rotations include *Kochia* spp., common lambsquarters, Russian thistle, puncturevine, common purslane, and cacti (*Coryphantha vivipara*, *Opuntia fragilis*, and *Opuntia tortispina*) (Gray, 1986).

Others nematodes

The sugarcane cyst nematode is one of the predominant nematode species in sugarcane (Fademi et al., 1997). This nematode was first reported as *Heterodera schachtii* from a sugarcane field in Congo in 1961 (Luc & Merny, 1963). Salawu (1994) studied the development of *Heterodera sacchari* in sugarcane and found that the nematode is fast reproducing as it completes the life cycle (J₂ to adult females) within a month under favorable conditions. The infected plants show stunted growth and leaf yellowing under high population levels.

The reniform nematodes, *Rotylenchulus parvus* and *R. reniformis*, have been reported to occur in sugarcane soils in different countries such as Venezuela, Dominican Republic, India, Puerto Rico (Singh & Misra, 1974), Australia (Stirling et al., 2002a, 2002b), Nigeria (Khan, 1991), and Brazil (Rosa et al., 2003). However, in one study, sugarcane was found to be immune to *Rotylenchulus reniformis* but its different strains may be pathogenic (Birchfield & Brister, 1962). The pathogenicity studies on *R. reniformis* in sugarcane showed all stages of females and males invaded the host (Mehta & Sundararaj, 1989). After egg laying, females dropped from the feeding sites leaving only egg masses attached to the roots. Little is known about the nature and extent of crop damage inflicted by reniform nematodes to sugarcane.

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A number of ectoparasitic nematodes have also been found aggregating in the root zone of sugarcane and cause notable damage when their populations exceed economic threshold levels. Sugarcane roots harbor a number of species of *Tylenchorhynchus*, viz., *T. shivanandi* (Shaw & Khan, 1992), *T. paracanalisis* (Khan, 1991), *T. microcephalus* (Siddiqui & Patel, 1990), and *T. annulatus* (Blair et al., 1999a). *T.* species are ectoparasites and feed on epidermal cells and root hairs (Siddiqui, 2005). The root system of cane inoculated with *T. annulatus* became sparse with signs of necrosis and moderate-to-severe stunting of the lateral roots. The overall number of root hairs was decreased and premature death of sett roots took place (Birchfield & Martin, 1956; Harris, 1974).

Species of *Xiphinema*, *Longidorus*, and *Paralongidorus* possess long stylet and have been found associated with the root damage in sugarcane (Horner & Jensen, 1954). A number of *Xiphinema* spp. (over 40 species) have been reported from sugarcane fields; the commonly occurring species are *X. americanum*, *X. brevicaudatum*, *X. elongatus*, and *X. basiri* (Renubala et al., 1991; Sankranarayana, 2010). Spaul and Heyns (1991) recorded 21 species of *Xiphinema*, four species of *Longidorus*, eight species of *Trichodorus*, and four species of *Paralongidorus*. *Xiphinema elongatus* was the most commonly occurring in 60% of the fields surveyed followed by *X. mampara* recorded from 46% fields in South Africa. The roots of infected cane plants with *X. elongatum* became coarse and sparse with tissue decay and swelling of root tips (Harris, 1974). *Xiphinema* and *Paratrachodorus* were dominant nematodes in West Indies (Cadet, 1989). Among the trichodorids occurring in sugarcane fields, *Paratrachodorus minor* has been reported to be most common species and is widespread in United States, Taiwan, South Africa, Zimbabwe, and Burkino Faso (Spaul & Cadet, 1990). *Paratrachodorus minor* feeds ectoparasitically on epidermal and subepidermal cells. The cells are killed and become typically stubby and lack fine feeder roots (Apt & Koike, 1962c).

There are several other ectoparasitic nematodes such as *Belonolaimus*, *Hirschmanniella*, *Criconemella*, and *Hemicycliophora* which have been reported from sugarcane rhizosphere (Mehta & Narayanaswamy, 1993). Razjivin et al. (1973) and Mehta (1986) reported that sting nematodes, *Belonolaimus gracilis* and *B. lineatus*, have been associated with sugarcane decline in some areas. In addition, *Rotylenchus* spp. in southern Rhodesia and *Scutellonema* spp. in Kenya have also been found infesting sugarcane roots (Razjivin et al., 1973; Razjivin & Milian, 1978). *Hirschmanniella abnormalis* (Renubala et al., 1992) and *Hemicycliophora* spp. (Carbonell, 1978) were among the most widespread and abundantly occurring plant parasitic nematodes in sugarcane cropping system causing distortion to the roots and suppressing growth of cane in Australia (Blair & Stirling, 2007), Burkina Faso, and South Africa (Cadet & Spaul, 2005). In Dominican Republic, El Salvador, Indonesia, South Africa, and Venezuela, *Criconemella* and related genera were reported to be widespread in sugar fields (Roman & Grullon, 1975; Spaul, 1981). Harper (1975) recorded *Criconema xenoplax* to be an important nematode-infesting sugarcane in Indonesia.

The needle nematodes, *Longidorus* spp., parasitize sugar beet in several countries in Europe. The most common species found in sugar beet fields are *L. elongatus*, *L. attenuatus*, and *L. macrosoma* (Bridge & Starr, 2007). *Longidorus* spp. often occur together with *Trichodorus* spp. and *Paratrachodorus* spp. on sandy soils. Infected plants often show stunted growth in patches. *Longidorus* spp. are ectoparasites. With the very long stylet, they typically attack roots in the root tips where the growing point is destroyed. This causes characteristic hook-like galls. *Longidorus* spp. is one of the largest plant parasitic nematodes and females can reach a length of 11 mm. The life cycle is 19 weeks at 20°C. *Longidorus* spp. can be several years old.

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The host range of *Longidorus* spp. is very wide including most cultural plants and weeds (Andersson, 2018).

Sugar beets are also attacked by pin nematodes, *Paratylenchus* spp. The genus *Paratylenchus* has a worldwide distribution (Van Den Berg et al., 2014). The symptoms are similar to those caused by other free-living nematodes on sugar beet, forking, and development of numerous lateral roots. The pin nematodes are very small, resistant to dehydration (Ghaderi, 2019). The pin nematodes range in size between 0.2 and 0.6 mm. Because of their short generation time, population can increase fast.

Nematodes in cohabitation

Sometimes, plant parasitic nematodes have been found to be more damaging at community level rather than their monoculture populations. Salawu (1992) recorded significant impact of infestation with *Meloidogyne incognita* and *Heterodera sacchari* in cohabitation on the growth of sugarcane. The shoot and root weights of sugarcane were significantly decreased, and severe necrosis and galling were developed due to concomitant inoculation with *M. incognita* and *H. sacchari*. A study involving four nematode species revealed negative impact of *Pratylenchus zae* with *Helicotylenchus dihystera* (Sundararaj & Mehta, 1993). In another multispecies interaction experiment involving *Hoplolaimus indicus*, *Helicotylenchus dihystera* and *Tylenchorhynchus annulatus* indicated that *Hoplolaimus indicus* had a negative interaction with *Helicotylenchus dihystera* and a positive interaction with *Tylenchorhynchus annulatus* while *Helicotylenchus dihystera* showed negative association with *Tylenchorhynchus annulatus* (Sundararaj & Mehta, 1995). Similarly, the concomitant inoculation of *Pratylenchus zae* and *Meloidogyne javanica* on sugarcane resulted in antagonistic impact on *Meloidogyne javanica* (Sujatha & Mehta, 1998). As a result, the development and reproduction of *Meloidogyne javanica* were slowed down in the presence of *Pratylenchus zae*. However, the concomitant inoculation caused considerably greater quantitative and qualitative reduction in the plant growth and productivity of sugarcane. Sujatha and Mehta (1997) reported that cohabitating *Pratylenchus zae* and *Meloidogyne javanica* resulted in lower buildup of their populations in the soil and root tissue in comparison to single inoculation because of mutual negative effects.

Economic importance of nematodes associated with sugarcane and sugar beets

The continuous monoculture, ratooning, and massive root system gradually lead to high-population buildups of nematodes in the sugarcane fields and subsequently cause economic loss to the crop. Populations of *Hoplolaimus* and *Helicotylenchus* were found very high in the fields where sugarcane was grown continuously for more than 20–25 years. In such fields, the sugarcane crop showed stunting, drying, and discoloration of leaves despite using improved agricultural practices (Sankranarayana, 2010).

According to CNRCP, United States, 15.3% annual yield loss to sugarcane occurs due to nematode infestation based on worldwide nematode survey of nematologists (Sasser &

Freckman, 1987). However, more recent estimates indicate that the loss in sugarcane yield caused by plant-parasitic nematodes may be equivalent to approximately US\$250 million annually (Berry et al., 2008). Due to ratooning as well as climatic conditions, the yield loss in sugarcane may vary with season, 11% loss in a very dry season, and about 32% under good rainfall areas (Spaull, 1995). In South Africa, the annual loss due to nematode infestation could amount to 0.9 million tons cane (Spaull et al., 1990). In India, Mehta (1992) estimated around 15% yield loss in sugarcane. Sasser (1979) reported that *Meloidogyne* spp. may be responsible for 6%–9% yield loss to sugarcane in Mexico, Central and South America, the Caribbean and South East Asia. The average cane losses due to nematode infestation in sugarcane crop have been estimated at more than 900,000 tons per annum in South Africa. Losses due to *Pratylenchus zae*, *Meloidogyne incognita*, *Hoplolaimus indicus*, and *Trichodorus goldeni* alone varied from 1% to 63% of the total loss caused by nematodes (Haider & Nath, 1996). In Australia, sugarcane root lesion nematode is reported to reduce yield equivalent to AU\$80 million annually (Blair & Stirling, 2007).

Nematode damage to sugar beet can result in approximately 11% loss in yield (Sasser & Freckman, 1987). The sugar beet nematode, *Heterodera schachtii*, is estimated to cause 90% of the damage to sugar beet caused by nematodes (Steele, 1984). *Heterodera schachtii* is estimated to cause an annual loss greater than US\$95 million in the European Union, and cause yield losses up to 60% of the crop (Muller, 1999).

Management

The nematode infestation in sugarcane and sugar beet is generally overlooked by growers unless the nematode population becomes very high, and severe stunting and leaf yellow occur. The methods of nematode management in sugarcane and sugar beet depend on region and species combination of nematodes and host. Some of the important sustainable methods which may prove effective and economic in suppressing nematode populations in sugarcane and sugar beet cropping system are summarized below.

Cultural practices

Intercropping and organic amendments

The intercropping with marigold (*Tagetes erecta*) or Sunhemp (*Sesbania bispinosa*, *S. aculeata*) along with application of pressmud (25 ton/ha) or neem cake (2 ton/ha) resulted in significant decline in the *Helicotylenchus multicinctus* infestation in sugarcane roots (Jonathan et al., 1999). Somasekhar and Mehta (1998) reported that cultivation of sesame, mustard, pulses, tomato, green manures, and spice crops may lead to a considerable decline in the nematode community as these crops support low populations of phytonematodes. Haider et al. (2001) observed that intercropping with *Nigella sativa* reduced the population of major nematodes inhabiting in sugarcane fields. In North Queensland, a single soybean crop increased free-living nematodes and reduced *Pratylenchus zae* by 44%–89% compared to sugarcane alone. An integrated farming system based on residue retention, minimum tillage, and crop rotation with a legume has been found quite effective in improving the sugar yields,

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reducing the costs, and providing additional income (Stirling, 2008). Oliveira et al. (2008) observed substantial decline in the population of *Pratylenchus* spp. when a cropping sequence of sugarcane-crotalaria-sugarcane was adopted.

Soil amendments with manure and cakes have been found considerably effective in suppressing soil populations of phytonematodes (Tiyagi & Alam, 1995). Soil amendment with cakes of groundnut, sesame, neem, cotton seed, and coconut significantly increased cane yield and suppressed *Pratylenchus zae* population (Mehta et al., 1994a, 1994b). Application of oilcakes of *Ricinus communis*, *Pongamia glabra*, *Brassica campestris* and *Azadirachta indica*, pressmud, and carbofuran greatly reduced nematode population in sugarcane (Haider & Wari, 1993). The lesion nematode population also decreased in the fields applied with Naemin, Neemark, FYM, pressmud, and *Calotropis procera* (Mehta & Sundararaj, 1995). The soil amendment with pressmud alone or in combination with Neemark/Naemin, carbofuran, or micronutrients reduced *Pratylenchus zae* population in sugarcane fields (Mehta & Sundararaj, 1999). Moussa et al. (2006) reported that the soil application of cattle, poultry, and pigeon manures induced a significant decline in the population of *Pratylenchus zae* and improvement in the length and fresh weight of shoot of sugarcane plants. Jonathan et al. (1991) found that soil application of neem cake (2 tons/ha) and pressmud (25 tons/ha) resulted in 81%–82% decline in the population of nematodes infesting sugarcane fields after 90 days and 60%–62% decline after 180 days of amendment. In a field experiment on sugarcane in Philippines, pressmud (80 tons/ha), FYM (30 tons/ha), or a combination of both (40 tons/ha) significantly reduced the population of plant parasitic nematodes up to 6 months after treatments (Estioko et al., 1988).

There are several varieties of oil seed radish (OSR, *Raphanus sativus* L. spp. *oleiformis* Pers.) and white mustard (WM, *Sinapis alba* L.) that are resistant to *Heterodera schachtii*. These varieties can be used as trap crops to actively reduce the number of nematodes in an infested field. The second-stage juveniles infect the trap crops but are unable to develop to mature females, the so-called dead-end trap crops (Vestergård, 2018). Many varieties of OSR also show resistance to some free-living and root-knot nematodes in addition to the resistance to *Heterodera schachtii*. The choice of OSR variety must be based on soil sampling and identification of the nematode species present in the field. Another strategy is to use a susceptible trap crop. This crop will stimulate hatching and infection. It is important that the trap crop is mulched before the life cycle of the nematode is completed (Vestergård, 2018). Monitoring of soil temperature is therefore needed. For the control of *Meloidogyne hapla*, mulching before 400-degree days above 8°C is necessary (Vestergård, 2018).

Biofumigation has been found effective to manage nematodes on sugar beet in warm climates. Glucosinolates are secondary metabolites found in Brassicas. When they are incorporated into soil, they break down and release isothiocyanates, similar to the isothiocyanates found in metam sodium nematicides. Placing a plastic sheet over the soil will slow down the rate at which isothiocyanates volatilize, improving efficacy (Bui & Desaeger, 2021; Westerdahl, 2021).

Crop rotation

Crop rotation of sugarcane with an economically viable nonhost crop is a very effective management practice. Peanut followed by the maize and *Crotalaria juncea* are good options,

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where maize and *Crotalaria juncea* support very low reproduction of root-knot nematodes (de Moura, 1991b). Two crops of peanut in a year, two crops of corn in a year, one crop of corn in the first half of the year, and a crop of peanut in the second half of the year may greatly suppress the soil population of *Meloidogyne javanica*. However, rotation of maize/peanut may increase the populations of *Pratylenchus zae* and *Helicotylenchus dihystra* and decrease the density of *Criconemella* and *Trichodorus* (de Moura et al., 1997). The combination of *Crotalaria juncea* and *Mucuna aterrima* followed by a peanut crop showed no effect on nematode populations except for the numerical increase in the population of *Trichodorus* spp. and the free-living group. Rashid (1981) found that growing a combination of maize and marigold or paddy and mustard drastically reduced the population of *Hoplolaimus indicus*, *Helicotylenchus* spp., *Pratylenchus* spp., and *Trichodorus goldeni*. The soybean/peanut rotation increased free-living nematodes and reduced the population of *Pratylenchus zae* and *Rotylenchulus parvus* by 75% and 93%, respectively (Stirling et al., 2002a, 2002b).

Developing a crop rotation program on sugar beet begins with sampling the field to determine the nematode species present. A nonhost crop can then be selected by referring to a published list of hosts or a database (Ferris, 2022). A more effective program can be developed if additional information on the biology of the nematodes present in the field is available. This would include knowledge of the rate at which nematodes increase during a growing season on a host crop and decline under nonhost crops; the economic damage threshold; and effects of planting and harvesting dates on nematode reproduction (Westerdahl, n.d.).

Additional hosts for sugar beet cyst nematode include cabbage, canola, brussels sprout, cauliflower, broccoli, mustard, spinach, turnip, and radish. Weed hosts include mustard, pigweed, lambs-quarters, shepherd's purse, and purslane. In addition to sugar beet, false root-knot nematode hosts include broccoli, cabbage, carrot, cucumber, lettuce, pea, pumpkin, radish, rutabaga, spinach, tomato, and turnip. Nonhost rotation crops include alfalfa, potato, and grain. Weed hosts that must be controlled during rotations include *Kochia* spp., common lambsquarters, Russian thistle, puncturevine, common purslane, and cacti (*Coryphantha vivipara*, *Opuntia fragilis*, and *Opuntia tortispina*). Because of their wide host ranges, crop rotation may not be an effective control measure for root knot, lesion, or stubby root nematodes (Gray, 1986).

Host-resistant

Sugarcane cultivars express varying degree of susceptibility to plant parasitic nematodes. Varieties like Co 290, Co 527, and a few others have shown moderate susceptibility to root-knot nematode (Rao, 1966). Suwarno (1991) reported that cultivars Ps 60, Ps 59, and Ps 56 were found highly resistant to *Meloidogyne* spp. Dinardo (1999) found the cvs IAC 83-4157 and RB 825336 expressed resistance to *M. incognita*. Dinardo (1994) screened eight sugarcane cultivars to *Pratylenchus brachyurus* and *P. zae*. The cvs. SP 70-1078 and SP70-1143 were found to be poor host. In a trial in Brazil, cvs. SP 71-1632, SP 72-1861, and RB 735275 were found tolerant and SP 70-1143 resistant to *Meloidogyne javanica* and the cv. IAC 77-51 tolerant to *Pratylenchus zae* (Dinardo et al., 1995). Among 24 sugarcane clones evaluated for resistance against *Pratylenchus zae* in India, the clones Co 93004, Co 93015, and Co 90010 were found resistant (Mehta & Somasekhar, 1998b). In another screening program, the

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cultivars Co 88020, Co 89009, and Co 89034 expressed resistance to *Pratylenchus zeae* (Mehta et al., 1994a, 1994b).

Development of sugar beet varieties resistant to plant parasitic nematodes is an important way of control. A source of resistance to *Meloidogyne* spp. was identified from sea beet in a study by Yu (1995). The resistance is mediated through a dominant single gene called R6m-1. Since then, molecular markers have been developed for use in plant breeding (Bakooie et al., 2015; Weiland & Yu, 2003).

Currently, there are no sugar beet varieties resistant to *Ditylenchus dipsaci* available for commercial use. In a study by Storelli et al. (2021a) and Storelli et al. (2021b), sugar beet breeding lines and prebreeding populations were investigated for their ability to reduce penetration and reproduction of *Ditylenchus dipsaci*. One genotype, DIT-119, was found to reduce penetration rate but not reproduction compared to the susceptible control. The authors conclude that the variation found among genotypes needs to be further investigated in large-scale screenings (Storelli et al., 2021a, 2021b).

Sugar beet varieties resistant to sugar beet cyst nematodes (BCN) do not allow reproduction since female development is not supported. The available commercial resistant varieties are seldom used since their yield level is low. However, the introduction of tolerant varieties has provided new possibilities to grow sugar beet without yield losses on infested fields. Tolerant varieties perform well on both uninfested and infested fields and are able to compensate for the damage made by the nematodes. In a study by Stevanato et al. (2015), a single nucleotide polymorphism (SNP) marker from the *Beta vulgaris* ssp. *maritima* source WB242 was identified. This marker, SNP192, was linked to the nematode tolerance gene HsBvm-1.

Constant monitoring of the population development of *Heterodera schachtii* in the field is needed since tolerant varieties allow infestation and multiplication of beet cyst nematodes to various degrees. Tolerant varieties seldom show any symptoms of BCN infestation and there is a risk that population increases may be overlooked. At very high population densities, tolerant varieties may also react with low yield levels (Hauer et al., 2016). Reuther et al. (2017) studied 5 tolerant varieties on 15 locations in Germany during three years. They classified the tolerant varieties as mostly moderately resistant. The authors suggest that new sugar beet varieties should be regularly tested and classified in four categories: moderately or highly susceptible, or moderately or highly resistant. This will help farmers in choosing management strategies for infested fields (Reuther et al., 2017).

Biological control

Biological control is an effective, ecofriendly, and sustainable method of nematode management (Khan, 2007). Application of biocontrol agents (BCA) at the time of planting is getting popularity in achieving sustainable nematode management especially in horticultural crops (Khan, 2007; Khan et al., 2020; Khan & Anwer, 2011; Sikora & Roberts, 2018; Stirling, 1991). The nematode antagonists such as *Pochonia chlamydosporia* (= *Verticillium chlamydosporium*), *Purpureocillium lilacinum* (= *Paecilomyces lilacinus*), *Aspergillus niger*, *Pasteuria penetrans*, etc. (Jatala, 1986; Kerry, 2000; Khan, 2016; Stirling, 1991), and phosphate

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solubilizing microorganisms such as *Pseudomonas*, *Bacillus*, *Penicillium*, and *Aspergillus* species/strains (Khan et al., 2009, 2016a, 2016b) may greatly contribute in protecting sugarcane and sugar beet, if applied at the time of planting. In recent decades, *Trichoderma* spp. have emerged as an important BCA in the management of plant pathogenic fungi and nematodes (Khan & Mohiddin, 2018; Mohiddin et al., 2010). The commercial formulations of *Trichoderma virens*, *T. harzianum*, and *T. hamatum* are available (Khan et al., 2011, 2017), which have been found highly effective against fungal and nematode diseases when applied on the planting material (Mohammed & Khan, 2021; Sikora & Roberts, 2018). The sugarcane rhizosphere ecosystem harbors diverse group of organisms including the nematode antagonists; hence there is a potential opportunity for exploiting the naturally occurring antagonists against nematodes infesting sugarcane. In early years of biocontrol research, a sporozoan infecting 34% of *Meloidogyne* females in sugarcane roots was recorded in Mauritius (Williams, 1960). A similar sporozoan was found suppressive to *Xiphinema* populations (Williams, 1967). Chu and Hsu (1965) isolated five species of nematode trapping fungi, *Arthrobotrys cladodes*, *A. conoides*, *A. oligospora*, *Dactylella ellipsospora*, and *Dactylella* sp. from sugarcane fields in Taiwan. Among these, *Arthrobotrys oligospora* was found to be suppressive to *Meloidogyne* spp. in a pot experiment. Some other nematophagous fungi, *Arthrobotrys cladodes*, *Dactylaria* sp., *Monacrosporium gephyrophagum*, and *Legenidium* spp. have also been isolated from sugarcane fields (Gowda et al., 1982). Agnihotri (1992) isolated *Catenaria vermicola*, *Alternaria alternata*, and *Protoascus subuliformis* from the sugarcane fields, and of these, only *Catenaria vermicola* effectively reduced the nematode population. *Pasteuria penetrans*, a potential nematode parasite, has also been isolated from sugarcane field (Lin & Chen, 1992).

Among various biocontrol fungi, *Purpureocillium lilacinum*, *Pochonia chlamydosporia*, *Trichoderma* spp., etc., have been found most effective candidates against plant-parasitic nematodes (Khan, 2008). Soil application of *Purpureocillium lilacinum* (200 or 400 kg/ha) along with Furadon 5 G (30 or 60 kg/ha) reduced *Meloidogyne incognita* population and improved cane yield by 17 tons/ha (Novaretti et al., 1986). *Paralongidorus buchae* was found infected with *Catenaria anguillulae* in sugarcane fields of Mauritius (Ciancio & Chinappen, 1987). Application of pressmud alone and pressmud loaded with *Trichoderma viride* gave significant enhancement in the plant growth and decline in *Pratylenchus zae* population (Somasekhar et al., 1998). The sugarcane invasion by *Pratylenchus zae* decreased due to application of antagonistic fungi, *Purpureocillium lilacinum*, *Pochonia chlamydosporium*, *Trichoderma viride*, *Beauveria bassiana*, *Chaetomium* sp., and *Humicola* sp. (Sankaranarayanan et al., 2002, 2007). An application of *Metarhizium anisopliae* reduced nematode population in the sugarcane root tissue (Rossi et al., 2006). Soil application of *Glomus fasciculatum* increased biomass of sugarcane plants and its application with phosphatic fertilizers reduced the *Pratylenchus zae* population by 42%–54% (Sankaranarayana et al., 2010). In addition, phosphate-solubilizing microorganisms may also be used to obtain plant growth improvement and nematode suppression (Khan et al., 2009).

Biological control of nematodes infesting sugar beet includes predators and parasites, soil amendments, killed microbials, bionematicides, and “natural” products. A variety of biological products are sold as soil amendments with only testimonial data that they suppress or control nematodes. An interesting finding with some of the newer products is that they may increase yields without reducing nematode populations (Westerdahl, n.d.). Several biological nematicides are available commercially in some sugar beet growing areas. DiTera is a

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killed microbial formulation of the fungus *Myrothecium verrucaria* (Valent, n.d.). NemaQ is a botanical extract of the soapbark tree *Quillaja* (Brandt, n.d.). Melocon is a formulation of the nematode parasitic fungus *Purpureocillium lilacinum* (Nehrer & Ocamb, n.d.). A commercial product has been developed in which sugar beet seeds are coated with *Pasteuria nishizawae*. The coating contains a mycelial and endospore-forming bacterial parasite of cyst nematodes (Syngenta, 2015). The relevant researches in these areas may lead for efficient sustainable methods (Chitambar et al., 2018; Westerdahl, 2011).

Conclusions and future prospects

The nematode infestation in sugarcane crop is generally overlooked by the farmers, although these pests have been involved in “slow yield decline.” The situation warrants need to survey the sugarcane fields along with adjoining fields to assess the nematode damage to sugarcane and to make realize the farmers about significance of nematode management in sugarcane and other crops. From scientific point of view, host-parasite relationship involving different nematode species needs to be examined to ascertain the role of phytonematodes in “sugarcane slow yield decline,” and necessary management strategies are needed to be devised and validated. Efforts to identify multispecies resistance should be intensified using the recent biotechnological approaches. Further, nanotechnology with regard to development of nanobiopesticides and nanofertilizers has great potential for use in nematode management in sugarcane. However, much greater emphasis should be given for exploration and commercial utilization of multifacious biocontrol agents for eco-friendly and sustainable management of nematode infestation in sugarcane. Pesticides may be applied as sett treatment in integration with biocontrol agents and other nonchemical measures. Research in recent years has developed new methods for sustainable management of nematodes on sugar beet. A number of biological nematicides are available commercially. Chemical nematicides that are safer for nontargets have been developed. Sugar beet varieties resistant to cyst nematode have been released. Yield enhancement and nematode suppression have been demonstrated with cover cropping, trap cropping, biofumigation, and other cultural practices. Continued research efforts in these and other areas hold promise for development of additional sustainable advances in nematode management.

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