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Review Article

From Genes to Fields: Marker-Assisted Selection for Nematode Resistance in Crops

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ABSTRACT

Plant-parasitic nematodes (PPNs) are one of the serious threats to agricultural production worldwide, causing enormous economic losses and posing a threat to food security. This review outlines a few important groups of PPNs, their economic losses, and current control approaches. Marker Assisted Selection (MAS) has been recognized as a precise and efficient approach for developing nematode-resistant cultivars and an environmentally friendly alternative to conventional control practices. Genome-Wide Association Studies (GWAS) thereby provide a way of identifying novel resistance loci and deciphering the genetic basis of resistance traits. MAS guided by validated GWAS results have therefore immense prospects for enhancing resistance breeding, reducing over-dependence on nematicides, and fostering healthy agricultural systems. Future efforts should focus on integrating molecular with field-based approaches to maximize benefits in the control of nematodes.

Keywords: Plant-parasitic nematodes, Marker-assisted selection, Genome-wide association studies, Nematode resistance, Sustainable agriculture

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INTRODUCTION

Plant parasitic nematodes (PPNs) seriously threaten global agriculture leading to annual crop losses worth over $152 billion worldwide. These nematodes are a diverse group of microscopic roundworms (Jones *et al.*, 2013; Ali *et al.*, 2017a; Khan, 2023) that infect thousands of plant species, including many economically important crops. PPNs cause damage by developing feeding sites or directly feeding on crop roots and in some cases tissues other than roots (Williamson and Hussey, 1996). PPN infestation thus causes interference with general plant activities because of the parasitic relationship culminating in the reduced uptake of nutrients and water, stunted growth, and in some cases, death of the plants (Davis *et al.*, 2004; Parrado *et al.*, 2024). Nematodes use their needle-like stylets to invade plant cells for nutrient uptake from plant tissues. They also use several enzymes and effectors that change the cellular environment of the plant for nematode

development and suppress immune responses from host plants (Ali *et al.*, 2017b; Davis *et al.*, 2004; Gheysen and Mitchum, 2011). Root-knot nematodes (RKNs) (*Meloidogyne* spp.), cyst nematodes (CNs) (*Heterodera* spp. and *Globodera* spp.), and root-lesion nematodes (RLNs) (*Pratylenchus* spp.) are among the most harmful PPNs worldwide (Moens *et al.*, 2009; Nicol *et al.*, 2011; Khan *et al.*, 2023).

The management approaches to control PPNs include crop rotation, planting resistant cultivars of plants, and the application of nematicides (Ali *et al.*, 2017a; Sikora *et al.*, 2018). However, environmental and health concerns associated with chemical control have prompted research on more sustainable management approaches (Kerry and Hominick, 2002). To present additional environmentally friendly options, research has focused on biological control agents, such as fungal and bacterial antagonists or beneficial nematode predators (Hallmann *et al.*, 2009; Stirling, 2014; Anwar *et al.*, 2022; Antill *et al.*, 2023). Biological soil amendments and plant extracts are also gaining interest in managing PPNs (Arshad *et al.*, 2020; Arshad *et al.*, 2021a; Fayyaz *et al.*, 2024; Tahir *et al.*, 2023). Recently, enzymatic extracts from bacterial antagonists have been successfully used to suppress different life stages of potato cyst nematodes (Hajjaji *et al.* 2024). There is a dire need for further research on the biology of PPNs and host interactions to develop practical and sustainable control measures, such as host resistance (Trudgill and Blok, 2001; Chitwood, 2003; Ali *et al.*, 2017).

Host resistance is considered one of the most economical and sustainable solutions for managing PPNs (Ali *et al.*, 2019; Mashavakure *et al.*, 2023). Conventional breeding is a time-consuming process that requires up to 12 years to develop resistant genotypes (e.g., wheat). Molecular marker techniques are important genomic tools for developing nematode-resistant germplasm to mitigate the crop losses posed by PPNs (Sahu *et al.*, 2017). The incorporation of molecular marker techniques into breeding programs helps scientists save time and resources during the development of nematode-resistant genotypes and limits the losses incurred by PPNs (Ali *et al.*, 2019). Marker-assisted selection (MAS) is an essential breeding method, as markers assist in tracing and eventually pyramiding genetic loci governing important traits, such as nematode resistance. Identification of quantitative trait loci (QTL) and allelic diversity, which localizes genomic areas related to polygenic resistance to nematodes, has so far been mainly accomplished largely using simple sequence repeats (SSRs) (Sahu *et al.*, 2017).

The emergence of new and more virulent populations of nematodes, specifically resistance-breaking RKN species, is a serious threat to global agricultural systems. These obstacles have necessitated the discovery of new resistance genes for sustainable nematode management. Polygenic resistance regulated by minor effect QTL means lifelong non-specific resistance to different nematode types or populations (Kumar, 2010). The use of next-generation sequencing technologies, such as genotyping by sequencing (GBS), has transformed exploring single nucleotide polymorphism (SNP), which then enables genome-wide association studies (GWAS) and identification of loci and more intense improvement of breeding aimed at nematode resistance (Ibrahim *et al.*, 2021).

GBS approaches followed by SNP hunting have developed into a tremendous platform for identifying resistant genotypes and for understanding host–nematode interactions (Ali *et al.*, 2019). These molecular techniques boost our ability to fight nematode-induced losses in crops and pave the way toward resilient agricultural systems. This review presents the impact of PPNs on agriculture, some important groups of nematodes, and nematode management strategies employed worldwide. This review also discusses the details of the molecular markers generated in various crop plants for different PPN species through bi-parental QTL mapping and GWAS.

IMPORTANT CATEGORIES OF PPNs

PPNs can be broadly classified based on the type of feeding behavior, life cycle, and host-plant interaction as endoparasitic, semi-endoparasitic, or ectoparasitic nematodes. They are among the most significant contributors to global agricultural losses. Endoparasitic nematodes such as RKNs and CNs (sedentary endoparasites) penetrate plant roots and form feeding structures. In the case of RKNs, the vascular tissues are transformed into giant cells on which the female nematode feeds, disrupting the transport of nutrients and water through xylem vessels, as root galls are eventually produced. CNs, on the other hand, form syncytia which are metabolically active feeding sites formed by breaking, destroying, and merging adjoining cells' walls (Ali *et al.*, 2015). In the case of both RKN and CN, feeding by the female induces the plant to form these feeding site cells, which are morphologically, physiologically, and biochemically altered. The eggs of CN develop into resistant cysts capable of surviving in the soil for over 10 years in the absence of host plants (Jones *et al.*, 2013). RLNs (migratory endoparasites) wound plant roots and gain access to the interior of the root, where they can move around and feed. These wounds create infection sites that allow plant roots to get infected by other fungal and bacterial pathogens. They have a wide host range and can infest many

crops, including cereals, legumes, and most horticultural plants, causing significant agricultural losses (Luc *et al.* 2005). These attributes make endoparasitic nematodes particularly harmful to crops, leading to significant economic impact

Semi-endoparasitic nematodes, such as *Rotylenchulus reniformis* (reniform nematode), partially penetrate the root and establish feeding sites in the cortex. These nematodes remain anchored at the point of entry while feeding on plant tissues, causing wilting, chlorosis, and reduced plant vigor. The reniform nematode is particularly problematic in tropical and subtropical regions, affecting crops such as cotton, soybean, and pineapple (Bridge and Starr, 2007). Their dual strategies of invasion and external survival allow them to persist in various cropping systems. Ectoparasitic nematodes, such as *Xiphinema* (dagger nematodes) and *Trichodorus* (stubby-root nematodes), feed externally on plant roots by inserting their stylet into the root cortex and withdrawing nutrients. Dagger nematodes are also vectors of plant viruses, including the grapevine fanleaf virus, making them an indirect but significant threat to agriculture (Luc *et al.* 2005).

ECONOMIC IMPACT OF PLANT PARASITIC NEMATODES

PPNs negatively impact agricultural systems and the economy by causing extensive yield losses (Ali *et al.*, 2017b). Their interference with nutrient and water uptake due to damage and obstruction in plant roots leads to stunted growth, reduced vigor, and huge reductions in yield (Jones *et al.*, 2013). Their infestation also causes an increase in management costs, making the largest possible economic impacts on staple and cash crops such as wheat, rice, maize, soybeans, potatoes, and vegetables (Singh *et al.* 2015).

PPNs develop a wide range of symptoms in plants, resulting from their feeding activity on roots, stems, leaves, or other tissues in different crops with special reference to the roots. These symptoms often overlap with those caused by nutrient deficiencies or other pathogens, complicating the disease diagnosis. However, nematode-specific symptoms can generally be categorized into below-ground root damage and above-ground signs. Below-ground symptoms are primarily observed in the roots, where most nematodes feed and establish their specialized structures (Ali *et al.*, 2017a). RKNs induce the formation of root galls, which are swollen, knot-like structures containing several giant cells that disrupt the vascular system and impair water and nutrient transport (Ali *et al.*, 2015). CNs cause stunted root systems, and the development of specialized feeding sites called syncytia, leading to reduced root efficiency and nutrient uptake. Root lesion nematodes (*Pratylenchus* spp.) infection leads to necrotic lesions on root surfaces due to their feeding activity, making the roots susceptible to secondary infections by fungal pathogens. These symptoms often weaken the root systems, making plants more vulnerable to environmental stress (Jones *et al.*, 2013).

Above-ground symptoms are indirect effects of root damage and nutrient transport disruption. Plants infected by nematodes often exhibit stunted growth, chlorosis (yellowing of leaves), wilting, and poor vigor. For example, nematode-infected crops may fail to reach their expected height or produce fewer flowers and fruits. In severe cases, plants can die prematurely, particularly under drought or nutrient-limitation conditions. Symptoms may vary depending on the crop and nematode species but are generally more pronounced in resource-poor soils (Bridge and Starr, 2007). Similarly, leaf and stem nematodes such as *Aphelenchoides* spp. directly attack aerial plant parts. These nematodes cause localized necrosis resulting in chlorotic spots, deformed leaves, or stem swelling. Foliar nematodes are particularly problematic in ornamentals, cereals, and other crops, where their activity can lead to significant economic losses. In many cases, the damage caused by such nematodes is misdiagnosed as fungal or bacterial infections, delaying appropriate management measures (Luc *et al.*, 2005). In addition, seed symptoms (e.g., discoloration) are caused by seed-gall nematodes (*Anguina tritici*) targeting wheat. The above-ground and below-ground symptoms are displayed in Figure 1.

The annual economic losses due to PPNs are estimated at $152 billion globally. RKNs are important in causing serious damage to an extensive range of crops, especially vegetables (Moens *et al.*, 2009), whereas CNs cause serious damage to crops such as potatoes and wheat (Nicol *et al.*, 2011). These losses are not limited to rich agricultural economies; rather, smallholder farmers, mostly in poor countries, have borne the brunt of losses from nematodes due to their lack of access to effective nematode management strategies (Coyne *et al.*, 2018). Thus, the indirect impact of PPNs has significant economic implications. These infestations often lead to the use of expensive nematicides, which can harm the environment and human health. Farmers generally rely on crop rotation and fallowing since they are common alternative cropping practices to control nematodes. Thus, overall land-use efficiency tends to be lower (Coyne *et al.*, 2018). The economic effect of PPN infestation is broad in terms of other

socioeconomic domains as well because increased food prices triggered by lower crop yields will probably lead to food insecurity at the local and global levels (Nicol *et al.*, 2011). Losses due to nematode damage have a ripple effect on rural incomes, livelihoods, and economic viability, especially where agriculture is the main source of income (Coyne *et al.*, 2018).

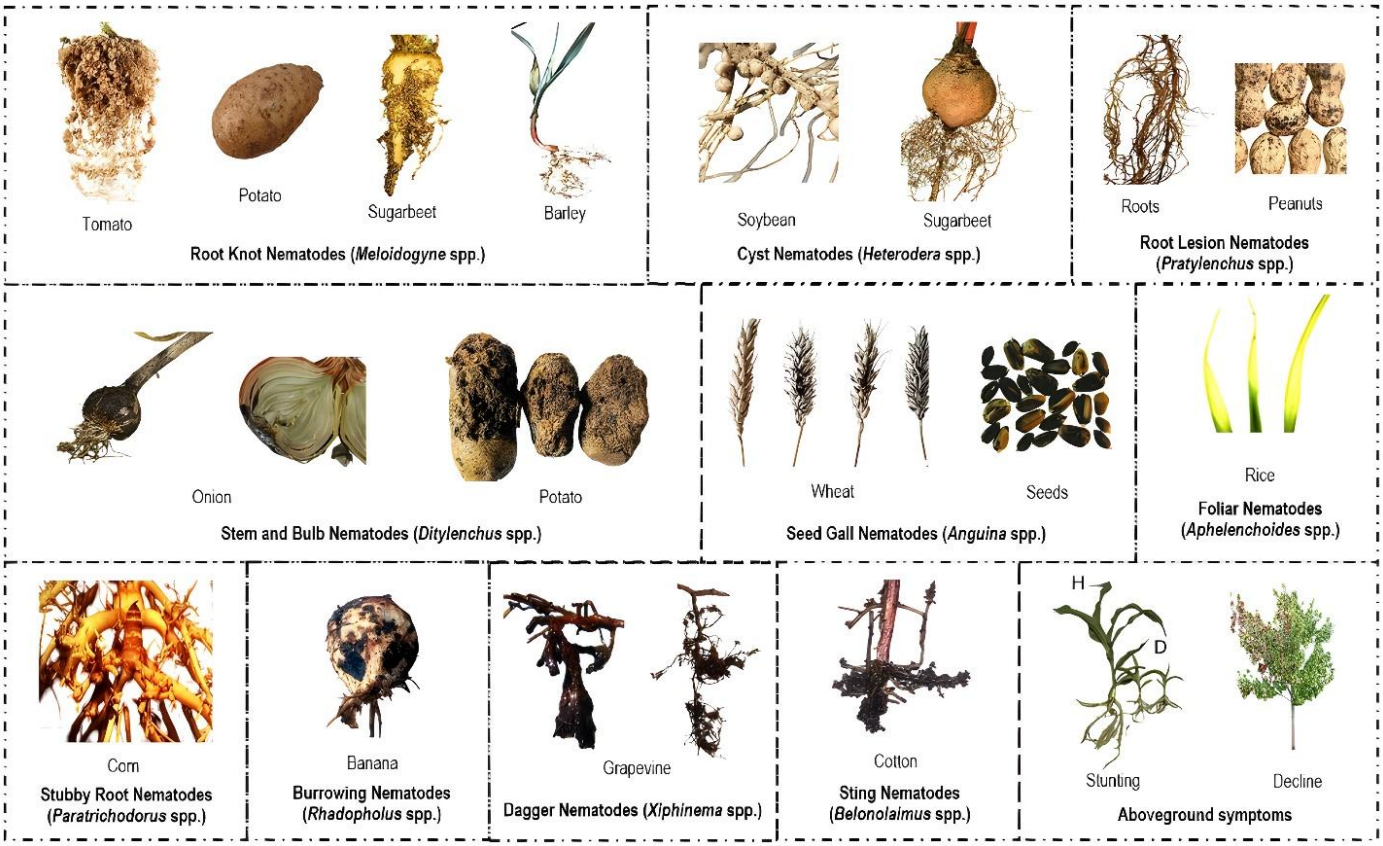

Figure 1. Main symptoms (belowground and aboveground) caused by plant parasitic nematodes on various crops.

NEMATODE MANAGEMENT

Effective management approaches integrate culture, biological, chemical, and host resistance strategies (Ali *et al.*, 2017a). These approaches encompass several aspects of nematode biology and cropping and provide effective control with minimal environmental and health risks (Jones *et al.*, 2013).

Cultural management involves modifications in farming conditions, making them unfavorable for the invasion and development of PPNs on crop plants. Crop rotation is one of the most common cultural practices in which farmers cultivate non-host or resistant crops to help reduce the population density of PPNs (Coyne *et al.*, 2018). For example, the application of rotation in which legumes or non-host crops such as marigold (*Tagetes* spp.) or alternate cereals can reduce root-knot nematodes (*Meloidogyne* spp.) (Nicol *et al.*, 2011). Soil types can also be solarized by covering fields with transparent plastics to raise soil temperatures to lethal levels for nematodes in the upper layers (Mostafa, 2008). Another practice is deep plowing together with leaving fields fallow, where nematodes can be exposed to desiccation and natural predators, thus making their populations even smaller.

Currently, biological control is gaining more significance where natural nematode enemies such as bacteria, fungi, and predatory nematodes have been used as suppressors against PPN infestations (Din *et al.*, 2017; Arshad *et al.*, 2021b). One important example is the endoparasitic bacterium *Pasteuria penetrans*, which infects and kills juvenile RKNs (Kamran *et al.*, 2014; Moens *et al.*, 2009). Different fungi such as *Trichoderma* spp. and *Pochonia chlamydosporia* use nematode eggs and cysts as their reproductive substrate, interfering with their propagation (Stirling, 2014). Although biocontrol is eco-friendly, its efficacy will always be limited under diverse environmental settings and interactions with biocontrol agents and other soil microbiomes present in the rhizosphere.

Chemical control remains the mainstay in agricultural systems, especially in profitable crops, where severe damage caused by PPNs could lead to more pronounced economic losses. Most of the general nematicide chemistries

comprise organophosphates and carbamates which damage the nervous system of PPNs. Fumigants, such as 1,3-dichloropropene and dazomet, target soil-dwelling nematodes (Chitwood, 2003). However, concerns about their adverse effects on the environment and human health, together with increasing regulatory obstacles against their use, are driving a decline in the application of such chemicals (Abbas *et al.*, 2019). Safer alternatives are under development in the form of newer products that incorporate rational principles derived from natural sources. For example, fluopyram, a fungicide with nematicidal activity, is widely used in integrated pest management (Coyne *et al.*, 2018).

Breeding nematode-resistant crops is one of the most durable and economical strategies for PPN management. Modern techniques such as molecular breeding and genomics can identify and transfer resistance genes into commercial cultivars (Ali *et al.*, 2017a). For instance, the use of the *Mi-1* gene in tomato provides resistance against various RKN species. The *Gpa5* gene is another example that is located on potato chromosome 1 and confers resistance to white potato cyst nematodes *Globodera pallida* (Nicol *et al.*, 2011). Approaches, such as marker-assisted selection (MAS) and genome-wide association studies (GWAS), are largely being used to develop resistant varieties because the durability of resistance genes will forever remain a challenge since virulent nematode biotypes emerge to warrant continued efforts to develop new resistant lines.

MARKER-ASSISTED SELECTION (MAS) FOR NEMATODE RESISTANCE

Marker-assisted selection (MAS) is an approach to breeding that combines basic breeding methods with molecular biology to develop disease resistance (Ali *et al.*, 2019). DNA markers are specific DNA sequences associated with characteristics of interest. These markers allow the breeders to efficiently identify and select wheat varieties that have improved resistance against diseases (Seid *et al.*, 2021). In this approach, breeding programs are accelerated as a result of molecular detection of favorable alleles early without depending on laborious time-consuming, and costly field selection of the phenotype (Francia *et al.*, 2005). MAS involves screening large numbers of plants in segregating populations using specific DNA markers, after mapping and validating the trait QTL of interest (Miedaner and Korzun, 2012). Advances in molecular genetics have expanded the use of DNA markers and MAS, which have great potential for the development of stress-resilient germplasms (Collard and Mackill, 2008). The scientific progress associated with major problems, such as climate change and limited water availability, food demand projections, and scarcity of arable land, makes it very important to have advanced approaches, such as MAS, in upholding the development of crop productivity and sustainability (Hickey *et al.*, 2019).

A major advantage of using molecular markers is that they do not depend on environmental variables or plant growth stages, which allows breeders to identify traits at a very early developmental phase (Todorovska *et al.*, 2009). The gene-related molecular markers are especially useful for traits controlled by major genes and QTLs. The availability of genetic maps and molecular markers has brought about rapid progress in this aspect (Hasan *et al.*, 2021). Several DNA marker types such as SCAR (Gold *et al.*, 1999), SSRs (Wang *et al.*, 2002), RAPD (Qi *et al.*, 1996), microsatellites (Ma *et al.*, 2001), RFLP (Metakovsky *et al.*, 2021), and SNPs (Wu *et al.*, 2018) have played important roles in identifying plant resistance genes and their associated QTL leading to enhanced breeding programs (Thomson, 2014; Ali *et al.*, 2019). Resistance to plant pathogens may be achieved with the help of molecular markers along with classical breeding to create crop varieties, which could help reduce crop losses by PPNs (Gupta *et al.*, 2010). MAS has proven to be very useful in tracing nematode resistance genes in several crops and has drastically enhanced the speed of breeding programs (Seid *et al.*, 2021).

MAS aims for the enhancement of resistance against PPNs by introgression and combining QTL. It thus depends on identified and validated QTL associated with nematode resistance (Jabran *et al.*, 2023) through QTL mapping of GWAS. QTL mapping involves crossing of two contrasting parents, one susceptible and the other highly resistant parent to develop biparental mapping populations, in filial generation 2 (F2) plants, ending with the establishment of near-isogenic lines (NILs), recombinant inbred lines (RILs), Backcross inbred lines (BILs), etc., segregating for nematode resistance. This is followed by accurate phenotyping for resistance to PPNs, genotyping to identify DNA-based molecular markers to evaluate genome-wide distributed polymorphisms, and comprehension of linkage maps. Subsequently, QTLs are statistically associated with resistance and/or susceptibility to a particular nematode species in a specific crop plant. A systematic flowchart diagram for QTL mapping is given in Figure 2.

Many QTL mapping studies reported nematode resistance in crop plants (Table 1). Galeng-Lawilao *et al.* (2018) mapped QTL for resistance to the rice root-knot nematode, *Meloidogyne graminicola* from a mapping population of doubled haploid lines. They reported 3 main effective QTLs from chromosomes 4, 7, and 9, and two epistatic

interactions were detected between loci on chromosomes 3 and 11, and between 4 and 8. Using a population of RILs, Usovsky *et al.* (2020) identified QTL for resistance to the soybean cyst nematode, *Heterodera glycines*, in *Glycine max* using SNP markers. They reported that several QTLs are located on chromosomes 8, 10, and 18. In sweet potato, researchers have identified a major QTL, qIbMe-4.1, for resistance to RKN, *M. enterolobii*, using a mapping population derived from a cross between resistant and susceptible varieties (Fraher *et al.*, 2024). They reported that QTL qIbMe-4.1 explained 70% of the variation in resistance, making it a significant marker for breeding nematode-resistant sweet potato varieties.

Recently, Pundir *et al.* (2023) mapped 8 QTL and 2 meta-QTL for resistance to the cereal cyst nematode, *H. avenae*, in common wheat (*Triticum aestivum*) on chromosomes 1B, 2A, and 3A in two repeated experiments. They used composite interval mapping and inclusive composite interval mapping on 149 RILs derived from the cross HUW 468 × C 306. They further reported that the two meta-QTLs discovered were associated with 57 candidate genes involved in nematode resistance (Pundir *et al.*, 2023). Recently, QTLs associated with resistance to RKN, *M. incognita*, were identified in cucumber (*Cucumis metuliferus*) (Xie *et al.*, 2024). This study used an F2 population and employed quantitative PCR and virus-induced gene silencing to identify candidate genes (EVM0025394 and EVM0006042) within QTL regions (QTL3.1) present on chromosomes 2 and 6. This study highlights the potential of these QTLs for marker-assisted breeding of RKN resistance in cucumbers (Xie *et al.*, 2024).

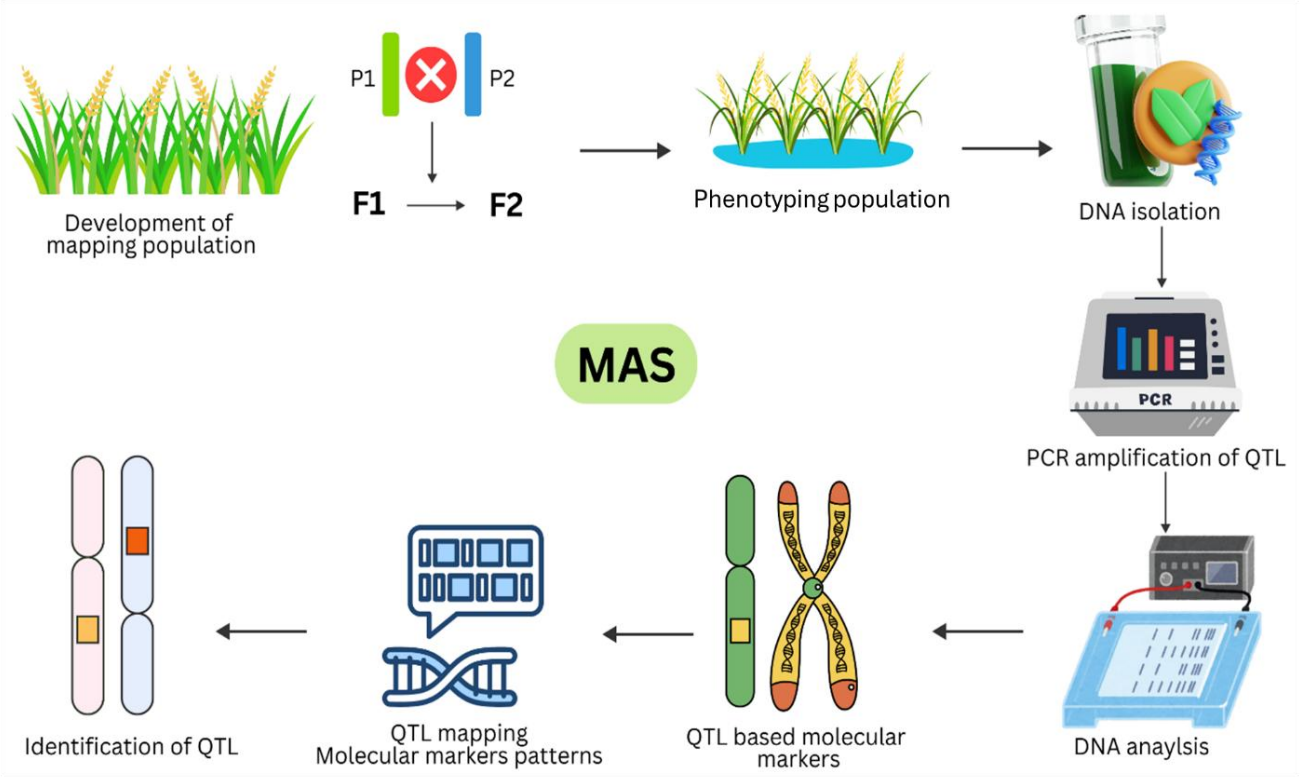

Figure 2. The general procedure of QTL mapping. This procedure involves the crossing of two contrasting parents, one susceptible and the other highly resistant parent to develop biparental mapping populations in F2 to develop NILs, RILs, BILs, etc., segregating for disease resistance. This is followed by precise phenotyping for resistance and PCR-based genotyping to identify molecular markers or QTL to evaluate genome-wide distributed polymorphisms and comprehend linkage maps. After this, the QTLs are statistically associated with resistance and/or susceptibility to a particular disease.

GENOME-WIDE ASSOCIATION STUDIES (GWAS) FOR NEMATODE RESISTANCE

GWAS is a genetic research tool that enables the identification of the genetic variants that underlie complex traits including quantitative disease responses. GWAS explores genomes and mainly uses SNPs that are found to be more frequent among individuals (Visscher *et al.*, 2017). In comparison to bi-parental QTL mapping, GWAS is applied in diverse sets of germplasm (Collard *et al.*, 2005). The identification of loci through GWAS may result in a substantial number due to the elevated number of alleles present in the diverse germplasm sets. However, only a limited number of loci are considered, given the presence of markers that exclusively represent the genetic diversity of the parent organisms and the specific population under study (Ali *et al.*, 2019).

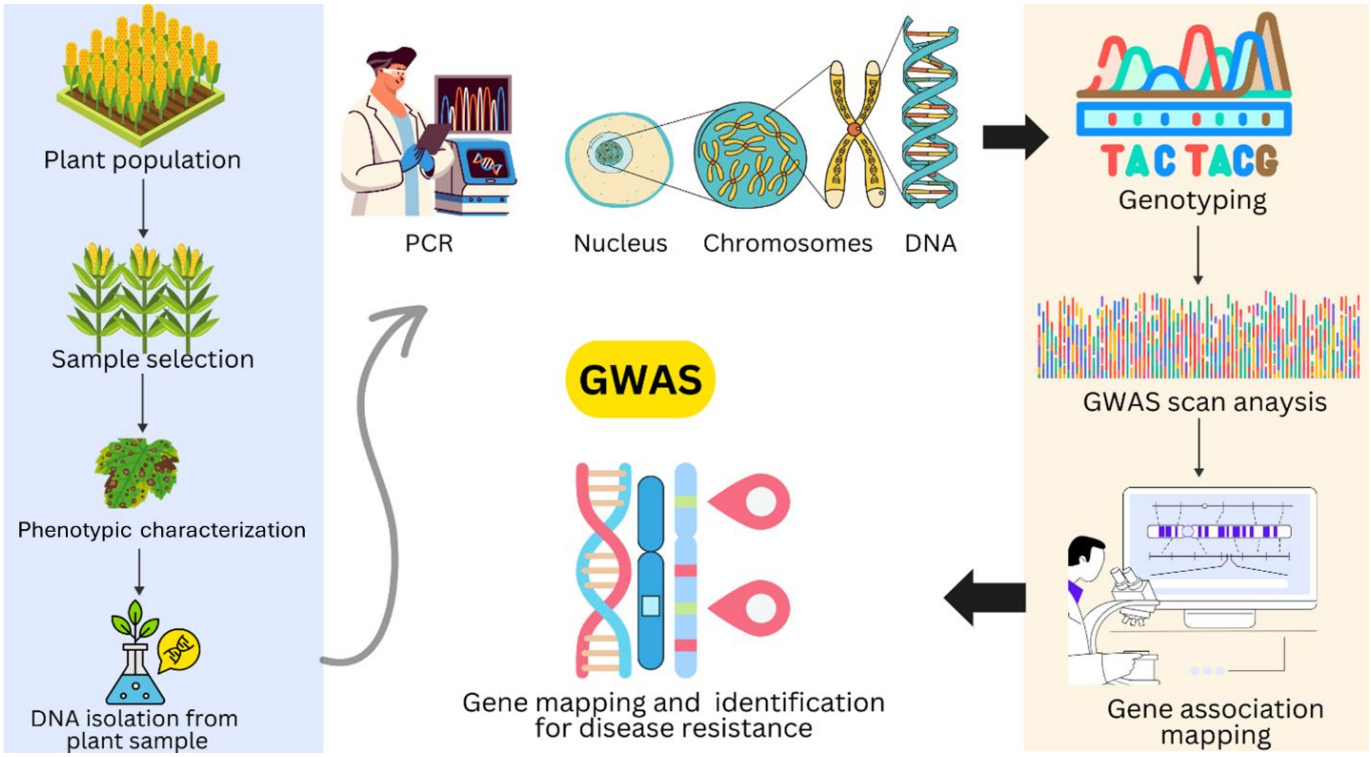

Figure 3. A Schematic diagram of GWAS showing phenotyping on the left panel and genotyping and association mapping on the right one.

Table 1. QTLs are associated with nematode resistance in different plant species.

Crop	Nematode Species	Resistance Gene/QTL	Chrom. No.	Reference
Glycine max	*Heterodera glycines*	rhg1	LG G	Guo *et al.* (2006)
G. max	*H. glycines*	Rhg4	LG A2	Cregan *et al.* (1999)
G. max	*H. glycines*	cqSCN-005	LG B1	Guo *et al.* (2006)
G. max	*H. glycines*	cqSCN-006	LG E	Guo *et al.* (2006)
G. max	*H. glycines*	cqSCN-007	LG G	Guo *et al.* (2006)
G. max	*H. glycines*	cqSCN-001	LG A2	Guo *et al.* (2006)
Solanum multidissectum	*Globodera pallida*	H2	5	Strachan *et al.* (2019)
S. sparsipilum	*G. pallida*	GpaV spl	5	Caromel *et al.* (2005)
S. sparsipilum	*G. pallida*	GpaXI spl	11	Caromel *et al.* (2005)
S. spegazzinii	*G. pallida*	Gpa	5	Kreike *et al.*, (1994) ; Caromel *et al.* (2005)
S. spegazzinii	*G. pallida*	GpaM1	5	Caromel *et al.* (2003)
S. spegazzinii	*G. pallida*	GpaM2	6	Caromel *et al.* (2003)
S. spegazzinii	*G. pallida*	GpaM3	12	Caromel *et al.* (2003)
S. spegazzinii	*G. rostochiensis*	Gro 1.2	10	Kreike *et al.* (1993) ; Park *et al.* (2019)
S. spegazzinii	*G. rostochiensis*	Gro 1.3	11	Kreike *et al.* (1993)
S. spegazzinii	*G. rostochiensis*	Gro 1.4	3	Kreike *et al.* (1996)
S. tarijense	*G. pallida*	GpaXII tar	11	Tan *et al.* (2009)
S. tuberosum ssp. andigena	*G. rostochiensis*	H1	5	Bakker *et al.* (2004) ; Finkers-Tomczak *et al.* (2011)
S. tuberosum ssp. andigena	*G. pallida*	H3	4	Bryan *et al.* (2004)

S. vernei	*G. pallida*	GpaV	5	Rouppe van der Voort *et al.* (2000); van Eck *et al.* (2017)
S. vernei	*G. pallida*	Gpa VI	9	Rouppe van der Voort *et al.* (2000) ; Bryan *et al.* (2002)
S. vernei	*G. rostochiensis*	GroVI	5	Jacobs *et al.* (1996)
S. tuberosum, S. oplocense, S. vernei (3 different) and S. tuberosum ssp. *andigena*	*G. rostochinesis, G. pallida*	Grp1	5	Rouppe van der Voort *et al.* (1998); Finkers-Tomczak *et al.* (2009)
S. tuberosum ssp. andigena and *S. vernei*	*G. rostochiensis*	Ro2_A	5	Park *et al.* (2019)
S. tuberosum ssp. andigena and *S. vernei*	*G. rostochiensis*	Ro2_B	5	Park *et al.* (2019)
S. tuberosum ssp. andigena and *S. vernei*	*G. pallida*	Pa2/3_A	5	Park *et al.* (2019)
S. tuberosum ssp. andigena and *S. vernei*	*G. pallida*	Pa2/3_B	10	Park *et al.* (2019)
S. tuberosum ssp. *andigena* and *S. vernei*	*G. pallida*	Gpa IV	4	Bradshaw *et al.* (1998)
Triticum aestivum	*Heterodera* spp.	*Cre8*	6B	Williams *et al.* (2003)
T. aestivum	*Heterodera* spp.	*Cre8*	6B	Williams *et al.* (2003)
T. aestivum	*Heterodera* spp.	*QCre-ma7D*	7DL	Cui *et al.* (2020)
T. aestivum	*Heterodera* spp.	*QCre-ma2A*	2AS	Cui *et al.* (2020)
T. aestivum	*Heterodera* spp.	*CreZ*	??	Dababat *et al.* (2021)
T. aestivum	*Heterodera* spp.	*CreY*	3BL	Dababat *et al.* (2021)
T. aestivum	*Heterodera* spp.	*QCcn-1B*	1BS	Al-Ateeq *et al.* (2021)
T. aestivum	*Heterodera* spp.	*TaPrx113-F*	??	Al-Doss *et al.* (2010)
T. aestivum	*Heterodera* spp.	*TaPrx112-D*	2B	Al-Doss *et al.* (2010)
T. aestivum	*Pratylenchus* spp.	*QRlnt.lrc*	6DS	Zwart *et al.* (2005)
T. aestivum	*Pratylenchus* spp.	*QRlnt.sk-2B*	2B	Rahman *et al.* (2020)
T. aestivum	*Pratylenchus* spp.	*QRlnt.sk-6D*	6D	Rahman *et al.* (2020)
T. aestivum	*Pratylenchus* spp.	*Rlnn1*	7AL	Williams *et al.* (2002)
Aegilops spp.	*Heterodera* spp.	*Cre2*		Delibes *et al.* (1993)
Aegilops spp.	*Heterodera* spp.	*Cre3*	2DL	Al-Doss *et al.* (2010)
Aegilops spp.	*Heterodera* spp.	*Cre4*	2DL	Eastwood *et al.* (1991)
Aegilops spp.	*Heterodera* spp.	*Cre7*	2BL	Montes *et al.* (2008)
Aegilops spp.	*Heterodera* spp.	*Cre5*	2AS	Williams *et al.* (2006)
Aegilops spp.	*Heterodera* spp.	*Cre6*	5N	Ogbonnaya *et al.*, (2001)
Dasypyrum villosum	*Heterodera filipjevi*	*CreV*	*6VL*	Zhang *et al.* (2008)
L. peruvianum, L. esculentum	*Meloidogyne* spp.	Mi-1	6	Milligan *et al.* (1998)
S. arcanum	*Meloidogyne* spp.	Mi-9	6	Jablonska *et al.* (2007)
L. peruvianum, L. esculentum	*Meloidogyne* spp.	Mi-3	12	Yaghoobi *et al.* (2005) El-Sappah *et al.* (2019)
L. esculentum	*Meloidogyne* spp.	Mi-HT	6	Wang *et al.* (2013)
L. peruvianum, L. esculentum	*Meloidogyne* spp.	Mi-2	6	Cap *et al.* (1993)

L. peruvianum	*Meloidogyne* spp.	Mi-5	12	Yaghoobi *et al.*, (1995)
L. peruvianum	*Meloidogyne* spp.	Mi-4	Not known	Veremis and Robertsc (1996)
L. peruvianum	*Meloidogyne* spp.	Mi-6	Not known	Veremis and Robertsc (1996)
L. peruvianum	*Meloidogyne* spp.	Mi-7	Not known	Veremis and Robertsc (1996)
L. peruvianum	*Meloidogyne* spp.	Mi-8	Not known	Veremis and Robertsc (1996)
Oryza sativa	*M. graminicola*	qMGR4.1	4	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qMGR7.1	7	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qMGR9.1	9	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qGR4.1	4	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qGR8.1	8	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qYR5.1	5	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qYR11.1	11	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qJ2RS2.1	2	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qJ2RS3.1	3	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qGR3.1	3	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qGR5.1	5	Galeng-Lawilao *et al.* (2020)
O. sativa	*M. graminicola*	qMGR11.1	11	Lahari *et al.* (2019)
Arachis hypogea	*M. arenaria*	Rma	A09	Boissot *et al.* (2010)
A. hypogea	*M. arenaria*	Ma-1	LG01, LG03, LG09.1	Burow *et al.* (2014)
Beta vulgaris	*H. schachtii*	Hs1pro-1	1	Galal *et al.* (2014)
Carrot	*M. incognita*	Mi-1	8	Parsons *et al.* (2015)
Cotton	*M. incognita*	qMi-C11	11	Shen *et al.* (2010)
Banana	*Radopholus similis*	RGA2	11	Habineza (2019)
Barley	*P. neglectus*	Rlnnp6H	6H	Sharma *et al.* (2011)
Pepper	*M. incognita*	Me1	P9	Djian-Caporalino *et al.* (2007)
Grapes	*Xiphinema index*	XiR1	19	Hwang *et al.* (2010)
Melon	*M. incognita*	Vat	5	Boissot *et al.* (2010)

For this reason, it usually produces results of low resolution and may not capture all the potential genetic variation affecting a particular trait (Xu and Crouch, 2008). However, the resolution of GWAS depends very much on the crop, LD thus germplasm used, and the genotyping platform.

GWASs use genetically heterogeneous populations and have a much higher potential for detecting genetic differences associated with different traits (Korte and Farlow, 2013). Such genetic diversity may improve the mapping resolution, leading to the identification of variants with small effects. However, it must involve analyses with large sample sizes for sufficient statistical power and must also take care of population stratification, as such might serve to raise false positives in most instances (Price *et al.*, 2006). This approach has been employed for many different traits in several crop plants in addition to the development of fungi and nematode-resistant cultivars (Ali *et al.*, 2019; Malosetti*et al.*, 2021; Younessi-Hamzekhanlu *et al.*, 2022). The process of GWAS involves the phenotyping of a large number of germplasm accessions in response to a particular PPN, followed by high-density genotyping of the phenotypically assessed germplasm (Jabran *et al.*, 2023), either using GBS or SNP arrays. The next step involves statistical data analysis and predictions of associated markers with QTL of interest and chromosomal mapping of identified QTL and their further functional validation. A schematic diagram of GWAS is given in Figure 3.

PPNs are parasites, which adversely influence the yield of several crops and require the need to scope out their resistance-associated genetic loci for breeding programs. GWAS of wheat can be taken as an example that reveals several SNPs associated with the resistance to *Heterodera avenae,* the cereal cyst nematodes, thereby providing markers that are important in developing resistant wheat varieties (Gao *et al.*, 2023). GWAS in soybean identified a locus on chromosome 13 that has several TIR-NB-LRRs also found to be associated with resistance against RKN (*M. javanica*) and revealed parts of the genetic architecture responsible for nematode resistance as well as possible breeding target sites (Sang *et al.*, 2023). Similarly, multi-locus GWAS in chickpea detected several genomic regions associated with root-lesion nematode resistance (*P. thornei*), which could assist in the breeding programs for the improvement of chickpea cultivars (Thudi *et al.*, 2023).

A single GWAS study on common bean resulted in the identification of SNPs associated with resistance against soybean cyst nematode (*H. glycines*) complex contributing both to understanding the genetic architecture of nematode resistance and to the development of resistant cultivars (Schmutz *et al.*, 2021). Another potato study reported genomic regions related to resistance against *Globodera pallida*, the potato cyst nematode which marks important alleles for breeding nematode-resistant potato cultivars to replace agrochemicals (Banik *et al.*, 2023). The efficacy of GWAS in mapping out the genetic loci responsible for nematode resistance in different crops is demonstrated by research studies. Markers identified through GWAS can be utilized in the marker-assisted selection programs that hasten the breeding of nematode-resistant cultivars, ultimately leading to sustainable agriculture practices. Different GWAS studies done for the association of nematode resistance with particular germplasm accessions in different plant species are given in Table 2.

Table 2. GWAS studies done for nematode resistance assessment in different plants

Nematode Species	Crop Name	# of germplasm accessions assessed	Marker System Used for GWAS	# of Associated Markers	References
M. graminicola	Rice	332 accessions	SNP array	11	Dimkpa *et al.* (2016)
M. javanica	Soybean	317 soybean accessions	SNP markers	2	Alekcevetch *et al.* (2021)
M. graminicola	Wild rice	272 diverse wild rice accessions	SNP markers (50K "OsSNPnks" genic Affymetrix chip)	8	Hada *et al.* (2020)
M. incognita	*Arabidopsis*	340 natural inbred lines	SNP array	2	Warmerdam *et al.* (2018)
Meloidogyne spp	*grapevine*	N/A	GBS followed by Sequenom MassARRAY validation	1 (*MJR1*)	Smith *et al.* (2018)
Rotylenchulus reniformis	Cotton	246 *G. arboreum* germplas	Genotyping-by-sequencing (GBS)	15	Li *et al.* (2018)

		m accessions	followed by SNP analysis		
Heterodera glycines	*Soybean*	461 soybean accessions	Illumina SoySNP50K iSelect BeadChips and three KASP SNP markers	12	Tran *et al.* (2019)
H. glycines	*Soybean*	553 soybean plant introductions (PIs)	SoySNP50K iSelect BeadChip	60	Vuong *et al.* (2015)
H. glycines	*Soybean*	120 *Chinese* collection	SNP markers	10	Zhang *et al.* (2017)
H. glycines	*Soybean*	234 soybean genotypes	SNP markers	6	Ravelombola*et al.* (2020)
H. glycines	wild soybean	235 (*Glycine soja* Sieb. & Zucc.) accessions	SNP markers	10	Zhang *et al.* (2016)
H. glycines		200 diverse soybean accessions	SNP markers	13	Zhao *et al.* (2017)
H. glycines	*common bean*	317 plant introductions (PI's)	SNP markers	6	Jain *et al.* (2019)
H. glycines	*common bean*	315 accessions of the USDA Common Bean Core collection	SNP markers	18	Shi *et al.* (2021)
H. glycines	*common bean*	363 accessions	SNP markers	3	Wen *et al.* (2019)
Globodera pallida and G. rostochiensis	*Potato*	222 accessions	SNP markers	Gp (9) Gr (11)	Sood *et al.* (2023)
Pratylenchus thornei	Wheat	143 wheat genotypes	SNP markers	9	Kumar *et al.* (2019)
Heterodera filipjevi	Wheat	161 winter wheat accessions	90K iSelect SNP chip	8	Priyar *et al.* (2016)
H. filipjevi	Wheat	255 diverse prebreeding lines (PBLs)	SNP markers	5	Dababat *et al.* (2021)
H. filipjevi	Wheat	188 accessions	152K SNP chip	11	Taheri *et al.* (2024)
Heterodera avenae	Wheat	141 Indian wheat germplasm	SNP markers	9	Singh *et al.* (2023)
Pratylenchus neglectus	Wheat	189 advanced spring bread wheat lines	SNP markers	11	Sohail *et al.* (2022)
Pratylenchus thornei	Chickpea	202 chickpea accessions	SNP array	5	Kumar *et al.*, (2024)
Belonolaimus longicaudatus	Peanut	775 USDA accessions	SNP markers	46	Ravelombola *et al.* (2022)

CONCLUSION AND PERSPECTIVES

The global challenge posed by PPNs demands innovative and sustainable management solutions. The conventional ways of control are becoming increasingly restricted due to environmental legislation, high costs, and developing

resistance in the nematode populations. Breeding nematode-resistant crops, underpinned by high-throughput molecular tools, is a promising direction forward. MAS has immense potential for precise delivery of certain resistance traits and hence reduction of time and effort used as compared to conventional methods. In addition, MAS has been proven effective in the pyramid of resistance genes that enable crops to resist an attack by several nematodes concurrently. GWAS has become one of the main approaches toward the discovery of new resistance loci and the definition of the genetic architecture underlying nematode resistance. The knowledge developed herein encourages a fuller understanding of the complex interactions between nematodes and their host plants, hence breeding and helping to deliver sustainability for resistance. Improved high-throughput genotyping or sequencing methods and phenotyping technologies make these approaches increasingly accessible even in resource-poor environments. Looking forward, integrating molecular tools into a unified breeding framework holds immense promise. Future research should prioritize the identification of broad-spectrum resistance genes and the development of molecular markers that are inexpensive, robust, and transferable across breeding programs. Expanding the use of genome editing tools, such as CRISPR-Cas systems, will further accelerate the creation of nematode-resistant varieties. Interdisciplinary efforts that combine molecular breeding, soil health management, and digital agriculture technologies are essential to translating laboratory findings into field-level impacts.

AUTHOR CONTRIBUTIONS

Abdelfattah A. Dababat: Writing – original draft, Writing – review & editing, Formal analysis, Conceptualization, Validation, Supervision, Resources, Funding acquisition. Timothy Paulitz: Validation, Writing – review & editing. Salah-Eddine Laasli: Writing – original draft, Writing – review & editing, Formal analysis. Rachid Lahlali: Writing – review & editing. Honglian Li: Writing – review & editing. Fouad Mokrini: Writing – review & editing. Susanne Dreisigacker: Validation, Writing – review & editing.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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