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Molecular marker-assisted selection for nematode resistance in crop plants

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Abstract

Plant parasitic nematodes are recognized as major agricultural pathogens and cause crop losses throughout the world. Conventional breeding tactic for nematode resistance in crop plants involves a laborious and time consuming task. Technical difficulties in selecting nematode-resistant plant accessions or progenies in a breeding program could be minimized by adopting more rapid and objective methods of genetic identification, such as marker-assisted selection (MAS). DNA based polymorphism, commonly known as DNA markers can be used for genetic improvement through selection for favourable traits. Molecular markers can play an important role in accelerating the introgression of genes conferring resistance to nematodes into high-yielding cultivars. It is clear that DNA markers hold great promise, but realizing that promise remains elusive. In future, chip-based, high-throughput genotyping platforms and the introduction of genomic selection will reduce the current problems of integrating MAS in practical breeding programs and open new avenues for a molecular-based resistance breeding.

Keywords: Molecular marker-assisted, nematode resistance, crop plants

1. Introduction

Plant parasitic nematodes (PPNs) are gaining significant importance worldwide due to their devastating effects on crops leading to major economic and social impacts. It is estimated that the 20 most important life sustaining crops undergo 10.7% yield losses due to nematodes, and other 20 economically important crops suffer 14% losses, the average amounts to 12.3% while the average losses in developing nations including India is 14.6% [1]. The majority of crop losses caused by plant parasitic nematodes are inflicted by relatively few species belonging to the two main groups of root-knot nematodes (RKNs, *Meloidogyne* spp.), cyst nematodes (*Heterodera* and *Globodera* spp.) [2] and reniform nematode (RN).

2. Nematode biology and life cycle

Most species of plant parasitic nematodes have a relatively simple life cycle consisting of the egg, four larval stages and the adult stage of male or female [3]. Development of the first stage larvae occurs within the egg where the first molt occurs. Second stage larvae hatches from eggs to find and infect susceptible plant roots or in some cases foliar tissues. Host finding or movement in soil occurs within thin film of water surrounding soil particles and root surfaces [3]. Depending on the nematode species, feeding will vary from root to foliar region. In root-knot nematode, infective juvenile (J₂) stages will invade root tissue, establishing permanent feeding sites within the root. Second stage juvenile will then molt three times, to become adult male or female [3]. For most species of root feeding nematodes, as many as 50-100 eggs are produced per female, while in case of root-knot nematodes, more than 2000 eggs may be produced [4]. Under suitable environmental conditions, the eggs hatch and new larvae emerge to complete the life cycle within 4 to 8 weeks. Nematode development is generally most rapid within an optimal soil temperature range of 70 to 80°F [5].

3. Plant damage symptoms caused by nematodes

The characteristic above ground symptoms of nematode damage include stunting, yellowing, wilting and yield loss, while below ground indicators are malformations of roots such as galls, lesions and distortions depending upon the type of nematode species [3]. In addition to the direct crop damage caused by the nematodes, many of these species have also been shown to predispose plants to the infection by fungal or bacterial pathogens or to transmit virus diseases,

which contribute to the additional yield reductions ^[3]. Yield reductions can be extensive but vary significantly between plant and nematode species.

4. Nematode management

Major methods to control nematodes include crop rotation, use of soil fumigants, chemical nematicides and resistant varieties. Each of these methods has certain advantages depending on application areas and cultivation period ^[6]. Chemical nematicides have been widely used for controlling plant parasitic nematodes (PPNs). Since most chemical nematicides have been banned due to environmental and public health issues, cultivation of resistant cultivars have become an important strategy against these pests ^[6].

Conventional breeding program for nematode resistance in crop plants involves successive crossing and selection steps based on careful phenotypic analyses, which make this procedure a laborious and time consuming ^[7]. This is particularly true in the case of root infesting pathogens such as plant-parasitic nematodes, for which reliable inoculation and screening of the plants is labour intensive ^[7]. Moreover, assessment of the level of resistance to nematodes is not a trivial task. In this context, it is obvious that marker-assisted selection holds great promise in plant breeding ^[7]. Technical difficulties in selecting nematode-resistant plant accessions or progenies in a breeding program could be minimized by adopting more rapid and objective method of genetic identification, such as marker-assisted selection, where molecular markers come mainly from DNA polymorphism ^[2]. In recent days, molecular marker techniques are integrated into nematode resistance breeding programs, although apparently limited to only a very few nematodes like root-knot nematodes and soybean cyst nematodes ^[7, 8]. Although resistant cultivars of some crops are available for root-knot and cyst nematodes, they are resistant to only a few races or species of nematodes and new races develop over time ^[9]. Effective resistance against plant parasitic nematodes is not available in the most economically important crops.

5. Application of molecular markers in nematode resistance breeding

Molecular markers are tools that can be used as chromosome landmarks to facilitate the introgression of genes associated with economically important traits ^[10]. It is an approach that has been developed to avoid difficulties associated with conventional plant breeding by shifting the selection criteria from selection of phenotypes towards selection of genes that control traits of interest, either directly or indirectly ^[10]. In recent years molecular markers such as RFLPs (Restriction Amplified Length Polymorphisms), AFLPs (Amplified Fragment Length Polymorphisms), RAPDs (Random Amplified Polymorphic DNA), CAPS (Cleaved Amplified Polymorphic Sequence), SCAR (Sequenced Characterized Amplified Regions), Simple sequence repeats (SSRs) and Sequence Tagged Site (STS) based methods and others have been developed and applied to a wide range of crop species for nematode resistance ^[11]. Different types of molecular markers utilized for breeding nematode resistance in major crops are listed in Table 1.

Application of markers for breeding nematode resistant varieties is especially interesting when conventional bioassays are expensive and unconvincing. A prominent example is the selection for resistance to nematodes ^[8]. In wheat, there is extensive use of DNA markers for cereal cyst nematode (*Heterodera avenae* Woll.) resistance ^[10], whereas, in soybean

the most prominent example for MAS application in breeding is resistance to soybean cyst nematode (*H. glycines*) ^[11]. In both cases, the disease is of economic importance, the resistance is due to a single gene and the bioassay is expensive and unreliable ^[10], thus MAS is a clear advantage.

Since, the effective resistance against the nematodes is not available in the economically important crops; it has been suggested that deploying sources of natural resistance against them will be the most effective and environmentally sustainable method of reducing the crop losses caused by them ^[6]. Owing to the above reason, marker-assisted selection for nematode resistance has been the major focus to improve the crops affected by nematodes. Because cyst nematodes infestation can cause major losses to most of the world's important staple crops including potato, soybean and wheat, it is not surprising that substantial breeding efforts have been undertaken to identify stable sources of resistance to different species and pathotypes of cyst nematodes ^[12]. For example, both polygenic and monogenic genes for resistance to potato cyst nematodes have been identified and markers closely linked to these alleles have been developed for use in potato resistance breeding programmes ^[12]. Similarly, different types of resistance genes have been identified, mapped and/or cloned from host plants that confer near complete and partial resistances to *H. glycines*, *H. avenae* and *H. schachtii* including the map based cloning of a gene encoding a serine hydroxymethyl transferase, at the Rhg4 locus, that confers resistance to soybean cyst nematode race 4 ^[13]. For soybean, identification and validation of RFLP, RAPD, SSR and AFLP markers linked to soybean resistance alleles in different races of *H. glycines* were reported by earlier workers ^[14].

5.1 Cotton

Cotton (*Gossypium* spp.) is the most important commercial fibre crop of India. Phytoparasitic nematodes such as root-knot, (*Meloidogyne incognita* Kofoid & White) Chitwood and reniform nematodes (*Rotylenchulus reniformis* Linford & Oliveira) are the major and extremely difficult pathogens to manage in the field and cause a reduction in cotton yield ^[15]. Major efforts have been taken to identify genetic markers linked closely to nematode resistance genes in cotton. SSR markers on chromosomes 11 and 14 were identified to be associated with resistance to RKN ^[16]. An AFLP marker has been further developed as a CAPS marker to facilitate its use for root-knot nematode resistance ^[17]. Using recombinant inbred lines (RIL), SSR marker CIR 316-201 allele on chromosome 11 and SSR marker BNL 3661-185 allele on chromosome 14 were shown to be closely associated with RKN resistance ^[18]. Two resistant SSR markers, (CIR 316-201 and BNL 3661-185) has been validated against root-knot nematode in cotton (*Gossypium hirsutum* L.) ^[19].

Simple sequence repeats have been discovered and applied in the marker-assisted selection of RN resistance in cotton. The introgression of RN resistance from *G. longicalyx* into *G. hirsutum* was facilitated by the discovery of tightly-linked associations between three SSR markers, BNL 3279_114, BNL 1066_156, BNL 836_215, and one phenotypic marker, green-colored fuzz (Fzglon) with the RN resistance locus (Renlon) located on chromosome 11. The Quantitative Trait Loci (QTL) regions and SSR markers associated with resistance to reniform nematode in *G. barbadense* accession GB 713 were identified. Molecular markers that are closely linked to gene(s) in *G. barbadense* accession GB 713 that confer a high level of resistance to reniform nematode was identified ^[20].

5.2 Soybean

Soybean (*Glycine max* L.) is an economically important bean in the world, providing vegetable protein, oil and therefore in high demand for food, feed, and industrial products. Among the biotic stress challenging the crop production, the soybean cyst nematode (SCN), *Heterodera glycines* (Inchinoe), is one of the most devastating pathogen on soybean [3]. In soybean, cyst nematodes pose serious problem and most of the varieties are susceptible to this parasite [21]. MAS has been used in soybean breeding for resistances to SCN. The most efficient and economical control method is the use of resistant cultivars, together with rotation with non-host crops [22]. However, the development of resistant cultivars is limited by factors such as phenotypic analysis of segregating populations, which is time consuming, labour-intensive and requires much space in the greenhouse [23].

Genetic diversity of RFLP markers have been identified and reported to facilitate soybean breeding for both *Rhg1* and *Rhg4* loci [23, 24] against soybean cyst nematodes [25]. New QTL has been mapped to the soybean linkage group D2 and, in conjunction with other QTLs already identified for SCN resistance [27].

The SSR markers have been applied in the marker-assisted selection of Soybean cyst nematode resistance [26, 28]. The development of 1,000 microsatellites (SSR) led to the construction of an integrated and saturated consensus map for soybean [29]. Thus, the markers near important QTL can be used as anchors for locating regions in the linkage map in

different populations [30]. Several QTL linked to the resistance to different SCN races were identified and validated in different soybean genotypes [23]. One of the QTL with major effect in LG (linkage group), G designated *rhg1*, confers resistance to several races [30], while another in LG A2 (*Rhg 4*), with major effect, confers specific resistance to race 3. The effectiveness of using microsatellite near the loci *rhg1* and *Rhg4* for the selection of soybean lines resistant to SCN race 3 was evaluated [30].

5.3 Potato

Potato (*Solanum tuberosum* L.) ranks fourth, after rice, wheat and maize as the most important human food crop worldwide. There are several nematode species that affect potato crops. The most challenging phytophagous nematode pests of potatoes are the potato cyst nematodes. There are two main species of Potato Cyst Nematode (PCN), *Globodera pallida* (white PCN) and *G. rostochiensis* (yellow PCN) [3]. Regarding PCN, the monogenic dominant *Gro1* gene from *Solanum spegazzinii* for resistance to all pathotypes of *G. rostochiensis* was mapped to the potato molecular map on chromosome VII [31]. Five more molecular markers to select for potato virus Y, *G. rostochiensis* and *G. pallida* resistance was identified [32, 33]. In addition, the SNP marker HC and GRO1-4 markers were utilized to identify the GpaVvrn QTL and *Gro1-4*, resistance genes of *G. pallida* and *G. rostochiensis*, respectively [33].

Table 1: Molecular markers used for screening nematode resistance in major crops

Crop	Nematode species	Resistance Genes	Marker type	References
Soybean	Soybean cyst nematode, <i>Heterodera glycines</i>	<i>Rhg1</i> and <i>Rhg4</i>	SNPs and QTL	[30]
	<i>H. glycines</i>	<i>Rhg1</i> and <i>Rhg4</i>	SNP	[34, 37]
Wheat	Cereal cyst nematode, <i>Heterodera avenae</i>		Sequence-tagged site (STS)	[36]
	<i>H. avenae</i>	<i>CreX</i> and <i>CreY</i>	SCAR	[37]
	Root-knot nematode, <i>Meloidogyne incognita</i>	<i>Mi</i>	RAPD	[37]
Tomato	<i>M. incognita</i>	<i>Mi 3</i>	RAPD and RFLP	[38, 39, 41]
Cucumber	<i>M. javanica</i>	<i>mj</i>	AFLP and SRAP	[40]
	<i>M. incognita</i>	<i>Mi-1</i>	SCAR	[40]
Potato	Potato cyst nematodes, <i>Globodera rostochiensis</i>	<i>H1</i>	RFLP	[42, 43]
	<i>G. rostochiensis</i> and <i>G. pallida</i>	<i>Hero A</i>	PCR-RFLP	[42]
Turmeric	<i>M. incognita</i>		ISSR	[44]
Sugar Beet	<i>Heterodera schachtii</i>	HsBvm-1	SNP	[45]
Cotton	<i>M. incognita</i>		SSR	[46]
			AFLP and derived CAPS markers	[47]
	<i>Rotylenchulus reniformis</i>		SSR	[48]
Coffee	<i>M. exigua</i>		SSR	[49]
Peanut	<i>M. arenaria</i>		SSR	[50]
	<i>M. arenaria</i>	<i>Rma</i>	RFLP	[51]
Banana	Burrowing nematode, <i>Radopholus similis</i>		CAPS, SSR, AFLP	[52]
			RAPD	[53]

6. Summary

The exploitation of natural resistance genes using genotype screening and marker-assisted selection will continue to be the standard approach for improving resistance and/or tolerance to nematodes for many staple food and horticultural crops. However, for many crops, this approach is slow, and in most cases adequate broad-spectrum resistance is not available. With advances in transgenic technologies, the releases of commercial varieties of major crops with transgenic nematode resistance traits are need of the hour. Even though there is no practical success in nematode management, real benefits have been derived through conventional plant breeding practices by introduction of the *H1* major resistance gene against the potato cyst nematode, *G. rostochiensis* and the *Mi* gene conferring host resistance

Meloidogyne spp. in tomato, which has been transferred to many different tomato varieties throughout the world.

Marker-assisted selection can also be used to pyramid and combine different desired traits into improved germplasm, and this has been an ongoing activity undertaken by plant breeders over many years. The more conventional application of biotechnology to nematode control by marker-assisted selection is now being complemented by the developing biotechnological approaches of transgenic plants, genome editing, developing new nematode control agents and new modes of delivery of control agents. The commercial implementation and delivery of these biotechnology-based technologies will undoubtedly contribute to future global food security.

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