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Rice Root-knot Nematode - Progress of Resistance Breeding in Rice

PANKAJ*, MANSI MACHAL and VISHAL SINGH SOMVANSHI

Division of Nematology, ICAR-Indian Agricultural Research Institute, New Delhi - 110012, India

*Principal Author E-mail: pankaj_nema@yahoo.com; ORCID ID: 0000-0003-2300-3223

ABSTRACT: For almost half of the world's population, rice is a staple food. In addition to the numerous challenges, rice production worldwide is seriously threatened by the rice root-knot nematode (RRKN), *Meloidogyne graminicola*. Developing resistant rice varieties is a priority for sustainable agriculture since *M. graminicola* infestations cause substantial yield losses and economic consequences. Understanding the intricate host-pathogen interaction between rice and rice root-knot nematode is fundamental for effective resistance breeding. Recent molecular studies have shed light on the underlying mechanisms, providing valuable insights into potential targets for genetic manipulation. Numerous resistance genes have been identified in rice, conferring varying resistance levels against RRKN. These genes, discovered through conventional breeding and advanced molecular techniques, serve as the foundation for developing resistant rice cultivars. The integration of marker-assisted selection techniques has expedited the breeding process by enabling the identification and selection of plants with desirable resistance traits more efficiently. This method proved significant in facilitating the development of rice variants resistant to RRKN. Advancements in genetic engineering techniques, such as CRISPR-Cas9, have opened new avenues for precise manipulation of the rice genome to enhance resistance against RRKN. The potential of transgenic approaches in creating durable resistance needs to be further explored while addressing regulatory and ethical considerations. Despite significant progress, challenges persist in developing resistant rice varieties with durable and broad-spectrum resistance against RRKN. The progress in resistance breeding against rice root-knot nematode marks a crucial step toward sustainable rice production. Continued research efforts, incorporating cutting-edge technologies and collaborative initiatives, are essential for addressing the complexities of RKN resistance and ensuring global food security through improved rice varieties. This paper provides a concise overview of the progress made in resistance breeding against RRKN, highlighting key advancements and challenges in this crucial area of research.

Keywords: Crop improvement, nematode, QTL, resistance, rice, rice root-knot nematode, RILs, traits

INTRODUCTION

Rice is among the world's most significant grain crops. More than 50 per cent of people in the entire globe, especially in Asia, rely on rice as their primary source of nutrition (FAO, 2008). Approximately 90 per cent of the world's rice is grown in China, India, Pakistan, Japan, Korea, south-east Asia, and other adjacent countries (USDA, 2014). Beyond Asia, Brazil and the United States are the two nations with the highest rice production (Poehlman and Sleper, 1995). The most common type of rice grown today, *Oryza sativa* (2n = 2x = 24), originated in southern and southwestern tropical Asia. The other type of cultivated rice, *Oryza glaberrima* (2n = 2x = 24), is grown exclusively in western tropical Africa and is indigenous to the upper Niger River basin. Ten distinct genome types (AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ, and HHKK) and 23 species of *Oryza* exist in the wild. *O. sativa* is closely related to the wild annual species *O. nivara* and the wild perennial species *O. rufipogon*. These weedy species are diploid and have the AA genome.

By 2030, the world will require roughly 25 per cent more rice to meet the projected demand of a growing world population (Wani and Sah, 2014). Growing rice over a larger area is one approach to address this challenge, but it is challenging because of rising urbanization and population growth in developing nations. The alternative is to use conventional and contemporary

biotechnology in breeding efforts to enhance varieties and raise the rice yields per ha (Ozawa and Takaiwa, 2010; Mahmood-ur-Rahman *et al*., 2014). A number of plant diseases significantly impact rice quality and yield. One of the most prevalent pathogens in rice production systems is *M. graminicola,* which can cause yield losses ranging from 17 to 32 per cent (Kyndt *et al*., 2014; Mantelin *et al*., 2017). Estimates suggest that *M. graminicola* is the most destructive nematode in India, causing losses of over Rs. 23,272.32 million annually (Kumar *et al*., 2020).

M. graminicola is an obligatory, stationary endoparasite with a broad host range (Abad *et al*., 2003). It infects upland, lowland, and deep-water rice and was recently found to be one of the significant soil diseases limiting aerobic or direct-seeded rice yield. Plants that are infected grow smaller and become chlorotic and stunted. There have been reports of alterations in photosynthetic rate and reductions in chlorophyll concentration of the infected plants (Swain and Prasad, 1988). The nematodes cause the roots to develop galls that resemble hooks, which progressively decrease the intake of water and nutrients and reduce rice yield by 20–30 per cent every year (Fortuner and Merny, 1979; Williamson, 1998). The infectious second-stage juveniles (J2) of *M. graminicola* make their way through the soil to find a suitable host before reaching the root tip. They proceed towards the meristem in an intercellular fashion, ultimately reaching the cell differentiation region (Williamson, 1998), where they establish their permanent feeding site. The nematode causes synchronous mitoses without cytokinesis, which results in the formation of giant cells (Williamson and Gleason, 2003). Galls are formed when nearby pericycle cells divide in tandem with this. The nematodes grow into adults and receive nourishment from the enormous, multinucleated, metabolically active giant cells. Under ideal circumstances, *M. graminicola* may complete multiple generations in a single rice-growing season, which causes the population sizes to expand to harmful levels quickly.

Most nematode management techniques today are ineffective (Starr *et al*., 2002). The most widely used methods in the field to reduce *M. graminicola* yield losses include crop rotation, continuous flooding, and the application of nematicides. In addition to other benefits, regular flooding can lower soil nematode populations by preventing J2 from infecting rice roots. Although most soil nematodes can be killed by flooding, artificial flooding is expensive and unfeasible (Stover, 1979) and has minimal impact on *M. graminicola* (Bridge, 1996). The growing scarcity of water available for agricultural usage, especially in South and Southeast Asia, is further limiting the potential benefits of this approach in the field. Using cultural techniques like crop rotation results in only a partial level of control. Crop rotation that includes *M. graminicola* non-hosts or poor hosts, including sesame, mung bean, and mustard can also successfully lower its population densities in the soil, minimising yield losses. However, moving to another crop, even for a part of the crop season, can come at an unreasonably high cost for a large number of small-scale rice farmers in Asia, where rice is a staple food source. Additionally, due to *M. graminicola*'s broad host range, crop rotation is not very effective (Whitehead, 1998), and chemical control options are restricted to carbofuran since DBCP (1,2-dibromo-3-chloropropane) and EDB (ethylene dibromide) have been banned (Boerma and Hussey, 1992). Using poisonous and environmentally harmful carbamates is the foundation of current RRKN management recommendations. New methods for eliminating this pest require immediate attention, and resistance and tolerance are useful tools for long-term pest management (Williamson, 1998).

Rice farming techniques will probably transition from extended floods to water-saving techniques due to reduced water availability brought on by climate change, increased labour expenses, and urbanisation. These

water-saving methods increase damage and yield loss by allowing *M. graminicola* to enter and accumulate at high densities in the roots of susceptible rice varieties. This will make the development of rice varieties that are tolerant or resistant to *M. graminicola* even more important. With a few notable exceptions, nearly all *O. sativa* cultivars evaluated to date are known to be susceptible to RRKN infection (Kumari *et al*., 2016). Evidence of resistance to *M. graminicola* has been found for *O. longistaminata* A. Chev. and Roehrich, Asian rice (*O. sativa* L.) (Jena *et al*., 2013), and African rice (*O. glaberrima* Steud.) (Soriano *et al*., 1999). Some of these so-called "resistant Asian rice cultivars" are resistant to *M. graminicola*, despite the fact that the great majority of Asian rice germplasm is susceptible to it (Bridge *et al*., 1982). Since the interspecific progenies failed to exhibit the same level of resistance as the African rice, attempts to transmit *M. graminicola* resistance from African rice to Asian rice have been unsuccessful (Plowright *et al*., 1999).

The attempt to combine advantageous features from these two rice species is hindered by sexual compatibility and hybrid sterility. Repeated backcrossing can restore the hybrids' fertility, but doing so involves the risk of losing the desired characteristics (Jones *et al*., 1997). However, recently, at the International Rice Research Institute (IRRI, Los Baños, Philippines), crosses and host-response evaluation experiments led to the identification of some promising Asian rice genotypes derived from *O. sativa* parents that are tolerant or resistant to *M. graminicola* (Shrestha *et al*., 2007). Previous research on rice resistance to *M. graminicola* has shown that this resistance is quantitative in character or controlled by many genes that work in conjunction.

MELOIDOGYNE GRAMINICOLA - RESISTANT RICE GERMPLASMS AND CONVENTIONAL BREEDING

In rice breeding, increasing yield and resistance to abiotic stresses have been major goals, but strategies for achieving these objectives have evolved over time. Developing high-yielding, stress-tolerant rice varieties with suitable nutritional qualities has greatly used conventional breeding techniques, including pedigree and backcross breeding. In cases when using wild relatives or donors with many unwanted features was necessary, advanced backcross lines had to be created to transfer the desired trait into a background that was phenotypically acceptable and to facilitate future breeding programmes. According to Kaloshian and Teixeira (2019), breeding and implementing resistant cultivars is the most efficient and environmentally friendly method of managing RRKN. The most practical and affordable way to lower agricultural losses due to plant diseases is to grow resistant cultivars of various crops. It is a constant effort to screen rice varieties or lines for resistance to RRKN and recommend those that are suitable for cultivation. Due to changes in agricultural practices, *M. graminicola* is becoming more common in the fields, endangering most rice cultivars (De Waele and Elsen, 2007).

Nearly all cultivated *O. sativa* cultivars studied thus far are known to be susceptible to RRKN infection, despite the fact that the non-cultivated African relatives *O. glaberrima* and *O. longistaminata* are assumed to be resistant to the infection of *M. graminicola* (Kumari *et al*., 2016). Dominant resistance (R) genes are used in conventional breeding because they encode nucleotide-binding leucine-rich repeat proteins (NLRs), which either directly or indirectly recognise pathogenic effector proteins and activate host innate immunity (Jones and Dangl, 2006; St Clair, 2010). Some highly resistant types are currently present in the Asian Rice Germplasm Bank: Thai aus rice Khao Pahk Maw (KPM), Sri Lankan indica rice LD24, and Chinese japonica rice Zhonghua11 (ZH11) and Huaidao 5 (HD5) (Dimkpa *et al*., 2016; Hada *et al*., 2020; Feng *et al*., 2022).

Furthermore, recent research (Phan *et al*. 2018; Lahari *et al*., 2019) showed that a major resistance gene

might be involved in the ZH11 resistance to *M. graminicola* infection and that *M. graminicola* resistance in *O. sativa* may be controlled by this key locus on chromosome 11. The putative dominant R gene has not been cloned yet. *O. glaberrima* was previously shown to be resistant to *M. graminicola*. However, the application of *O. glaberrima* genotype resistance in conventional breeding is restricted due to the challenge of hybridizing *O. sativa* and *O. glaberrima* (Soriano *et al*., 1999). Many rice cultivars were identified as resistant as the root galls failed to form, *e.g*., TKM 6, Patnai 6, N 136 (Israel and Rao, 1971), and Garem, Dumai (Cox, 1980). Certain TNAU (ADT) rice lines have been shown to be resistant to the rice root-knot nematode, according to Prasad *et al.* (1986). Similarly, rice *cvs*., Loknath 505 and M-36 were resistant to RRKN (Hassan *et al*., 2004). Several screening programmes have been carried out, but the majority of the rice cultivars screened were reported to be susceptible to RRKN (Sharma-Poudyal *et al*., 2002; Devi and Thakur, 2007; Amarasinghe, 2011; Devi, 2014). Of the 87 cultivars investigated, Achhoo and Naggardhan were shown to be resistant to RRKN (Narasimhamurthy, 2014).

M. graminicola resistance was detected in only one genotype out of twenty, KMP-179. A study by Devaraja *et al*. (2017) evaluated 33 genotypes of Asian rice against *M. graminicola* in DSR conditions. Based on the multiplication factor and root-knot index, the *cv*. NDR-97 showed strong resistance to RRKN with less than two galls per plant. To develop an F_2 mapping population, the rice cultivar Abhishek, which showed the least galls and significant resistance to RRKN, was crossed with the susceptible genotype Bangla Patni. Through bulked segregant analysis, a marker HvSSR10-21 was possibly connected to the resistant locus in cultivar Abhishek. The marker's linkage to the resistant locus Mg1(t) against *M. graminicola* was indicated by a significant LOD score. Previously, NRRI Cuttack discovered two F_9 recombinant inbred lines (RILs), Accession nos. CR3003-11-186 and CR3003-184, which were obtained from crossings of Annapurna × Ramakrishna, had a high level of resistance against the nematode. *In vitro* and soil tests conducted at IARI New Delhi revealed that the genotypes Vandana, Suraksha, Phule Radha, and EK 70 were resistant to RRKN at different inoculum levels. Additionally, RILs (F_7) were produced by crossing PB1121 × Phule Radha to map QTLs. Researchers have started breeding programmes to make rice resistant to nematodes. Currently, these resistance lines are being utilized in a number of nematode resistance breeding initiatives, which could result in the development of rice lines and cultivars resistant to RRKN.

However, this approach has long been hampered in rice cultivation due to the lack of nematode resistance sources in the cultivated *O. sativa* species. As mentioned above, genetic resistance to PPNs, particularly *M. graminicola*, has been identified in African rice, *O. glaberrima*, and wild relatives such as *O. glumaepatula*, *O. longistaminata*, *O. nivara*, and *O. rufipogon* (Soriano *et al*., 1999; Hada *et al*., 2020). Although most of these are quantitative resistance sources, some have been effectively used in breeding for resistance to other PPNs (Lorieux *et al*., 2003), but not for *M. graminicola*. Asian *O. sativa* cultivars exhibit strong resistance to *M. graminicola*, according to more recent research on global rice panels. Based on genetically and geographically diverse sources, three of these resistances have been partially characterized: Zhonghua 11 (Zh11) in the Chinese temperate japonica variety, KPM in the Thai aus subpopulation variety Khao Pahk Maw (KPM) (Dimkpa *et al*., 2016), and LD 24 in Sri Lanka. Similarly, *O. glaberrima*, the African rice plant, exhibits resistance to *M. graminicola* through a complex transcriptome response for which no single hormonal mechanism has been found to be the primary determinant (Petitot *et al*., 2017).

However, *M. graminicola* juveniles that penetrate the roots are tenacious and can initiate the development of giant cells. Histopathological investigations suggest that interactions in *M. graminicola*-resistant *O. glaberrima* lines may result in an HR-like response (Cabasan *et al*., 2014). Seemingly, late giant cell disintegration and poor nematode penetration are the main factors associated with resistance (Cabasan *et al*., 2014; Petitot *et al*., 2017). However, as the resistant *O. sativa* Zh11 cultivar demonstrates, *M. graminicola* infection appears to result in rapid cell death, as indicated by potentially necrotic cells observed in the root mesoderm during nematode migration. This accounts for *M. graminicola*'s total suppression of nematode multiplication and gall formation (Phan *et al*., 2018). Both the genetic components generating the resistance and the nature of the HR-like symptoms that develop during the incompatible interaction between *M. graminicola* and Zh11 rice are yet unknown.

IDENTIFICATION OF QTLS AND GENES RESPONSIBLE FOR *M. GRAMINICOLA* RESISTANCE

The field of genotyping technology advanced quickly, resulting in new, quicker, and less expensive ways to sequence plant genomes. High-density single-nucleotide polymorphisms (SNPs) allow for whole-genome scanning, which has been extensively utilized to identify MTAs for a number of yield-related traits. These haplotype blocks are often modest and strongly correlated with quantitative trait variation. To comprehend the underlying molecular mechanisms of resistance and to utilize these genes to produce rice cultivars resistant to nematodes, it is essential to identify and characterize the genes/QTLs generating resistance to root-knot nematodes. Genes and QTLs for a number of rice attributes have been mapped using various molecular mapping techniques. Bulk segregant analysis (BSA) is a helpful method for mapping genes or QTLs from a population with two extreme phenotypic traits (Michelmore *et al*., 1991; Venuprasad *et al*., 2009). The ability to efficiently find SNPs and other structural variants throughout the entire genome has been made possible by recent developments in next-generation sequencing technologies. Furthermore, genotyping has accelerated studies on genetic mapping and the generation of markers (Huang *et al.,* 2009). A "BSA-seq" approach that combines whole-genome resequencing with BSA of severe phenotypes is thought to be an efficient and cost-effective means of identifying genomic regions associated with a desired trait (Takagi *et al.,* 2013; Deokar *et al*., 2019). This technique has been successfully used in recent years to map QTLs with different genetic complexity, ranging from single genes to large QTLs, in a range of crops, such as brassica, rice, tomato, chickpea (Takagi *et al*., 2013; Illa-Berenguer *et al*., 2015; Deokar *et al*., 2019; Zhang *et al*., 2020). There is only one report of QTL identification for rice root-knot nematode resistance by the BSA-seq analysis using mapping populations obtained from indica and aus cultivar (Lahari *et al*., 2019).

A number of research have reported the quantitative nature of resistance to *M. graminicola* as QTLs for root galling, and the number of galls and eggs per root system has been determined by RIL populations (Shrestha *et al*., 2007; Jena *et al*., 2013; Galeng-Lawilao *et al*., 2018). *O. longistaminata*, *O. glaberrima* (African rice), and a few lines of *O. sativa* (Asian rice) are RRKN resistant, but the interspecific crosses did not exhibit resistance similar to that of *O. glaberrima*; therefore, the breeding programme to transmit RRKN resistance from *O. glaberrima* to *O. sativa* were unsuccessful. Numerous national screening initiatives have discovered a number of germplasms with variable resistance to RRKNs. RRKN resistance is quantitative, as demonstrated by mapping studies and QTL. These QTLs on *O. sativa* chromosomes 1, 2, 3, 6, 7, and 9 have been linked to root galling and eggs per root system. Eleven QTLs were discovered, including many putative lectin-domain-

containing genes and genes on chromosome 11 that were homologous to the Hordeum Mla locus. In yet another investigation, phenotypic characteristics such as the number of galls, egg masses, eggs/egg mass, and multiplication factor (MF) per plant were significantly correlated with 17 novel SNPs. These SNPs were associated with transcription factors such as WRKY, ARF, SCARECROW, MYB, bZIP, Cf2/Cf5 resistance protein, and NBS-LRR. They were found in QTLs on chromosomes 1, 2, 3, 4, 6, 10, and 11.

Similar to this, QTLs for resistance and tolerance to RRKN as well as other yield-related traits (such as plant height, weight of the roots and shoots, and the percentage of grains filled) were mapped on different chromosomal regions in RILs that were derived from different *O. sativa* accessions, like "IR64," "IR78877–208-B-1-2," and *O. glaberrima* accession "CG14." Das *et al*. (2011) screened 45 breeding genotypes of the *O. sativa* that have been enhanced for aerobic adaptability as well as 14 commonly grown traditional upland varieties against *M. graminicola*. The results of the experiment conducted in an indoor growth chamber showed that the fresh root weight and nematode population varied greatly both between and within the two rice ecotypes. Second-stage juveniles in aerobic rice genotypes had an average final and starting population ratio (RF value) of 6.5, much lower than that of upland cultivars (87.1). Accessions CG 14 and TOG 5674 of *O. glaberrima* demonstrated true resistance (RF=1). The aerobic rice genotypes IR 81426-B-B186-4 and IR81449-B-B-51-4, along with the traditional cultivars WAB 638-1 and IRAT 216, exhibited notable resistance to *M. graminicola*. Furthermore, resistance among the assessed rice genotypes is heritable, according to heritability study. They found that newly developed aerobic rice genotypes were more resistant to the RRKN than traditional upland cultivars and that it is possible to enhance these genotypes' resistance. Twelve QTLs with main effects and two epistatic interactions were found by Galeng-Lawilao *et al*. (2018, 2019, 2020) to be associated to *M. graminicola* resistance and tolerance in the first and second seasons, as well as other agronomic variables such as plant yield, the percentage of full grains, and the weight of fresh and dry roots. Additionally, genotypes of rice that are either resistant or partially resistant and tolerant, and that possess the favourable alleles for tolerance (qGR4.1, qMGR7.1, qMGR9.1, qGR4.1, qGR8.1) and resistance (qMGR4.1, qMGR7.1, qGR4.1, qGR8.1) QTLs, were chosen. Although they are vulnerable to *M. graminicola* infection, these chosen genotypes and the discovered QTLs provide essential information in developing MAB for the enhancement of high-yielding rice genotypes.

RILs produced from a hybrid of *O. sativa* accessions Bala and Azucena to report QTLs linked with root galling on five (1, 2, 6, 7 and 9) chromosomes (Shrestha *et al*., 2007). The percentage of variance explained by significant QTLs varied from 8.3 to 10.3. Using RILs derived from a cross of Annapurna and Ramakrishna, two traditional rice varieties from India, Jena *et al*. (2013) reported another QTL linked to the number of root galls per root system, eggs per root system, and eggs per g of roots on chromosomes 1 and 3. Additionally, Dimpka *et al*. (2016) mapped QTLs also linked to root galling on chromosomes 1, 3, 4, 5, 11, and 12 from a diverse rice panel. Hsa-1Og, a gene that gives resistance to the cyst nematode *Heterodera sacchari*, was the first nematode resistance gene found in rice. This gene was found in a segregating population that was descended from TOG5681 and IR64, and it is found on chromosome 11 (Lorieux *et al*., 2003). According to Bimpong *et al*. (2010), *O. glaberrima* accession TOG5681 is resistant to *M. graminicola* infection.

In order to understand the nematode genes involved in parasitizing rice plants, as well as to probe the immune responses of rice plants at different times following infection by *M. incognita*, *M. graminicola*, or *Hirschmaniella oryzae*, gene expression analysis by

RNA-sequencing has been employed (Petitot *et al*., 2017). Compared to *O. sativa* genotype "Nipponbare," the RRKN-resistant African rice *O. glaberrima* line TOG5681 exhibited induced genes for defence responses, phenylpropanoid and hormone pathways in response to *M. graminicola* infection. Several candidate genes conferring resistance against *M. graminicola* were identified (Petitot *et al*., 2017). The study of the functions of a small number of defensive response genes or plant hormone pathways involved in immune responses has been the subject of several studies on plants' response to RRKN infection (Hatzade *et al*., 2019). All of these investigations, however, do not directly compare the global gene expression response of resistant and susceptible nematode lines with the same genetic background. In an Indica rice land race with the genetic background JBT 36/14, a forward genetic screen identified several activation-tagged mutants resistant to RRKN (Hatzade *et al.,* 2019). Among the nematode-resistant mutants, line-9 was noteworthy because it exhibited lower nematode multiplication factor and post-penetration resistance to RRKN in comparison to the wild-type JBT 36/14 and the well-known basmati rice cultivar Pusa Basmati 1121 (Hatzade *et al.,* 2019). Despite numerous attempts, the location of the T-DNA insertion site in line-9 remains unknown. The nematodes were able to enter line-9 roots, however they were unable to form galls or multiply within the roots in contrast to JBT 36/14 (Hatzade *et al*., 2019).

A transcriptomic investigation of rice lines resistant to *M. graminicola* was done 24 hours post nematode infection to understand better the molecular pathways responsible for nematode resistance in the susceptible parent JBT 36/14 and mutant line-9 (Dash *et al*., 2021). In line-9, a total of 674 transcripts with differential expression were found and a number of genes were found to be involved in the production of secondary metabolites, such as diterpenoid biosynthesis (CPS2, OsKSL4, OsKSL10, Oscyp71Z2, oryzalexin synthase, and momilactone A synthase), as well as wall-associated receptor kinases (likely involved in nematode damage-associated molecular pattern recognition), signalling (Nucleotide-binding, Leucine-Rich Repeat, NLRs), pathogenesis-related (PR) genes (PR1, PR10a), defense-related genes (NB-ARC domain-containing genes), and a plethora of genes connected to pathogenesis. It was suggested that post-nematode juvenile penetration, early nematode J2 recognition led to phytoalexin-mediated plant immune responses, supported by PR proteins and obstructed nematode reproduction and growth.

MARKER-ASSISTED SELECTION BREEDING FOR RESISTANCE AGAINST RRKN

The primary concerns for sustainable crop development and resilience to biotic and abiotic pressures are the introduction of new diseases and pests, as well as the changing climate (Hasan *et al*., 2015). Over time, considerable advancements in the development of cultivars ideal for addressing various biotic and abiotic restrictions that impact rice productivity have been made possible by traditional breeding procedures. In order to provide a wider spectrum of resistance, the appearance of new biotypes and stressors has necessitated stacking multiple resistance genes into high-yielding cultivar backgrounds. With this increased resistance, crops are able to withstand attacks from multiple diseases at once. Technology advancements and the creation of DNA-based molecular markers have made it easier to transmit genes that confer resistance to various biotic (such as blast and gall midge), and abiotic (such as salinity and submergence) stresses in recent years.

By tracking the markers associated with each resistance gene, it is now possible to track the resistance genes due to advances in the understanding of molecular markers. The use of DNA markers to select resistant plants for gene pyramiding has been acknowledged as an

established technique (Sundaram *et al*., 2008; Dutta *et al*., 2014). Abad *et al*. (2003) found that *Mi* from *Lycopersicon peruvianum* provides resistance to some of the root-knot nematode species in tomato. Wang *et al.* (2006) found that RKN1 in cotton confers resistance to *M. incognita*, while Lorieux *et al*. (2003) found that Hsa-1Og provides resistance against the cyst nematode (*Heterodera sacchari*) in rice. In Asian rice, cultivar Zhonghua11, Mhatre *et al*. (2017) have identified a hypersensitive reaction (HR) against *M. graminicola*. Their results suggest that resistance is caused by key genes rather than quantitative resistance. There is a need for research on related rice species and their possible resistance to *M. graminicola*. According to Galeng-Lawilao *et al*. (2018), 300 RILs were produced from two well-known, high-yielding rice mega varieties, *i.e*., IR64, which is sensitive to *M. graminicola*, and IR78877-208-B-1-2, an aerobic rice genotype with enhanced tolerance and resistance to *M. graminicola*. Using this, the tolerance and resistance of *O. sativa* to *M. graminicola* were mapped. During the dry seasons of 2012 and 2013, RILs were phenotyped for tolerance and resistance.

The QTL study employed 131 single nucleotide polymorphism (SNP) and 32 simple sequence repeat (SSR) markers. This study discovered two epistatic interactions in the first and second seasons, as well as a total of 12 QTLs with main effects associated with tolerance and resistance to *M. graminicola*, along with other agronomic factors as plant yield, percentage of whole grains, and fresh and dried root weight. Additionally, genotypes of rice that are either resistant or partially resistant and tolerant and that possess the favourable alleles for tolerance (qGR4.1, qMGR7.1, qMGR9.1, qGR4.1, qGR8.1) and resistance (qMGR4.1, qMGR7.1, qGR4.1, qGR8.1) QTLs, were chosen. Although they are vulnerable to *M. graminicola* infection, these chosen genotypes and the discovered QTLs provided essential information in developing MAB to enhance high-yielding rice genotypes. QTL mapping and trait development programmes have made it possible to identify genomic areas that can be transferred through marker-assisted breeding to improve existing cultivars for one or more attributes. The development of Sub1 gene-based submergence-tolerant cultivars was a significant early success in marker-assisted breeding for resistance to abiotic stresses. RRKN found that five QTLs associated with root galling were present in RILs produced by crossing the *O. sativa* accessions "Bala" and "Azusena".

To produce NILs of Swarna with the Sub1 gene, Neeraja *et al*. (2007) described a systematic approach that sequentially uses background, recombinant, and foreground markers. The first rice cultivar created using a scientific marker-assisted backcrossing approach was Swarna-Sub1. MAS has two benefits over traditional selection, the primary one being a reduction in the time required to develop products. With MAS, 99 per cent of the recipient genome may be recovered by BC4, but with traditional backcross breeding, this process cannot be completed until BC6. The introduction of phenotype-diagnostic markers not only requires fewer generations of backcrosses but also decreases the necessity for expensive and time-consuming phenotyping.

GENOME WIDE ASSOCIATION STUDIES

A method for identifying marker-trait associations (MTAs) in a group of unrelated germplasm is linkage disequilibrium mapping (LD) or genome-wide association research (GWAS). Compared to normal bi-parental QTL mapping, GWAS allows for faster analysis of quantitative traits at greater resolution because it is based on past recombination events. It might be used to identify significant MTAs for wheat nematode resistance. *H. avenae* resistance and *H. flipjevi* resistance in wheat have only been the subject of a few number of GWA investigations (Mulki *et al*. 2013; Dababat *et al*. 2016, 2021; Pariyar *et al*. 2016). The degree of genetic

variation, population structure, and LD all affect the power of association studies. Numerous factors, including population structure, selection, recombination rate, and allele frequency, influence it (Flint-Garcia *et al.,* 2003; Mulki *et al*., 2013). According to multiple research, LD decreases with increasing distance between SNPs and varies between sub-genomes and each chromosome (Mulki *et al*., 2013; Dababat *et al*., 2016; Pariyar *et al*., 2016; Guerra *et al*., 2021). Mulki *et al*. (2013) have reported that long-distance LD can exist, but it can also diminish for close loci. LD degradation in the wheat panel is between 1.09 kbp and 23 Mb, according to earlier research (Appels *et al*., 2018; Kidane *et al*., 2019; Li *et al*. 2019; Luján Basile *et al*., 2019; Pang *et al*., 2020; Guerra *et al*., 2021). GWAS has only been utilized in a small number of studies so far to find novel QTLs for phytonematode susceptibility or resistance in a variety of plants, including rice, wheat, soybean, and *Arabidopsis*. QTLs associated with root galling were mapped to chromosomes 1, 3, 4, 5, 11, and 12 in an Asian rice global panel. Eleven QTLs linked to nematode resistance were identified by a GWAS, two of which were in close proximity to epistatic loci found in the Bala × Azucena population. This investigation showed many lectin-domain-containing genes on chromosome 11 (Dimpka *et al*., 2016).

However, more research on rice panels from various geographic locations (such wild rice accessions with more genetic variety) will expand the pool of resistance genes that can be used in rice breeding initiatives in the future. The availability of wild rice is rapidly declining due to urbanization and the strain of an ever-increasing population. The Indo-Burma area is regarded as a hotspot for wild rice populations' biodiversity. Hada *et al*., 2020 examined 272 distinct wild rice accessions (*O. nivara*, *O. rufipogon*, and *O. sativa* f. *spontanea*) to identify genotypes resistant to RRKN. They revealed the genetic basis of RRKN resistance by using 50K "OsSNPnks" genic Affymetrix chips in a genome-wide association study to genotype SNPs. A study of the population structure showed that these accessions were divided into three main subpopulations. A total of 40 resistant accessions (multiplication factor/MF < 2 and nematode gall number) were found, and 17 new SNPs were shown to be substantially correlated with phenotypic variables, including MF per plant, number of galls, egg masses, and eggs/egg mass. SNPs were found around the QTL on chromosomes 1, 2, 3, 4, 6, 10, and 11 that contain potential genes such as WRKY transcription factors, MYB, bZIP, ARF, Cf2/Cf5 resistance protein, NBS-LRR, and bZIP. Seven days following inoculation, RRKN-infected plants exhibited considerably higher expression of these identified genes than mock-infected plants. The discovered SNPs expand the pool of possible genes for future marker-assisted breeding projects, which will help reduce the damage caused by RRKN in rice.

CRISPR/CAS9-MEDIATED RESISTANCE AGAINST *M. GRAMINICOLA*

In order to effectively control plant disease, CRISPR crops containing mutations in susceptibility (S) genes offer a method that is "transgene-free" and typically exhibit a more robust and broad-spectrum form of resistance. Alterations to the S gene can potentially result in disease resistance (Zaidi *et al*., 2018). In order to either reduce host immune signals or to aid in host recognition, penetration, nutrition acquisition, proliferation, and spread, pathogens activate, target, or recognise plant genes known as S genes (van Schie and Takken, 2014; Zaidi *et al*., 2018). The resistance that results from inactivating the S gene is long-lasting and genetically recessive. Genetic editing has made strides in breeding new resistant materials through S gene editing possible. No reports of CRISPR/Cas9-mediated editing of S genes to create resistance to plant parasitic nematode disease exist. Huang *et al*., 2023, produced genetically stable homozygous rice mutants, either with or without transgenic elements, by introducing a targeted mutation

of the rice copper metallochaperone heavy metal-associated plant protein 04 (OsHPP04) S gene using CRISPR/Cas9 technology. Furthermore, the "transgene-free" homozygous mutants showed an increase in the defence-related gene expression, reactive oxygen species burst, and callose deposition - all of which are plant immunological responses that are initiated by flg22. Based on an examination of the agronomic traits and rice development of two distinct mutants, no discernible variations were found between wild-type plants and the mutants. These results imply that OsHPP04 might be an S gene that negatively regulates host immunity and that genetically modifying S gene using CRISPR/Cas9 technology can be a potent method of creating plant varieties resistant to PPN.

The malectin-like receptor kinase GmLMM1 regulates pattern-triggered immunity and cell death in soybeans during *M. incognita* infection. Nematode-expressed RALF-like ligands bind to GmLMM1, inhibiting the host's immune response and promoting *M. incognita* infection. Using CRISPR/Cas9, GmLMM1 has been demonstrated to negatively influence *M. incognita* resistance in soybean *cv*. Williams 82 and DN50 (Zhang *et al*., 2021). It has been revealed that a heavy metal-associated plant protein (OsHPP04) acts as a negative regulator of rice defence against infection by *M. graminicola*. To scavenge reactive oxygen species and reduce host immunity, *M. graminicola* effector MgMO289 interacted with the copper metallochaperone OsHPP04 (Song *et al*., 2021). After OsHPP04 was eliminated using CRISPR/Cas9, rice (*cv.* Nipponbare) exhibited enhanced resistance to *M. graminicola*. Moreover, Huang *et al*. (2023) reported that there were increases in reactive oxygen species generation, callose deposition, and defence gene expression in mutant lines.

FUTURE OF INNOVATIVE BREEDING IN RICE

Apart from the different traditional breeding techniques mentioned above, genome editing is predicted to play a significant role in applied plant breeding in the future. The classical novel method of genome editing for rice enhancement is CRISPR-Cas9. It has gained popularity over other genome-editing methods, including zinc finger nucleases and transcriptional activator-like effector nucleases (TALENs), because of its increased efficiency in editing several target genes simultaneously (Liu *et al*., 2017). Few studies have used genome editing to produce rice suitable for DSR/AWD conditions. Attempts have been made to enhance plant growth and stress response by employing modified ABA receptor genes (pyrabactin resistance 1-like; PYL1, 4 and 6) (Miao *et al*., 2018). As genome-editing methods continue to progress and new strategies are proposed, it is expected that novel solutions may surface. For example, vector-based RNA delivery modifies traits in agronomic practice without requiring heritable genome editing (Torti *et al.,* 2021). These solutions may enable pursuing breeding targets that are currently unsatisfactorily addressed, like reducing methane emissions or improving photosynthetic efficiency. The first set of targets for genome editing might be major gene-controlled traits in directly sown rice. Some traits associated with crop establishment, such as anaerobic germination and regular, early emergence, could be among them. Moreover, rapid advancement can be attained by modifying targets that have been demonstrated to enhance resistance against predominant biotic stressors, including brown spots, nematodes, and blast. Furthermore, genome editing can help confirm important target genes identified by expression investigations for trait development studies.

CONCLUSIONS

Numerous screening studies have been carried out and several RRKN-resistant rice germplasm/lines have been identified in India and abroad. Several QTLs have been identified as associated with RRKN resistance. Molecular and gene expression studies have identified several RRKN resistance pathways and mechanisms.

Several rice breeding programmes have been initiated and are in advanced stages. As of now, no RRKN resistant cultivar has been notified. Concerted and sustained efforts are required to convert the basic research on RRKN resistance in rice into resistant cultivars in the near future.

CONFLICT OF INTEREST

Authors declare no conflict of interest.

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