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RESEARCH ARTICLE

Genome-wide association studies (GWAS) for resistance to *Meloidogyne graminicola* in an association panel of *Oryza rufipogon*

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Abstract

The rice root-knot nematode (RRKN), *Meloidogyne graminicola*, is an obligate pathogen responsible for considerable yield losses in both upland and rainfed lowland rice cultivation in India. Identifying and mapping quantitative trait loci (QTLs) associated with resistance to *M. graminicola* could provide a sustainable and cost-effective management strategy for farmers. Genetic resources for resistance to *M. graminicola* are limited in Asian rice (*Oryza sativa*) cultivars. Therefore, a study was conducted to identify potential sources of resistance in wild rice. In this study, 93 accessions of *Oryza rufipogon* were screened for resistance to RRKN, alongside the susceptible check PR126, under artificial inoculation conditions over 2 years at the Department of Plant Pathology, Punjab Agricultural University, Ludhiana, Punjab, India. The evaluation of RRKN resistance was based on the root galling index (RGI), soil nematode population and reproduction factor (Rf). A genome-wide association study (GWAS) for RRKN traits identified significant associations for RGI on chromosomes 1, 2, 5, 6 and 11. For soil nematode population, significant associations were found on chromosomes 2, 4, 5, 6 and 7. Notably, QTLs on chromosomes 2 and 6 were consistently detected across traits and models, providing robust candidate regions for resistance. Among these, SNP S6_23144943 on chromosome 6 showed consistent association across all models and may represent a stable genetic source of resistance. These loci highlight the polygenic nature of resistance to *M. graminicola* in wild rice and represent valuable resources for marker-assisted breeding.

Keywords: quantitative trait loci; rice breeding; root galling index; soil nematode population; wild rice

Introduction

The rice root-knot nematode, *M. graminicola,* has emerged as a significant bottleneck in the production of Asian rice (1). This endoparasite sedentary nematode infests a wide range of rice production systems, lowland, upland, irrigated, rainfed and deep-water conditions. It is known to cause considerable economic yield losses (2-5). Managing *M. graminicola* involves a combinatorial approach comprising of cultural, biological and chemical control methods. To mitigate yield losses caused by *M. graminicola*, effective management strategies include crop rotation, continuous flooding, the use of resistant rice varieties and practices that promote healthy soil conditions. Nematicides may be used in severe infestations, but their use requires careful consideration due to potential environmental impacts. All these practices have their limitations. However, continuous flooding can effectively decrease nematode populations in the soil by preventing infective second-stage juveniles (J_2) from entering rice roots. Despite this, its use is limited due to the growing scarcity of water for agricultural purposes (6). Crop rotation with poor or non-hosts of *M. graminicola*, such as mung bean, mustard and sesame, can effectively lower nematode population densities in the soil (7, 8). However, switching to another crop, even for part of the growing season, may impose an unacceptable cost for many small-scale rice farmers in Asia, where rice is the staple food. Although nematicides may provide some control over *M. graminicola*, this approach is not a practical solution, particularly for small-scale farmers, as these chemicals are costly and can be harmful to the environment. Furthermore, many chemicals used for nematode control, such as DBCP (1, 2-dibromo-3-chloropropane) and EDB (ethylene dibromide), have already been banned from the market (9). In this context, cultivating resistant or tolerant rice varieties could provide an effective, cost-efficient and environmentally sustainable approach for keeping *M. graminicola* population densities below economically damaging threshold levels.

Resistance to *M. graminicola* has been identified in *Oryza longistaminata* in African cultivated rice (*O. glaberrima* Steud.) (10, 11), as well as in Asian rice (*Oryza sativa* L.) (12-16). However, the majority of Asian rice germplasm is susceptible to *M. graminicola* (3). Efforts have been made to transfer resistance to *M. graminicola* from African rice into Asian rice. Still, the interspecific progenies did not

exhibit the same level of resistance as African rice (10). Sexual incompatibility and hybrid sterility hinder the effort to combine beneficial traits from these two rice species. Although hybrid fertility can be restored through repeated backcrossing, there is a risk of losing the desirable characteristics in the process (17).

Oryza rufipogon, the wild ancestral species of rice, has been recognized as a valuable donor for yield-related traits and resistance to several biotic and abiotic stresses (18, 19). We have already identified resistance sources to *M. graminicola* in a collection of *O. rufipogon* accessions (20). Based on this, we hypothesized that *O. rufipogon* harbors novel alleles and stable QTLs conferring resistance to *M. graminicola*, which can be exploited for rice improvement. Therefore, the present study was undertaken to evaluate diverse accessions of *O. rufipogon* for resistance under controlled inoculation, to identify genomic regions associated with resistance using GWAS and to detect stable QTLs across traits and models that can serve as robust candidates for marker-assisted breeding to enhance nematode resistance in cultivated rice.

Materials and Methods

Plant material

A collection of 93 *O. rufipogon* accessions was used in this study. Of 93 *O. rufipogon* accessions, 33 have their origin from Thailand, 23 from India, 9 from Cambodia, 8 from Nepal, 6 from Myanmar, 3 from China, 2 from Srilanka, 2 from Papua New Guinea, 2 from Taiwan, 1 each from the Philippines, Malaysia, Indonesia, Bangladesh and Australia. Seeds of all the accessions were received from the School of Agricultural Biotechnology, Punjab Agricultural University (PAU), India. A high- yielding cultivar, PR 126, recommended by PAU for sowing under direct-seeded conditions but highly susceptible to RRKN, was kept as a susceptible check. The germplasm set was evaluated against *Meloidogyne graminicola* for 2 years in India, *viz.* PAU.

Nematode inoculum and screening procedure

The nematode culture of *M. graminicola* was maintained on the susceptible cultivar PR126 in a sterilized soil-sand mixture under glasshouse conditions (28 ± 2 °C; 70 - 80 % RH). Second-stage juveniles (J_2) were extracted from infected roots and soil using a modified Cobb's sieving and decanting method (21, 22). The inoculum density was standardized to approximately 1000 freshly hatched J_2 per plant, which were applied around the root zone of 21-day-old seedlings transplanted into sterilized soil-filled pots (15 cm diameter). Plants were maintained with a shallow water layer (2-3 cm) and received recommended nutrient management practices. Screening was carried out in a randomized complete block design (RCBD) with 3 replications, each with at least 5 plants per accession. Resistance to *M. graminicola* was assessed 45 days after inoculation using 3 parameters: (i) RGI, recorded on a 1-5 scale (23); (ii) soil nematode population (SnP), determined by extracting J_2 from 250 cc of soil using the modified Cobb's sieving and decanting method (21, 22); and (iii) reproduction factor (Rf), calculated as the ratio of final nematode population to the initial inoculum. Based on these parameters, accessions were categorized into resistant and susceptible classes.

Genome Wide Association Study (GWAS)

Genotypic data for the 93 *O. rufipogon* accessions were obtained from previously generated restriction-site associated DNA sequencing (RAD-seq) datasets (24). The raw reads were aligned to the rice reference genome and single-nucleotide polymorphisms (SNPs) were filtered using the following criteria: ≤ 20 % missing data, minor allele frequency (MAF) > 0.05 and exclusion of multi-allelic SNPs and indels. After filtering, a set of 196652 high-quality SNPs was used for GWAS. Genome-wide association analyses were conducted using the GAPIT version 3.0 package (25). Three complementary models were applied: the Generalized Linear Model (GLM), which considered only fixed effects; the Mixed Linear Model (MLM), which included both fixed and random effects (26); and the Fixed and Random Model Circulating Probability Unification (FarmCPU), which iteratively incorporates both impact (27). Principal components were included as covariates to account for population structure and a kinship matrix was used as a random effect. A threshold of -log10 (p) ≥ 3.0 (p ≤ 0.0002) was selected, corresponding to a LOD score of 3.0, a widely used threshold in GWAS of rice. While stricter corrections, such as Bonferroni or FDR, can minimize false positives, they may be overly conservative for complex traits like nematode resistance. Therefore, SNPs consistently detected across models and traits were considered robust associations.

Results and Discussion

Phenotypic variation and GWAS analysis

Of the 93 accessions evaluated, one accession (IR93070) exhibited a highly resistant reaction. In comparison, 12 accessions showed a resistant response, 17 accessions were moderately resistant, 44 accessions showed a moderately susceptible response and 19 accessions were highly susceptible. This wide phenotypic variation, as assessed through both RGI and soil nematode population (SnP), highlights the genetic diversity available within *O. rufipogon*. The use of both RGI and SnP as phenotypic traits provides a more reliable measure of resistance than earlier studies that relied solely on gall scores (28).

Genome-wide association analysis of resistance traits

GWAS was conducted using 196,652 high-quality SNPs, along with phenotypic data for RGI and SNP from 93 *O. rufipogon* accessions to identify genomic regions associated with resistance to *Meloidogyne graminicola*. A total of 11 QTLs were identified across seven chromosomes using GLM, MLM and FarmCPU models (Table 1; Fig. 1 & 2). The Manhattan plots (Fig. 1 for RGI and Fig. 2 for SnP) display the distribution of SNP associations across the genome, highlighting significant peaks on chromosomes 2 and 6. The corresponding Q–Q plots (Fig. 3 & 4) showed a good fit to the expected distribution, confirming the reliability of detected associations. These distinct association peaks on chromosomes 2 and 6, supported by consistent signals across models, suggest the presence of stable QTLs contributing to resistance against *M. graminicola* in *O. rufipogon*. The maximum number of SNPs was associated with RGI using the FarmCPU model on chromosomes 1, 2, 5, 6 and 11, whereas both GLM and MLM models consistently detected associations on chromosomes 2 and 6. Among these, SNP S6_23144928 on chromosome 6 had a relatively high minor allele frequency (MAF = 0.42), suggesting its practical breeding relevance. Based on all 3 models, 3 SNPs (S2_35534567, S6_23144943 and S6_17170302) were consistently associated with RGI. Similarly, GWAS for SnP identified 7 SNPs distributed across chromosomes 2, 4, 5, 6 and 7 with FarmCPU detecting all associations, while GLM and MLM again confirmed associations only on chromosomes 2 and 6.

Table 1. Significant SNP associations for RGI and soil nematode population (SnP) identified through GWAS using GLM, MLM and FarmCPU models

Sr. No.	SNP ID	Chromosome	Position	*p* value			MAF[#]	Trait[$]
				GLM	MLM	FarmCPU		
1	S1_19340782	1	19340782			0.000127	0.06451	RGI
2	S2_2241346	2	2241346			0.000152	0.06451	RGI
3	S2_9563684	2	9563684			0.00019	0.27419	SnP
4	S2_35534567	2	35534567	0.000296	0.000296	8.80E-05	0.09677	RGI, SnP
5	S4_22201160	4	22201160			0.000142	0.22043	SnP
6	S5_87587	5	87587			0.000131	0.22580	SnP
7	S5_977868	5	977868			0.000147	0.06451	RGI
8	S6_23144943	6	23144943	9.05E-05	9.05E-05	1.65E-05	0.42473	RGI, SnP
9	S6_17170302	6	17170302			0.000123	0.19892	RGI, SnP
10	S7_25207219	7	25207219			0.000102	0.19354	SnP
11	S11_5441870	11	5441870			0.000162	0.09677	RGI

[#]MAF= Minor Allele Frequency,

[$]RGI=root galling index, SnP=soil nematode population

Note**:** SNPs in bold are consistently detected across traits (RGI and SnP) and across all 3 models (GLM, MLM, FarmCPU)

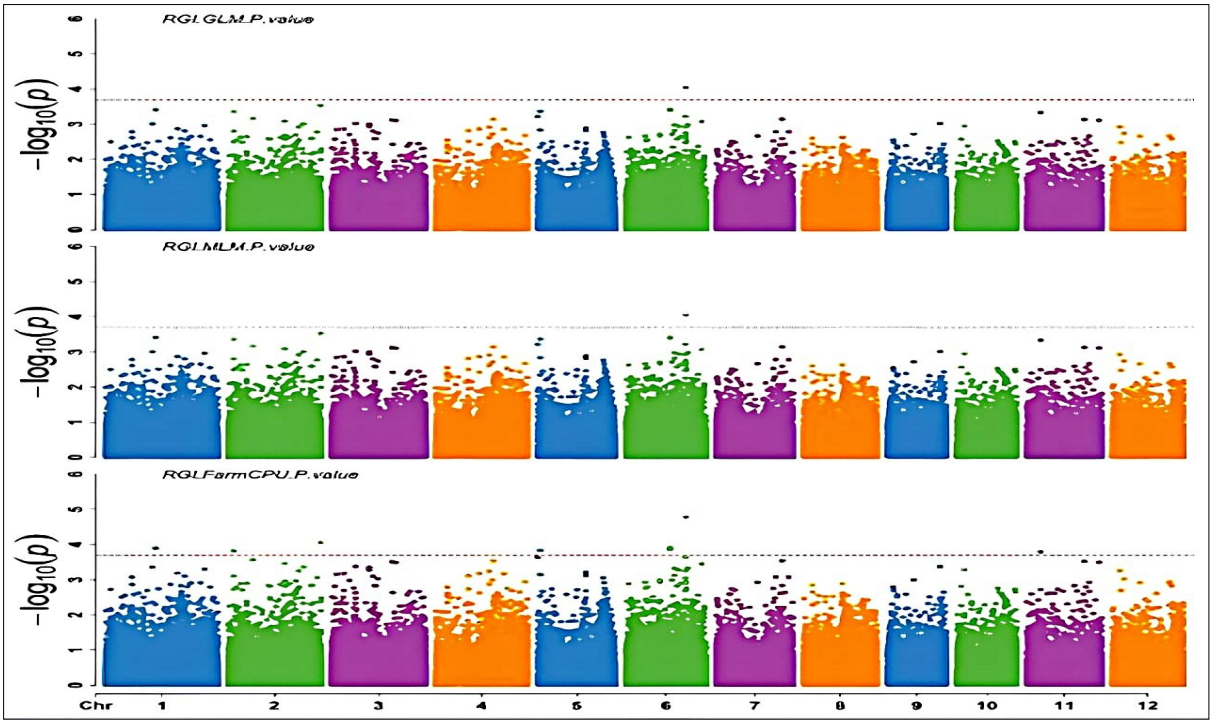

Fig. 1. Manhattan for RGI of rice root-knot nematode *(Meloidogyne graminicola)* in 93 *Oryza rufipogon* accessions.

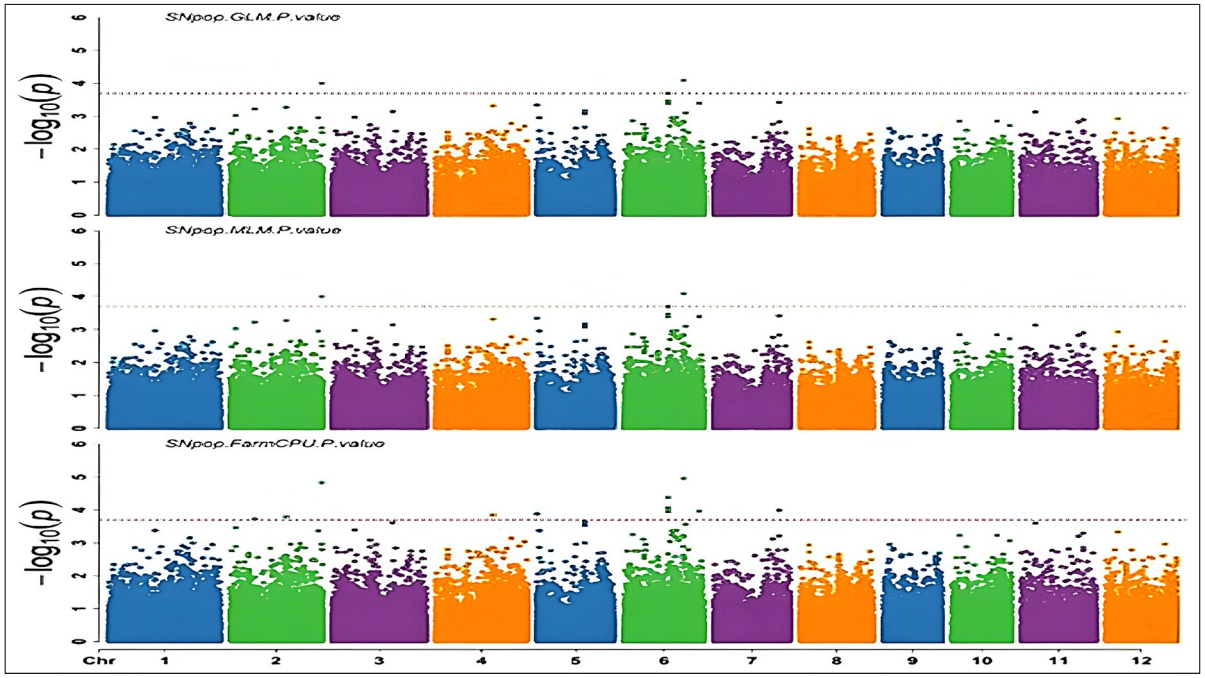

Fig. 2. Manhattan for SnP of rice root-knot nematode (*M. graminicola*) in 93 *O. rufipogon* accessions.

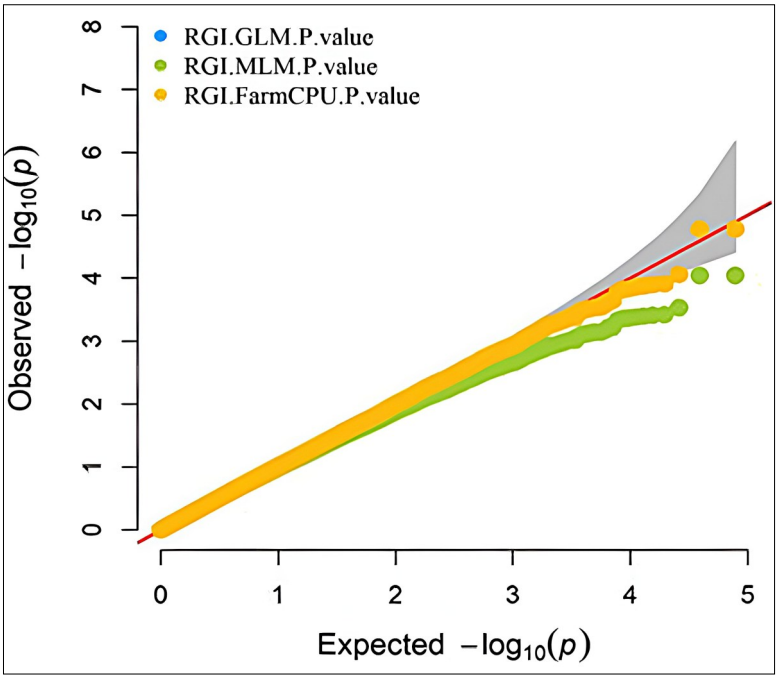

Fig. 3. Q–Q plots for root galling index (RGI) of rice root-knot nematode (*Meloidogyne graminicola*) in 93 *Oryza rufipogon* accessions.

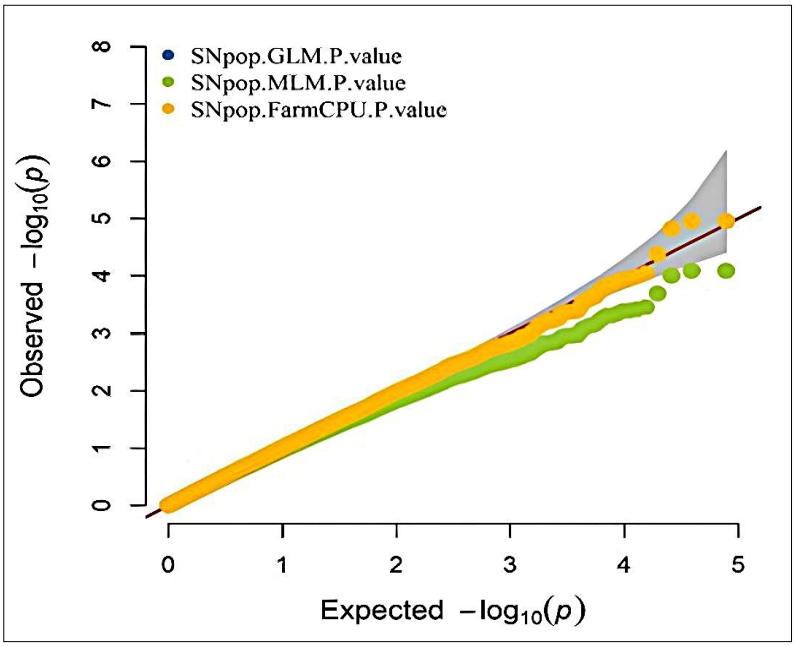

Fig. 4. Q–Q plots for SnP of rice root-knot nematode (*M. graminicola*) in 93 *O. rufipogon* accessions.

Taken together, 3 SNPs on chromosomes 2 and 6 were found to be consistently significant across both traits and models and these were considered as putative QTLs for resistance to *M. graminicola* in *O. rufipogon*. Notably, SNP S6_23144943 on chromosome 6 was repeatedly detected across traits and models (Fig. 1 & 2), confirming its strong association with both galling and nematode multiplication. Its relatively high MAF (0.42) indicates that the allele is common in the population, making it a suitable candidate for use in breeding programs targeting resistance to *M. graminicola*.

The consistent detection of SNPs across multiple models indicates robustness of the associations. Notably, SNP S6_23144943 on chromosome 6 was repeatedly detected across traits and all three models, suggesting its strong role in resistance to both galling and nematode multiplication. Its relatively high MAF (0.42) indicates that the allele is common in the population, making it a suitable candidate for use in breeding programs targeting resistance to *M. graminicola*. Collectively, the Manhattan and Q-Q plots (Fig. 1-4) illustrate the robustness and reproducibility of the GWAS signals obtained for both traits.

The presence of significant SNPs across different chromosomes (1, 2, 4, 5, 6, 7 and 11) suggests that multiple genomic regions contribute to resistance. The identification of QTLs, particularly on chromosomes 2 and 6, confirms the polygenic nature of resistance to *M. graminicola* in wild rice. These results agree with earlier reports of QTLs for partial resistance on chromosomes 1, 2, 6, 7, 9 and 11 in Asian rice (*O. sativa*) using recombinant inbred lines (29, 30). Likewise, a GWAS conducted in Indian wild rice accessions also reported multiple loci for resistance (31), further validating wild species as reservoirs of resistance alleles.

Breeding for nematode resistance remains the most cost-effective and sustainable strategy to reduce nematode-induced yield losses. Several resistance (R) genes and QTLs for sedentary endoparasitic nematodes have been mapped in other crops (32, 33), although only a few have been cloned (34, 35). In rice, the use of wild relatives such as *O. rufipogon* and *O. glaberrima* has shown

considerable potential as donors of resistance. Previous studies also emphasized the value of these species as untapped sources of nematode resistance (36). For example, *O. glaberrima* has been reported as a promising donor for *M. graminicola* resistance (37), supporting our present findings from *O. rufipogon*. Collectively, these studies highlight the potential of introgressing resistance loci from wild relatives into elite *O. sativa* cultivars. Candidate regions on chromosomes 2 and 6 harbor genes related to NBS-LRR proteins, WRKY transcription factors and auxin-responsive elements, all of which are implicated in plant-nematode interactions. These candidate genes warrant further fine mapping and transcriptomic validation.

Beyond mapping resistance loci, understanding the underlying molecular mechanisms is crucial. Transcriptomic and functional genomic studies have revealed that *M. graminicola* manipulates host pathways involved in auxin biosynthesis and reactive oxygen species (ROS) regulation, which are essential in plant defense (38). QTL mapping and GWAS studies specific to *M. graminicola* remain limited compared to those of other nematodes, such as *Heterodera* spp. and *M. incognita*. While marker-assisted selection has been successfully applied in wheat and other crops for nematode resistance (39), its use in rice is still underdeveloped. The advantage of GWAS is that it can complement QTL mapping by detecting novel alleles with small effect sizes, making it particularly powerful for dissecting complex traits such as nematode resistance (40). Interestingly, whereas earlier studies primarily relied on galling scores (30, 41), our integration of both RGI and soil nematode populations provides a more comprehensive phenotypic assessment. This is one of the few GWAS studies in rice to include soil J_2 count as a trait, which adds novelty and reliability to the identified QTLs.

The QTLs consistently identified on chromosomes 2 and 6 thus emerge as strong candidates for further functional validation. Fine mapping and cloning of these loci, along with transcriptomic profiling of resistant and susceptible accessions, will be essential to confirm their role in nematode resistance. Once validated, these loci can serve as starting points for pyramiding resistance genes through marker-assisted backcrossing or genomic selection in rice breeding. Similar strategies have been used successfully in other crops. For example, the *Mi-1.2* gene in tomato provides resistance to several *Meloidogyne* spp. (34), while the Hsa-1Og gene in African rice confers resistance to the cyst nematode *Heterodera sacchari* (42). Numerous other nematode resistance QTLs have been mapped in crops such as soybean, potato and pepper, but such information remains limited for *M. graminicola* in rice. In fact, previous studies identified QTLs for partial resistance on chromosomes 1, 2, 6, 7, 9 and 11 using recombinant inbred lines from Bala × Azucena in Asian rice (34) and 12 QTLs with main effects and epistatic interactions were also reported (12). In addition, a primary root-knot nematode resistance locus on chromosome 11 in rice (*O. sativa*) has recently been identified (43). Taken together, our results confirm that resistance to *M. graminicola* in *O. rufipogon* is polygenic and that chromosomes 2 and 6 harbor robust loci that can be targeted for marker-assisted selection. These findings not only validate earlier reports but also introduce novel evidence using both RGI and soil nematode populations as traits, thereby providing new avenues for functional validation and resistance breeding in rice.

Conclusion

In our study, we report 3 consistent QTLs on chromosomes 2 and 6 that can be used for breeding nematode resistance in rice. To our knowledge, no published studies have mapped QTLs for resistance to *M. graminicola* in rice using the number of J2 in the roots as the resistance trait. Additional studies on rice panels from different geographic regions will expand the resistant gene pool, which can be utilized in future rice breeding programs. In conclusion, the identification of these SNPs has laid the foundation for gaining valuable insights into the genetic architecture of resistance to *M. graminicola*. Further validation and functional characterization of these SNPs are necessary to confirm their role in nematode resistance. Still, these findings pave the way for future genetic studies and breeding strategies aimed at improving crop resistance to nematode damage.

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Authors' contributions

AS, HSB and NKD jointly planned and executed the research work. AS and HSB carried out phenotyping, data collection for root galling index and soil nematode population and statistical analysis. DB contributed valuable insights on genetic resources and supported genotypic data handling. NKD supervised the entire study, guided the GWAS analysis and critically reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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