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GENOME-WIDE ASSOCIATION MAPPING OF EARLY LEAF SPOT RESISTANCE AND YIELD TRAITS IN GROUNDNUT (*ARACHIS HYPOGAEA* L.) REVEALS NOVEL SNP MARKERS FOR MARKER-ASSISTED BREEDING

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ABSTRACT

Groundnut, an important food and oilseed crop globally, but its productivity is constrained by early leaf spot (ELS) disease and limited genetic diversity. This study aimed to assess the genetic diversity, population structure, linkage disequilibrium (LD), and identify marker-trait associations (MTAs) for ELS resistance and pod weight sing 3,592 SNP markers in a mini core collection of groundnut accessions. After quality filtering, 964 SNPs were retained for downstream analyses. Population structure analysis using STRUCTURE software revealed two subpopulations, consistent with cluster analysis based on geographic origin. LD decay was moderate, dropping to $r^2 = 0.1$ at approximately 2 Mb, which is suitable for genome-wide association studies (GWAS). Nineteen significant MTAs ($p < 0.001$) were identified across environments and conditions. SNP marker SM01 on chromosomes A05 and B05 showed a remarkably high phenotypic variance explained (PVE) of 63.56% for ELS at 65 days after sowing (DAS), indicating a strong potential for marker-assisted selection (MAS). Other moderate-effect SNPs such as SM02 and SM07 demonstrated stable associations across locations and conditions, particularly for ELS at 90 DAS and pod weight. The findings confirm the feasibility of using SNP-based GWAS for dissecting complex traits in groundnut and highlight genomic regions of interest for breeding ELS-resistant and high-yielding cultivars. The identified markers provide a valuable genomic resource for accelerating genetic improvement in groundnut through MAS and genomic selection. Future work should focus on validating these markers across diverse germplasm and environments to ensure robust application in breeding programs.

Keywords: Groundnut, Marker-trait association, Population structure, genome wide association study, foliar disease.

INTRODUCTION

Groundnut (*Arachis hypogaea* L.) is a globally significant legume crop due to its high oil content, protein-rich composition, and adaptability to various agro-ecological zones. It is cultivated in over 100 countries and ranks as the fourth most important source of edible oil and third most important source of vegetable protein worldwide (Niazi *et al.,* 2023). Recent FAO estimates place the global groundnut cultivation area at approximately 26.5 million hectares, producing 43.9 million tons of pods annually (Pooniya *et al.,* 2020). Nigeria remains one of the top producers in sub-Saharan Africa, where groundnut serves both commercial and subsistence roles. Despite its importance, groundnut productivity remains constrained by biotic stresses, particularly foliar fungal diseases. Early and late leaf spots caused by *Passalora arachidicola* and *Nothopassalora personata* (formerly *Cercospora* spp.), and rust caused by *Puccinia arachidis*, are among the most destructive pathogens, responsible for yield losses ranging from 15% to 70% (Prabhu & Vindhiyavarman, 2017). These diseases thrive in warm and humid climates and continue to limit yield gains despite conventional control strategies. One of the core challenges in breeding for resistance is the complex genetic nature of disease resistance, often controlled by multiple recessive genes, and further complicated by the low genetic diversity among cultivated groundnut varieties. This limited diversity arises from the crop's origin via a single hybridization event between two diploid progenitors (*Arachis duranensis* and *Arachis ipaensis*) (Shanthala *et al.,* 2022). Consequently, the development of polymorphic DNA markers critical for breeding and genetic mapping has been slow, posing a major hurdle to QTL mapping and marker-assisted selection (Motagi *et al.,* 2022). Modern biotechnological tools offer promising alternatives. The use of single nucleotide polymorphisms (SNPs), powered by next-generation sequencing technologies such as genotyping-by-sequencing (GBS) and restriction site-associated DNA sequencing (RAD-seq), has enabled large-scale identification of genetic variations in groundnut (Shanthala *et al.,* 2022). These advances are crucial for genome-wide association studies (GWAS), which have shown high resolution in identifying marker-trait associations (MTAs) using natural populations (Reager *et al.,* 2024). GWAS not only accelerates the identification of genomic regions linked to traits of interest but also avoids the need for labor-intensive bi-parental populations. Understanding the extent of linkage disequilibrium (LD) and genetic diversity in germplasm collections is essential to harnessing GWAS power. SNP-based GWAS has become the method of choice due to its precision and ability to dissect complex traits like disease resistance. Therefore, leveraging GWAS and SNP marker data, this study aims to: Assess the genetic diversity of groundnut lines for early leaf spot resistance, and Identify

significant marker-trait associations (MTAs) related to early leaf spot resistance.

MATERIALS AND METHODS

Groundnut leaf samples were collected at two weeks after sowing (2 WAS) and placed into 96-deep well sample collection plates for genotyping. These samples were sent to the Integrated Genotyping Service and Support (IGSS) platform at the Biosciences Eastern and Central Africa–International Livestock Research Institute (BecA-ILRI) Hub in Nairobi, Kenya. DNA was extracted using the Nucleomag Plant Genomic DNA extraction kit, yielding genomic DNA concentrations ranging from 50–100 ng/µl. DNA quality and quantity were assessed using 0.8% agarose gel electrophoresis. Genotyping was performed using the Diversity Arrays Technology sequencing (DArTSeq) platform. The DArTSeq method involves a complexity reduction step through enzymatic digestion of genomic DNA, followed by ligation with barcoded adapters and PCR amplification of adapter-ligated fragments. Sequencing was carried out on an Illumina HiSeq 2500 platform using single-read runs of 77 base pairs.

The DArTSeq protocol followed the procedures outlined by Kilian *et al.* (2012). In summary, fluorescently labelled genomic representations from each sample were hybridized to microarray slides containing a large collection of DNA probes derived from bacterial clones representing the groundnut gene pool. Each probe was printed in replicate on the array. A reference DNA fragment cloned into a multiple cloning site vector was co-hybridized with each target sample. Following hybridization, slides were washed and scanned using an imaging system capable of detecting fluorescence intensities from the dyes: FAM (reference), and Cy3/Cy5 (target samples).

Image analysis was conducted using DArTsoft, which automatically identifies array features using a reference image and calculates signal intensity ratios between sample and reference channels. Polymorphic clones were identified based on significant variation in hybridization signal intensity among the tested samples. To ensure data integrity and reproducibility, a subset of samples was genotyped in technical replicates. These replicates enabled evaluation of marker quality based on consistency and reproducibility of hybridization signals (Kilian *et al.,* 2012).

Data Analyses

Diversity and cluster analysis

Genotypic data were analyzed using DArTsoft version. The following statistics were determined: polymorphic information content (PIC), Allele count, Call rate, Reproducibility, and minor allele frequency, for each marker. Cluster analysis was carried out on the genotypic data using KDCompute. The unweighted pair-group method was used to cluster the accessions into a dendrogram.

Population structure and linkage disequilibrium analysis:

The genetic structure and number of subgroups of the genotypes were estimated using the model-based Bayesian clustering method implemented in STRUCTURE software version 2.1 (Pritchard *et al.,* 2000). STRUCTURE analysis and sub grouping were decided following Kulwal *et al*., (2012). Estimated likelihood values [LnP(D)], log likelihood of the observed genotype distribution in K clusters obtained from STRUCTURE were used to predict the most probable number of subgroups in the population. The delta-K value which best describes the population structure based on the criteria of maximizing the log probability of data was calculated in order to have appropriate subgroups in the population. The parameter r^2 was used to estimate LD between SNPs on each chromosome via the LD plugin of KDCompute. The LD plugin was also used to visualize the r^2 distribution against the genetic distance and distribution of markers across the genome.

Marker-Trait Association Analysis

Genome-wide association studies (GWAS) were conducted using the GAPIT package implemented through the KDCompute platform (https://kdcompute.igss-africa.org/kdcompute/home). Both SilicoDArT and biallelic SNP markers were analyzed. GAPIT employed a suite of algorithms including EMMA (Efficient Mixed-Model Association), CMLM (Compressed Mixed Linear Model), and P3D (Population Parameters Previously Determined).

Significant marker-trait associations were identified at a threshold of $p < 0.001$. To control for population structure and relatedness, the first three principal components and a kinship matrix were included in the model. SNPs with a minor allele frequency below 5% or with more than 20% missing data were excluded. Missing genotypic data were imputed using the nearest neighbor algorithm in TASSEL version 5.0.

Diversity and Cluster Analyses

Genotypic data were analyzed using DArTsoft to assess key marker statistics including polymorphic information content (PIC), allele count, call rate, reproducibility, and minor allele frequency (MAF). For cluster analysis, the KDCompute platform was employed. Accessions were grouped into clusters using the unweighted pair-group method with arithmetic mean (UPGMA), and a dendrogram was constructed to visualize genetic relationships among the genotypes.

RESULTS AND DISCUSSION

SNP Marker Data and Distribution

Genotyping of groundnut accessions using the DArTSeq platform generated a total of 3,592 biallelic SNP markers. Of

these, 3,396 SNPs had a call rate above 0.70, with 88.1% exceeding a call rate of 0.90, indicating high data quality and reproducibility. However, only 396 SNPs had a minor allele frequency (MAF) greater than 0.05. This low number of informative polymorphic markers reflects the limited genetic diversity in cultivated *Arachis hypogaea*, which is attributed to its narrow domestication bottleneck and polyploid genome origin (Shanthala *et al.,* 2022). Similar patterns were observed in the GINA study, which also reported low diversity across African groundnut breeding programs (Abdela *et al.*, 2020; Ma *et al.,* 2021; Conde *et al.,* 2023).

The polymorphic information content (PIC) values of the 3,396 SNPs ranged from 0.006 to 0.499 (Table I), further confirming the limited allelic diversity. A total of 257 SNPs could not be assigned to any chromosome, while 743 and 642 SNPs remained unanchored to the A and B genomes, respectively. After filtering SNPs with MAF < 0.05 and missing data > 20%, a refined dataset of 964 high-quality SNPs was retained for subsequent analyses.

The chromosomal distribution of SNPs revealed that chromosomes B04 and A04 contained the highest number of markers (116 and 113, respectively), whereas chromosomes B05 and B09 had broader inter-marker distances. This uneven distribution is consistent with prior studies, where chromosomes with higher gene density or recombination activity tend to accumulate more SNPs (Shaibu *et al.,* 2020).

Table 1: Summary of biallelic SNP marker data

	SNP	
	Minimum	Maximum
Allele count A	1	118
E-value A	9.65E-29	2.62E-10
Allele count B	1	100
E-value B	1.18E-28	4.35E-10
Polymorphic information content (PIC)	0.006	0.499
Call rate	0.374	1
One ratio SNP	0.006	1.00
Reproducibility	0.93	1.00
MAF	0.003	0.5

A total of 257 SNPs were not assigned to any chromosome. Additionally, 743 SNPs were unassigned to the A genome, and 642 were unassigned to the B genome. After applying quality control filters to exclude SNPs with MAF < 0.05 and missing data > 20%, a final dataset of 964 high-quality SNPs was retained for downstream analyses. The chromosomal distribution of these SNPs (Figure 1) revealed that chromosomes B04 and A04 contained the highest number of markers (116 and 113, respectively). However, SNPs were more widely spaced on chromosomes B05 and B09, indicating broader genomic coverage in these regions.

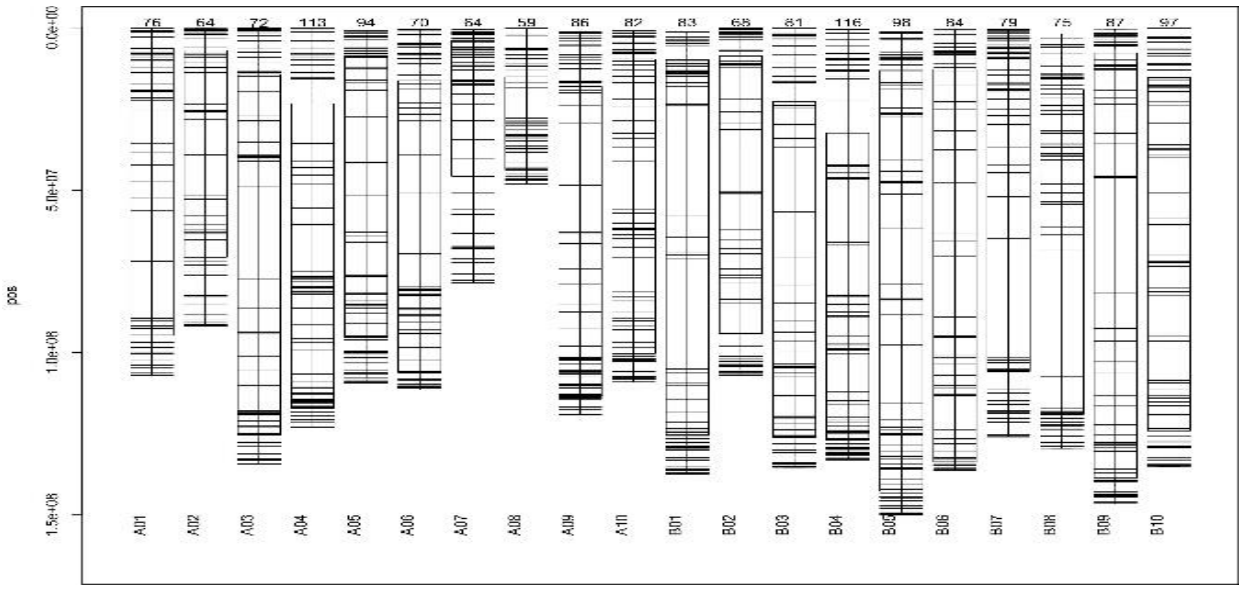

Figure 1: SNP Marker distributions

Linkage Disequilibrium (LD) Patterns

Linkage disequilibrium (LD) was assessed across the genome to understand the recombination landscape and marker informativeness. The decay of LD was not uniform across chromosomes (Figure 2), which indicates variable historical recombination rates in different genomic regions. LD decayed to $r^2 = 0.1$ at a distance of approximately 2 Mb, suggesting moderate LD decay in the studied panel. This finding is in line with the self-pollinating nature of groundnut, which often results in extended LD blocks due to limited recombination events (Daudi *et al.,* 2020; Shaibu *et al.,* 2020). Such patterns allow broader genomic coverage with fewer markers but reduce the resolution of association mapping.

Genome-wide LD estimates also demonstrated that most chromosomes exhibited LD values below $r^2 = 0.14$, highlighting moderate recombination in the population (Figure 3). Importantly, LD decay curves showed considerable fluctuations across different chromosomes, reinforcing the importance of chromosome-specific marker density optimization for GWAS. The analysis also showed that LD estimates were strongly influenced by minor allele frequency, particularly over longer distances. Rare alleles tend to inflate LD estimates, potentially leading to false positives in marker-trait associations. Filtering SNPs by MAF prior to LD estimation is therefore a crucial step in ensuring reliable downstream analysis (Tomar *et al.,* 2022).

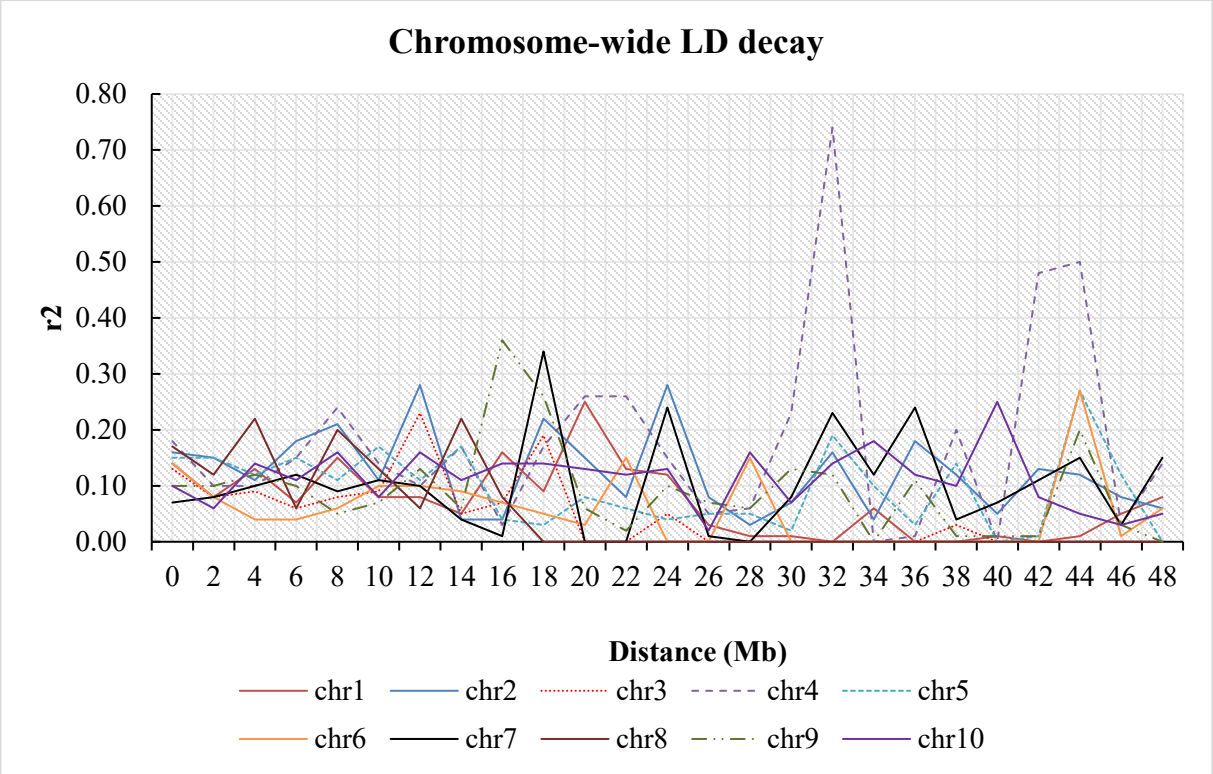

Figure 2: Chromosome-wide Linkage disequilibrium (LD) decayover distance

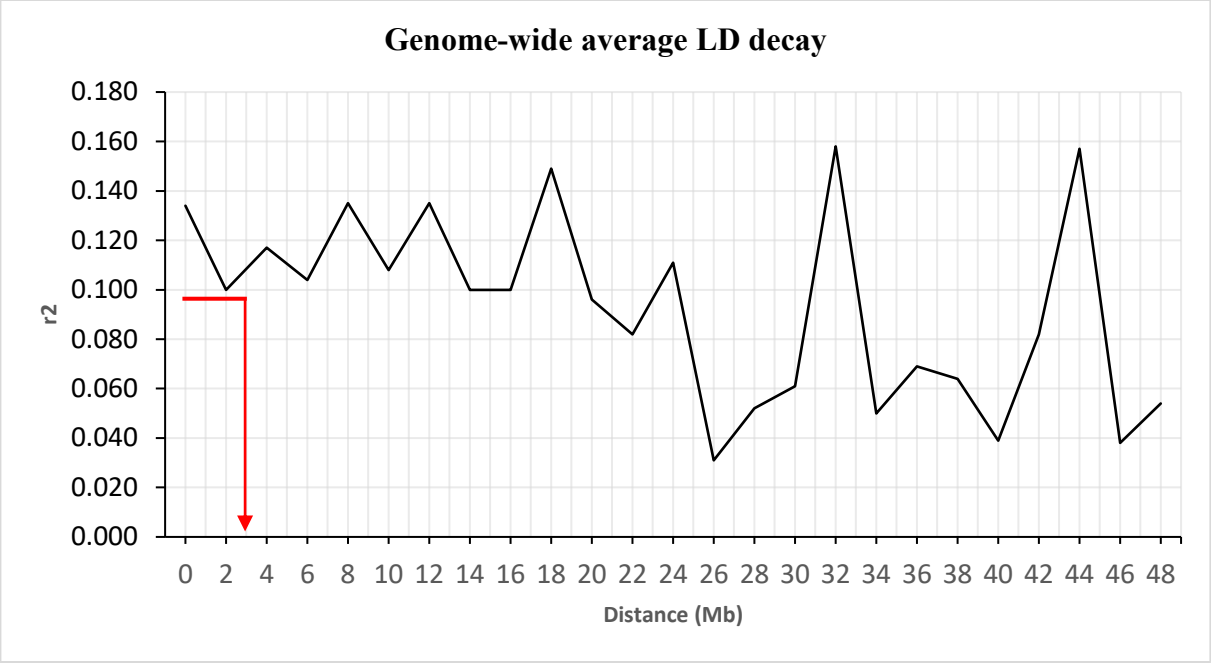

Figure 3: Genome-wide average Linkage disequilibrium (LD) decay. Rate of LD decay it dropped down to r2 = 0.1 at a distance of 2Mb

Population Structure and Association Analysis

The genetic structure of the groundnut mini core collection was analyzed using the model-based Bayesian clustering approach implemented in STRUCTURE software. The optimal number of subpopulations (K) was determined by evaluating the likelihood values and the ΔK method proposed by Evanno *et al.* (2005). The peak ΔK value at K = 2 indicated the presence of two distinct subpopulations within the studied panel (Figure 4). This result suggests a clear genetic subdivision among the accessions, likely shaped by their different geographical origins or breeding histories. STRUCTURE analysis effectively grouped genotypes based on their molecular similarities, demonstrating that SNP markers used in this study possess strong discriminatory power for detecting population stratification. The formation of two subgroups is supported by the accompanying cluster analysis, which also grouped accessions by origin, reinforcing the association between molecular diversity and geographic source.

These findings are consistent with those of Abady *et al.* (2021), who reported two to three subpopulations among improved groundnut lines using over 16,000 SNP markers, highlighting moderate genetic differentiation largely based on botanical types and adaptation zones. Similarly, Tomar *et al.* (2022) found three major subgroups using molecular and biochemical trait analysis, confirming that structure is often governed by both genetics and trait-based divergence. Furthermore, Uba *et al.* (2021) observed that accessions from different African regions grouped into genetically distinct clusters, indicating historical divergence due to regional selection and breeding practices. Although some accessions in the present study showed evidence of admixture, the overall pattern reflects a largely bipartite genetic structure a useful feature for designing association mapping and breeding programs.

These findings underline the importance of accounting for population structure in genome-wide association studies (GWAS) to reduce false positives and improve the accuracy of marker-trait association. Understanding the underlying subpopulations also aids in the effective use of genetic resources and helps guide the selection of parents for crossing to maximize genetic gain and heterosis.

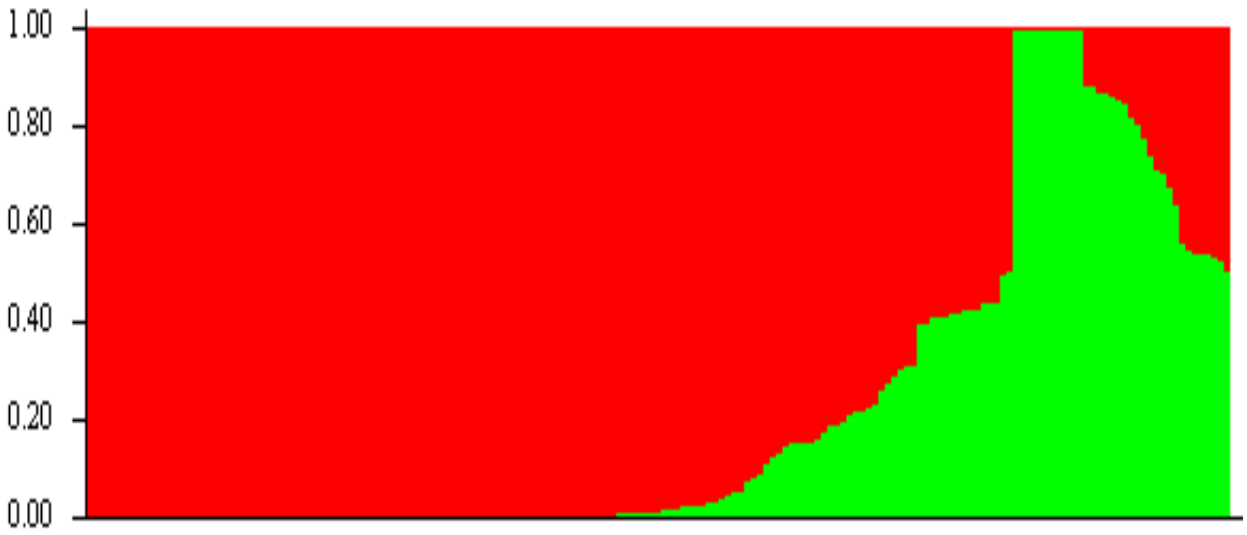

Figure 4: The results of genetic association analysis of groundnut mini core performed by STRUCTURE software version 2.3.4. The membership coefficients of genotypes are given on the y-axis. Each of the two identified subpopulations is shown by a different color

Marker-Trait Association (MTA)

Genome-wide association analysis using biallelic SNP markers identified 19 significant marker-trait associations (MTAs) ($p < 0.001$) across multiple traits and environments (Table 2). These MTAs involved nine distinct SNP markers detected under both inoculated and non-inoculated conditions at BUK and Samaru locations. At BUK under inoculated conditions, two MTAs were detected for early leaf spot (ELS) at 65 days after sowing (DAS), involving a single SNP marker (SM01) located on chromosomes A05 and B05. This marker exhibited a high phenotypic variance explained (PVE) of 63.56% and a marker effect of 0.27, indicating strong genetic control of resistance at this stage. This magnitude of PVE is notably higher than most ELS-associated QTLs reported in previous studies, where values typically range between 10–47% (Pandey *et al.,* 2014; Agarwal *et al.,* 2018).

For ELS at 90 DAS under inoculated conditions, four MTAs involving two SNPs (SM02 and SM03) were identified on chromosomes A05/B05 and A04/B04. These markers had PVEs of 13.36% and 10.65%, respectively, values within the range commonly associated with moderate-effect loci for ELS resistance (Han *et al.,* 2018). Under non-inoculated conditions at BUK, two MTAs were detected for ELS at 65 DAS, linked to SNP marker SM04 on chromosomes A03 and B03. This marker exhibited a lower PVE of 7.55% and a negative allelic effect (−0.38), suggesting its contribution to reduced disease severity. No significant associations were found for ELS at 90 DAS or for pod weight under these conditions.

At Samaru, four MTAs involving SNPs SM05 and SM02 were significantly associated with ELS at 90 DAS under inoculated conditions. These markers showed moderate PVE values (8.32% and 7.71%) and allelic effects of 1.24 and 1.11, respectively. The repeated detection of SM02 at both BUK and Samaru suggests its stability across environments, which is a valuable trait in marker-assisted breeding programs (Shaibu *et al.,* 2020). Under non-inoculated conditions at Samaru, SNP marker SM06 was associated with ELS at 90 DAS on chromosomes A03 and B03, with a PVE of 5.53% and a negative allelic effect of −0.63. These findings align with QTL reports identifying resistance loci on A03 and B03 (Han *et al.,* 2018; Shaibu *et al.,* 2021).

In terms of pod weight, five MTAs involving three SNP markers (SM07, SM08, and SM09) were detected under non-inoculated conditions at Samaru. These markers, mapped to chromosomes A02/B02, A09, and A10/B07, explained 10.39%, 8.09%, and 7.74% of phenotypic variance, respectively. The corresponding allelic effects were large (527.60, 365.13, and 313.76), indicating that these loci may influence yield-determining traits such as seed size or pod filling. These results are in line with recent GWAS studies that have identified significant associations for pod-related traits on similar chromosomes (Oteng-Frimpong *et al.,* 2023), and underscore the polygenic nature of yield in groundnut.

The overall range of PVE observed for ELS in this study (5.53% to 63.56%) mirrors ranges reported in earlier work. For instance, Pandey et al. (2014) identified QTLs with PVE values of 9.18%–10.99%, and Sujay et al. (2012)

reported up to 67.98% PVE for late leaf spot (LLS), but not for ELS. The detection of a high-PVE SNP (SM01) in this study is a noteworthy discovery and may represent a major-effect locus requiring further validation for marker-assisted selection (MAS).

Table 2: Marker-trait associations of SNP markers for ELS and pod weight of groundnut in the groundnut mini core

Trait	Location	SNP	Chromosome	Position	P.value	PVE	Effect
ELS65	BUK_Inoculated	SM01	A05	3564904	0.000948	63.56	0.27
		SM01	B05	3478279	0.000948	63.56	0.27
ELS90		SM02	A05	7919776	0.000039	13.36	1.69
		SM02	B05	8320889	0.000039	13.36	1.69
		SM03	A04	116960088	0.00038	10.65	0.82
		SM03	B04	126825346	0.00038	10.65	0.82
PW		-	-	-	-	-	-
ELS65	BUK_Non inoculated	SM04	A03	13526824	0.000733	7.55	-0.38
		SM04	B03	16442363	0.000733	7.55	-0.38
ELS90		-	-	-	-	-	-
PW		-	-	-	-	-	-
ELS65	IAR_ Inoculated	-	-	-	-	-	-
ELS90		SM05	A08	48135080	0.00052	8.32	1.24
		SM05	B08	128643588	0.00052	8.32	1.24
		SM02	A05	7919776	0.00087	7.71	1.11
		SM02	B05	8320889	0.00087	7.71	1.11
PW							
ELS65	IAR_ Non inoculated						
ELS90		SM06	A03	86470156	0.000764	5.53	-0.63
		SM06	B03	84856104	0.000764	5.53	-0.63
PW		SM07	A02	13672196	0.000088	10.39	527.60
		SM07	B02	1353944	0.000088	10.39	527.60
		SM08	A09	16858584	0.000574	8.09	365.13
		SM09	A10	56041006	0.000763	7.74	313.76
		SM10	B07	27037625	0.000763	7.74	313.76

ELS = early leaf spot; SM = SNP marker; PVE = phenotypic variance explained.

CONCLUSION AND RECOMENDATIONS

This study provided comprehensive insights into the genetic architecture of early leaf spot (ELS) resistance and pod weight in groundnut using high-throughput SNP genotyping and genome-wide association studies (GWAS). Despite the narrow genetic diversity observed, as reflected in the low number of polymorphic SNPs with MAF > 0.05, population structure and cluster analyses effectively delineated two subpopulations, which likely reflect distinct geographic origins and breeding histories. Linkage disequilibrium (LD) decayed to $r^2 = 0.1$ at 2 Mb, indicating moderate recombination rates suitable for GWAS resolution.

A total of 19 significant marker-trait associations were identified across environments and conditions. Notably, SNP marker SM01 on chromosomes A05 and B05 exhibited a high phenotypic variance explained (PVE) of 63.56% for ELS, suggesting its potential as a major-effect QTL for marker-assisted selection. Several moderate-effect markers such as SM02 and SM07 showed stable associations across multiple environments, highlighting their utility for breeding climate-resilient and disease-tolerant cultivars.

Given these findings, we recommend the validation of major SNPs (SM01 and SM02) across broader genetic

backgrounds and multiple environments. Their integration into marker-assisted selection (MAS) pipelines could greatly accelerate breeding for ELS resistance. Furthermore, expanding the genetic base through the inclusion of diverse landraces and wild relatives is crucial for increasing polymorphism and enhancing future mapping precision. The SNPs identified in this study can also contribute to the construction of high-resolution QTL maps and genomic selection models for yield and disease traits.

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