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Article

Genome-Wide Analysis to Identify SNP Markers Associated with Plant Height in *Sorghum bicolor*

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Abstract: Understanding the genetic basis of plant height (PH) in sorghum is essential for improving crop performance and breeding efficiency. This study analyzed 309 sorghum accessions using genome-wide association studies (GWAS) to identify significant single nucleotide polymorphism (SNP) markers associated with PH. Genotyping was conducted using SeqSNP with 5000 markers, of which 3143 high-quality SNPs were selected for analysis. Principal component analysis (PCA) and kinship analysis revealed two distinct genetic clusters. GWAS was performed using seven models: GLM, MLM, MLMM, CMLM, ECMLM, SUPER, FarmCPU, and BLINK. While GLM and SUPER identified a large number of significant SNPs, their Manhattan and QQ plots indicated high false-positive rates. FarmCPU and BLINK proved to be the most reliable models, detecting 10 and 8 significant SNPs, respectively, with four SNPs shared between both models. The most influential SNPs were located on chromosomes 1 and 8, in genes Sobic.001G017500 and Sobic.008G050800, known for their roles in plant growth and development. These findings demonstrate the advantage of multi-locus GWAS models in reducing false positives and enhancing SNP detection accuracy. The identified markers provide valuable insights for sorghum breeding programs, enabling the selection of desirable traits to optimize plant height and improve overall yield potential.

Keywords: BLINK; farmCPU; GWAS; sorghum

Introduction

Approximately 29% of the total population is moderately or severely food insecure (FAO, 2023). Even though there has been some progress towards reducing chronic hunger in the last four years in regions such as Asia and Latin America and the Caribbean, projected numbers of undernourished indicate that the world is far off from achieving zero hunger by 2030 (FAO et al., 2024). In addition, global food supply and demand are expected to notoriously increase, especially in developing countries, because the world population is expected to grow 1.6 billion people by 2050 (FAO, 2023). To meet these challenges, crop yield needs to increase by 70% by 2050 to satisfy the demands of a growing population (Hussain et al., 2021). Efforts to increase crop yield have included agronomical practices such as intercropping, breeding high-yield crops, better fertilizers and pesticides, and the development of stress-tolerant plants (Hussain et al., 2021). However, the implementation of these techniques is not sufficient to satisfy future food demands (Murchie et al., 2009).

While the majority of studies looking at boosting crop production have focused mainly on C3 species, the genetic factors controlling yield in C4 species are not well understood (Sales et al., 2021). C4 species such as maize, sorghum, and sugarcane are among the top ten crops with the highest annual global production, with sorghum being the fifth most important among cereal crops in terms of both annual metric production and yield (FAO, 2023). Sorghum (*Sorghum bicolor* L.) is known for its dual-purpose crop (staple food for humans and feed crop for livestock) and its greatest drought tolerance among C4 plants (Hossain et al., 2022), vital to secure future food security. The small relative genome makes sorghum an ideal model crop for crop genomic studies. Moreover, the availability of the sorghum genome sequences in public databases has made it possible to conduct different

analyses, including genome-wide-association (GWAS) analysis for the identification of molecular markers associated with key physiological traits.

Genome-wide association studies (GWAS) are known for their efficiency in identifying quantitative traits nucleotides (QTNs) associated with genomic regions of interest (CITATION). However, differentiating true from false QTNs, most often caused by population structure issues, has been challenging (CITATION). Given that, more powerful models have been developed in the last 10 years to overcome GWAS limitations. Among those new models, fixed and random model circulating probability unification (farmCPU) (Liu et al., 2016) and bayesian-information and linkage-disequilibrium iteratively nested keyway (BLINK) (Huang et al., 2018) are the most powerful models for GWAS. The farmCPU model is a multi-locus linear mixed model (MLMM) that analyzes multiple markers at the same time as cofactors to partially eliminate the confounding effect of markers and kinship coefficients (Liu et al., 2016). As a result, farmCPU has higher statistical power and better computational power compared to other GWAS models. Although the farmCPU model is good for reducing confounding effects caused by multiple markers, it is still inefficient when a large number of markers and genotypes are involved in the analysis. In contrast, BLINK, which uses Bayesian methods, is more time-efficient due to it replaces random effects with a fixed effects model, and therefore, removes the assumption that causal genes are evenly distributed across the genome.

Although GWAS analysis often reveals novel genomic regions associated with important traits that have a high impact on crop productivity and resilience, the genetic variation within and among different plant accessions along with genotype-by-environment interactions (G x E) limits GWAS results robustness and validation, especially when comparing studies conducted under multi-environment field trials. In addition, the development of newer GWAS models with higher power statistical analysis and computational speed needs to be considered when selecting the right model for a given data set. Therefore, this study aimed to conduct GWAS analysis to identify significant SNP makers associated with plant height of 309 independent sorghum accessions. This study hypothesizes that using newer models with higher statistical power and computational speed will help to identify SNP markers associated with plant height in sorghum accessions.

Material and Methods

Plant Material

The number of sorghum accessions was obtained as outlined by Enyew et al. (2025), with the difference that only 309 accessions were used in this study.

Phenotyping Data

Plant height (cm; PH) was measured from each sorghum accession before the flowering stage.

SNP Selection and Genotyping

The 309 accessions were genotyped using SeqSNP. This genotyping method used 5000 SNP makers that were previously identified in the genetic diversity analysis of sorghum accessions by Enyew et al. (2022). The SNP markers are targeted on chromosome 1 to chromosome 10. The majority of the SNP markers (93.7%) came from the sorghum DNP database SorGSD (<http://sorgsd.big.ac.cn>) and the remaining (6.3%) were identified as outlined by Enyew et al. (2022). Among the 5000 SNP markers, the polymorphic SNP loci and bi-allelic loci were identified as described by Enyew et al. (2025). In addition, from the bi-allelic SNP loci group, further SNP filtering analysis through minimum allele frequency (MAF) was performed to identify high-quality SNP loci (3142 SNP).

Genome-Wide Association (GWAS)

All data were analyzed using R software version 4.2.2. GWAS analysis was performed using the statistical package Genome Association and Prediction Integrated Tool (GAPIT version: 3.0). The GWAS used a total of 3143 SNP markers with phenotype data (plant height, PH) from 309 sorghum accessions. Principal component analysis (PCA) and pairwise genetic association (kinship matrix)

were calculated as outlined by Enyew et al. (2022). Five different GWAS models, GLM (general linear model), MLM (mixed linear model), MLMM (multiple loci mixed linear model), CMLM (compressed MLM), SUPER, ECMLM (enriched CMLM), farmCPU (Fixed and random model circulating probability unification), and BLINK (Bayesian-information and linkage-disequilibrium iteratively nested keyway) were used to determine significant SNPs for PH. Significant associations between PH and SNPs were determined at $P < 0.05$ with Bonferroni correction. Manhattan and QQ plots were generated with GAPIT functions in the R software. To assess the statistical power among the GWAS models used in this experiment. FarmCPU and BLINK along with earlier models GLM, MLM, MLMM, CMLM, ECMLM, and SUPER were compared using the GAPIT.Power.compare test (number of replicates = 10) from the GAPIT function (Wang & Zhang, 2021).

Results and Discussion

Principal Components (PCA)

The principal components analysis (PCA) of the 309 sorghum accessions was determined by the package GAPIT. The number of principal components that better explained the population variability was established by the eigenvalues (Figure 1A). Based on these values, 3 principal components (PC) were used to determine the population stratification of the 309 sorghum accessions (Figure 1B). Because PC3 contributed less than 5% of the population variability, only 2 PCs were selected to depict the clustering pattern of the 309 sorghum accessions (Figure 1C). The kinship analysis also showed that sorghum accessions were clustered into 2 groups (Figure 2).

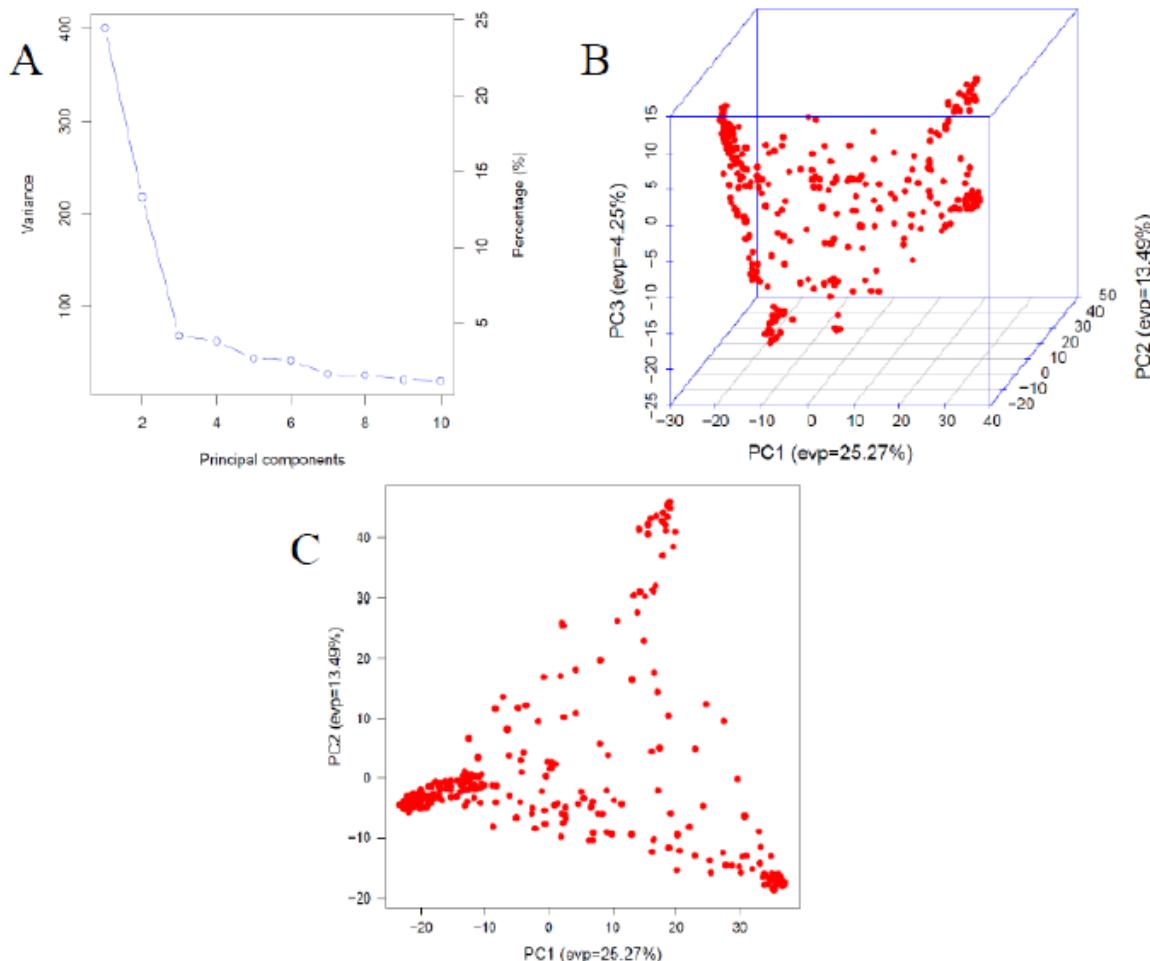


Figure 1. Eigenvalues that show the percentage (%) of variability explained by the most significant components and PCA scatter plots with 3 and 2 components depicting the clustering pattern of the 309 sorghum accessions.

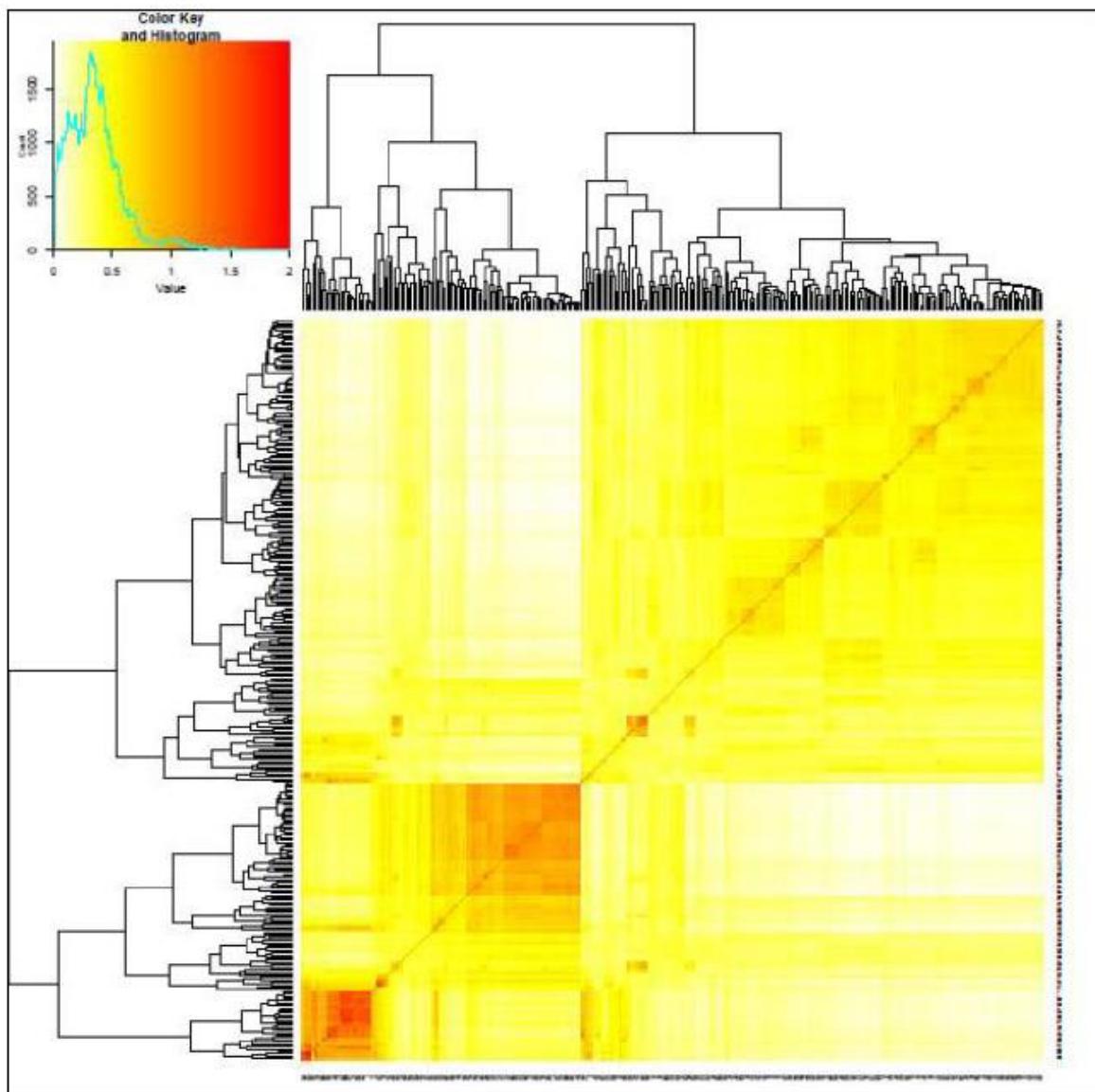


Figure 2. Heat map diagram of kinship matrix depicting that the 309 sorghum accessions are grouped into two clustering groups.

Markers-Trait Associated with Plant Height (PH)

Table 1 shows the significant markers associated with PH. The GLM and SUPER model identified 78 and 124 significant SNP markers, however, based on its QQ plot, the observed vs. predicted values were not correlated, indicating that the majority of significant SNPs identified through GLM were false positives.

FarmCPU and BLINK identified 10 and 8 significant SNP markers, respectively associated with the trait plant height, whereas the other two models MLM and MLMM did not identify any significant SNP markers associated with PH (Figure 3). Among the significant SNP markers for PH, four SNPs were identified by both farmCPU and BLINK. The Manhattan and QQ plots of FarmCPU and BLINK showed that the observed vs. the predicted *P*-values for the 3143 SNPs are matching, therefore, false positive results are less likely (Figure 3). The use of multi-locus GWAS models is better to overcome the limitations associated with single-locus models (Li et al., 2015) because they include kinship values and principal components to avoid confounding effects caused by population structure (Enyew et al., 2022). Moreover, the statistical power analysis showed that only farmCPU and BLINK reduced the likelihood of identifying false positives compared to GLM, MLM, MLMM, CMLM, and SUPER (Figures 4A and 4B). The comparison between multi-locus GWAS models and single-locus models has been also assessed to identify SNP markers associated with plant traits in

the vegetative stage of different sorghum accessions (Zou et al., 2024) suggesting that BLINK and farmCPU are models with improved statistical power. Similarly, a study assessing the disease rating for resistance to grain mold in 635 sorghum accessions found that the use of multiple models including those that avoid overfitting and eliminate confounding effects between kinship and testing markers (Nida et al., 2021). Even though these studies have assessed different GWAS models to identify SNP markers in different maturity stages of sorghum accessions, farmCPU and BLINK were still the most powerful models with less likelihood to identify false positives.

Both farmCPU and BLINK identified four markers in chromosomes 3, 4, 6, and 8 (Figure 5). The phenotypic variation explained by these markers ranged between 0.11 (chromosome 3) to 12.6% (chromosome 8). Additionally, four SNP markers were identified by BLINK on chromosomes 1, 5, and 7 with 2.38, 8.19, and 15.3% of phenotypic variation, respectively. Likewise, farmCPU identified 6 additional SNP markers on chromosomes 1, 3, 6, 9, and 10 with 27.4, 8.23, 0.65, 0, and 0.96% of phenotypic variation, respectively. The SNP markers that had the largest effect on PH, in chromosome 1 (PVE = 27.4%) and 8 (PVE=12.6%), were located in the genes Sobic.001G017500 and Sobic.008G050800, respectively. The former encodes for hydroxysteroid dehydrogenase, oxidoreductase, and short-chain dehydrogenase regions, while the latter plays an important role in protein expression. These genes are known for their importance in plant vegetative and reproductive growth (Enyew et al., 2022).

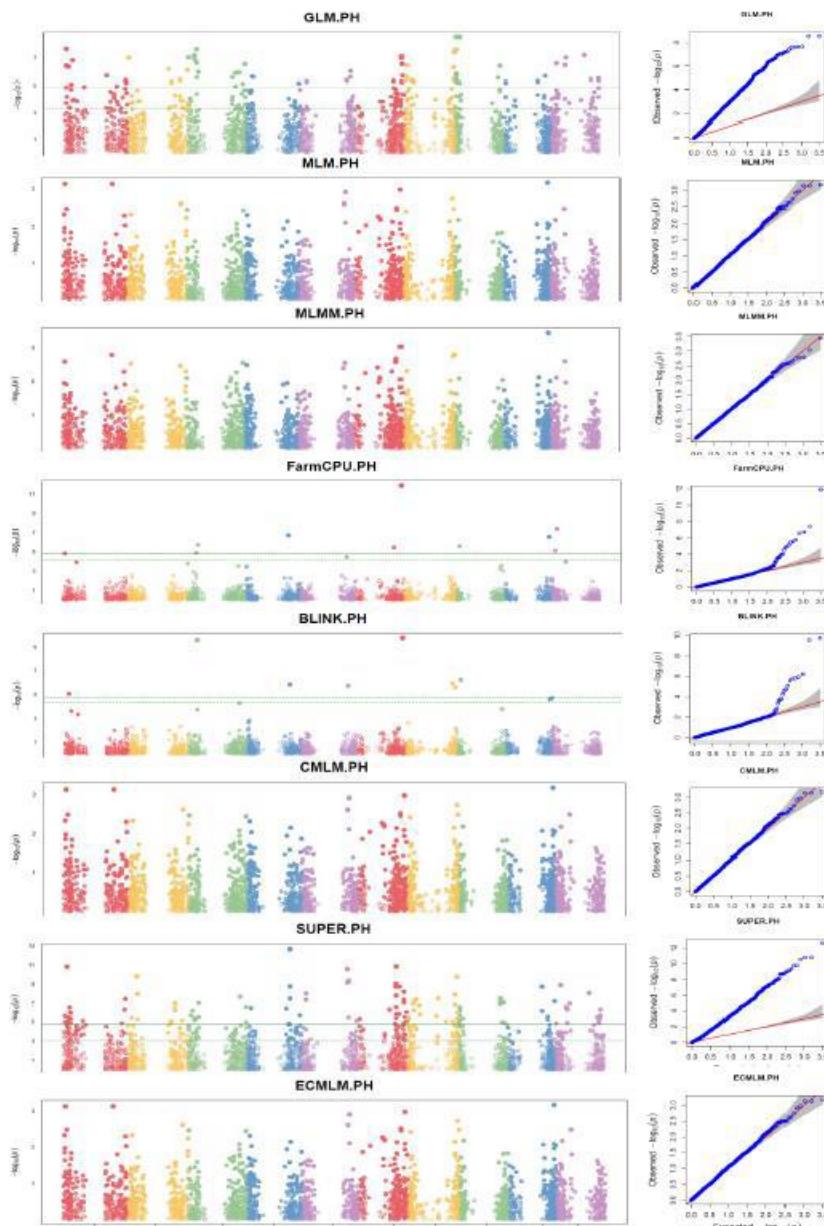


Figure 3. Manhattan and WW plots from GLM (general linear model), MLM (mixed linear model), MLMM (multiple loci mixed linear model), CMLM (compressed MLM), SUPER, ECMLM (enriched CMLM), farmCPU (Fixed and random model circulating probability unification), and BLINK (Bayesian-information and linkage-disequilibrium iteratively nested keyway) GWAS analysis of 309 sorghum accessions using 3143 SNP markers (P values threshold were corrected by Bonferroni correction).

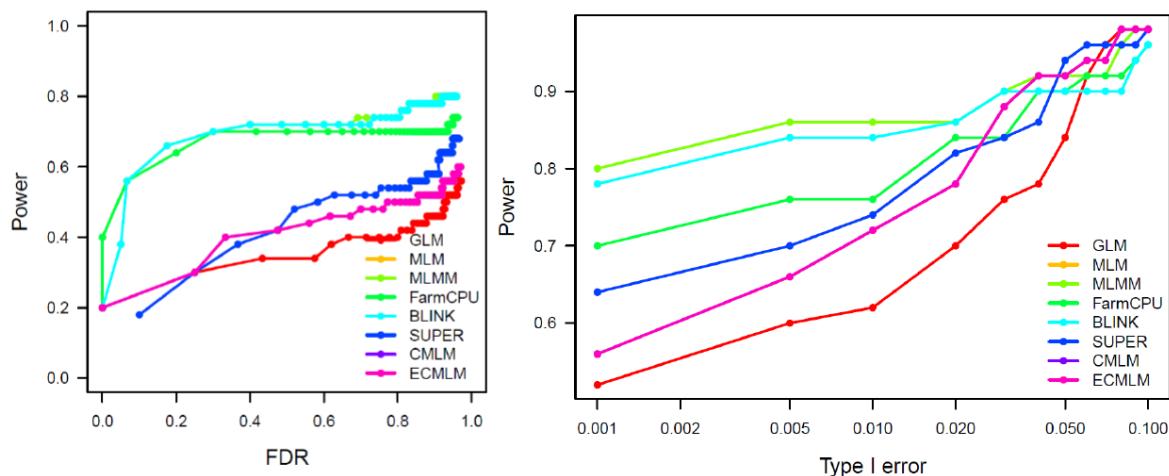


Figure 4. Statistical power comparison between GLM (general linear model), MLM (mixed linear model), MLMM (multiple loci mixed linear model), CMLM (compressed MLM), SUPER, ECMLM (enriched CMLM), farmCPU (Fixed and random model circulating probability unification), and BLINK (Bayesian-information and linkage-disequilibrium iteratively nested keyway) with simulated phenotype data from 309 sorghum accessions.

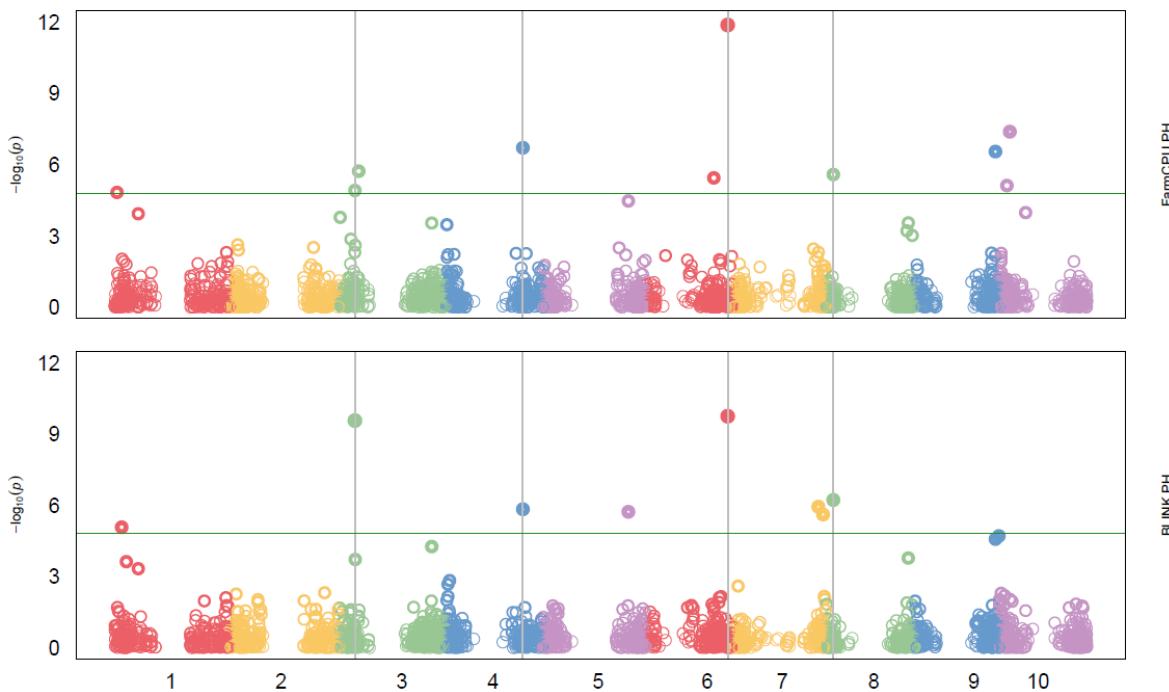


Figure 5. Manhattan plots from farmCPU (Fixed and random model circulating probability unification), and BLINK (Bayesian-information and linkage-disequilibrium iteratively nested keyway) GWAS analysis to identify the number of SNP markers identified by both models..

Table 1. List of significant SNP markers associated with plant height (PH) of 309 sorghum accessions from GWAS analysis.

Trait	GWAS model	SNP ID	Chromosome number	Position	MAF ¹	P-value	PV E (%) ²
-------	------------	--------	-------------------	----------	------------------	---------	-----------------------

PH ³	GLM	snp_sb00100000303 3	1	1803311 5	0.1165048 0	2.10E-08	0
		snp_sb00100000304 3	1	1803552 7	0.0679611 0	3.59E-07	1.17
		snp_sb04206017337 4	1	2053226 4	0.2071197 0	1.30E-05	3.06
		snp_sb04206017649 8	1	4583054 5	0.1229773 0	4.58E-07	3.30
		snp_sb04206017673 3	1	4778713 4	0.4045307 0	4.12E-07	0
		snp_sb04206018318 5	1	8066218 2	0.2621359 0	7.89E-06	4.04
		snp_sb04005763575 0	1	9985873	0.0987055	1.46E-07	7.01
		snp_sb00100004060 2	1	2476916 5	0.3867313 9	1.23E-05	0
		snp_sb04206023382 0	1	5345659 1	0.4401294 5	2.01E-06	0
		snp_sb04206026011 2	1	6625808 9	0.2508090 6	1.09E-05	0.75
		snp_sb04206027365 0	1	7774446 6	0.0614886 7	4.51E-06	0
		snp_sb04206027484 7	1	7846428 8	0.3252427 2	6.09E-06	0
		snp_sb04206027905 4	2	1028568 7	0.1877022 0	9.40E-08	0
		snp_sb04206033432 7	2	5176469 5	0.1504854 4	6.59E-07	3.89
		snp_sb04206033913 5	2	5566536 3	0.3495145 6	5.71E-06	0.51
		snp_sb04206035503 9	2	6660486 5	0.1245954 7	3.85E-06	0
		snp_sb04206036315 7	2	7599475 9	0.1262135 9	7.87E-07	0
		snp_sb04206036519 3	3	542076 2	0.2621359 0	8.95E-08	1.09
		snp_sb04206037544 6	3	8002244	0.1828479	6.13E-08	3.06
		snp_sb04206037549 1	3	8012102 5	0.2216828 0	1.16E-07	0.42
		snp_sb04206037960 4	3	1073411 8	0.0614886 7	2.10E-07	0
		snp_sb04206037994 0	3	1083653 5	0.0776699	2.23E-08	0
		snp_sb04206038015 0	3	1092195 4	0.0809061 5	2.30E-07	0
		snp_sb04206038019 9	3	1093272 0	0.0728155 3	2.71E-06	5.54
		snp_sb04206038404 0	3	1286637 2	0.2443365 7	1.10E-06	0.21
		snp_sb04206042145 5	3	5632224 6	0.2896440 1	2.65E-06	0

snp_sb04206042841	3	6047270	0.0566343	1.07E-05	1.77
8		7			
snp_sb04206042858	3	6050138	0.0533980	1.29E-06	0
5		6	6		
snp_sb04206042923	3	6081199	0.0566343	1.24E-06	0
2		4			
snp_sb04206043428	3	6483000	0.0614886	1.19E-06	0
0		3	7		
snp_sb04206043947	3	6976457	0.2038835	6.96E-06	0
7		6			
snp_sb04206044564	3	7228423	0.0582524	2.79E-07	0
5		7	3		
snp_sb04206046377	4	7424990	0.0614886	2.38E-06	0
7			7		
snp_sb04206052646	4	8890484	0.0825242	2.51E-06	1.30
4			7		
snp_sb04206052323	4	6685887	0.2588996	6.67E-06	0.11
1		7	8		
snp_sb04206054583	5	8563133	0.0517799	5.31E-06	0
0			4		
snp_sb04206058986	5	5984424	0.4158576	4.13E-06	4.45
2		3	1		
snp_sb04206060078	5	6444708	0.2491909	2.52E-06	0
4		5	4		
snp_sb04206060154	5	6466948	0.0663430	9.37E-07	0
4		1	4		
snp_sb00100070214	6	4759975	0.3559870	4.80E-06	0
1		7	6		
snp_sb00100070306	6	4789724	0.4239482	1.42E-05	0.68
8		7	2		
snp_sb00100071912	6	5764704	0.3932038	7.47E-08	0
3		3	8		
snp_sb00100071912	6	5764728	0.3802589	1.01E-07	0.43
7		7			
snp_sb00100071925	6	5770411	0.3106796	5.42E-06	4.23
4		0	1		
snp_sb00100072011	6	5853746	0.2022653	2.75E-07	0
1		5	7		
snp_sb00100072109	6	5927626	0.1407767	2.04E-06	0
7		1			
snp_sb04206076008	7	2622240	0.1003236	2.83E-06	0
1			2		
snp_sb04206076009	7	2623348	0.1035598	2.29E-06	0
8			7		
snp_sb04206076009	7	2623635	0.0987055	3.48E-06	0
9					
snp_sb04206076149	7	3776173	0.0711974	3.33E-07	7.40
0			1		
snp_sb04206076635	7	6455441	0.2944983	1.57E-05	0
8			8		
snp_sb04206077202	7	9428572	0.1650485	4.27E-06	0
6			4		

snp_sb04206077498	7	1201877	0.4304207	5.26E-06	0
5		2	1	06	
snp_sb04206085037	7	6322742	0.4563106	3.42E-06	0.50
3		5	8	06	
snp_sb04206085045	7	6330034	0.1278317	4.78E-07	5.09
8		6	2	07	
snp_sb04206085272	7	6431859	0.2233009	3.69E-08	0
7		3	7	08	
snp_sb04206085273	7	6431920	0.2249190	2.58E-08	0
5		5	9	08	
snp_sb04206085643	8	606304	0.197411	2.44E-08	0.13
6					
snp_sb04206085705	8	1016470	0.2734627	2.70E-09	0.27
0					
snp_sb04206085764	8	1241472	0.0922330	3.50E-06	0
9					
snp_sb04206085770	8	1243863	0.0809061	1.82E-06	3.31
1					
snp_sb04206085824	8	1459101	0.3689320	1.40E-06	0.16
4					
snp_sb04206085824	8	1462792	0.3673139	5.57E-06	0
6					
snp_sb04206086716	8	5053406	0.0857605	6.16E-06	1.54
2					
snp_sb04206086773	8	5247147	0.2330097	2.68E-09	0
1					
snp_sb04206093982	8	5461543	0.1941747	2.82E-06	2.26
0		7	6	06	
snp_sb04206094514	8	5684774	0.0938511	3.71E-07	0
9		5	3	07	
snp_sb04206095854	9	2005306	0.1537216	5.86E-06	0
8					
snp_sb04206100513	9	4284923	0.0825242	5.11E-06	0
4		8	7	06	
snp_sb04206102114	9	5237344	0.2605178	2.16E-06	0
8		7			
snp_sb00100104969	10	7303004	0.0598705	2.49E-07	8.78
6					
snp_sb00100107548	10	1838816	0.2330097	3.25E-07	0
7		0	1	07	
snp_sb04206106203	10	1945131	0.1941747	9.11E-08	3.57
6		5	6	08	
snp_sb00100112574	10	4287279	0.4029126	5.98E-08	0
1		1	2	08	
snp_sb00100114349	10	5145504	0.2394822	3.66E-06	1.23
0		8			
snp_sb00100115981	10	6097725	0.4012945	1.39E-05	0.12
3		0			
snp_sb00100115993	10	6106950	0.1391585	2.99E-06	0
4		0			
snp_sb00100116006	10	6114425	0.2006472	3.98E-06	0
2		0	5	06	

SUPER	snp_sb04206017335				1.10E-	-
	0	1	2036942	0.15534	05	
	snp_sb04206017337				2.30E-	-
	4	1	2053226	0.20712	06	
	snp_sb04206017673				1.60E-	-
	3	1	4778713	0.404531	11	
	snp_sb04206017723				1.14E-	-
	8	1	5073279	0.493528	05	
	snp_sb04206017774				9.13E-	-
	7	1	5705669	0.461165	06	
	snp_sb04206017783				3.18E-	-
	3	1	5736900	0.307443	06	
	snp_sb04206018303				3.49E-	-
	3	1	8034619	0.210356	06	
	snp_sb04206018318				2.99E-	-
	5	1	8066218	0.262136	07	
	snp_sb00100001453				9.51E-	-
	3	1	8870319	0.423948	07	
	snp_sb04206018410				5.03E-	-
	3	1	9022825	0.315534	06	
	snp_sb04206018457				1.08E-	-
	1	1	9291528	0.457929	06	
	snp_sb00100001531				1.40E-	-
	4	1	9412963	0.449838	05	
	snp_sb00100004060				7.69E-	-
	2	1	2476916			
	5		0.386731	06		
	snp_sb04206026716				1.36E-	-
	4	1	7373725			
	3		0.349515	05		
	snp_sb04206027326				4.72E-	-
	9	1	7743201			
	9		0.199029	07		
	snp_sb04206027484				3.62E-	-
	7	1	7846428			
	8		0.325243	08		
	snp_sb04206028788				3.69E-	-
	4	2	5838445	0.459547	06	
	snp_sb04206030200				1.62E-	-
	8	2	1224357			
	2		0.331715	10		
	snp_sb04206030443				5.33E-	-
	4	2	1317757			
	4		0.18123	06		
	snp_sb04206030463				1.07E-	-
	8	2	1329372			
	3		0.427184	08		
	snp_sb04206033847				1.32E-	-
	6	2	5529238			
	2		0.31877	05		
	snp_sb04206033913				8.25E-	-
	5	2	5566536			
	3		0.349515	06		
	snp_sb04206034798				3.55E-	-
	1	2	5981010			
	6		0.480583	07		
	snp_sb04206034886				6.24E-	-
	2	2	6037473			
	8		0.451456	07		
	snp_sb04206034920				9.69E-	-
	2	2	6041554			
	6		0.470874	08		
	snp_sb04206034921				1.16E-	-
	6	2	6041663			
	8		0.438511	07		

snp_sb04206035899		6958631	6.97E-	-
0	2	9	0.072816	06
snp_sb04206036869			2.09E-	-
1	3	3720735	0.364078	06
snp_sb04206037096			6.31E-	-
8	3	5535752	0.375405	07
snp_sb04206037544			3.91E-	-
6	3	8002244	0.182848	06
snp_sb04206037549			6.55E-	-
1	3	8012102	0.221683	06
snp_sb04206037885		1037019		3.87E-
2	3	3	0.122977	06
snp_sb04206038404		1286637		3.43E-
0	3	2	0.244337	06
snp_sb04206038520		1349421		2.88E-
9	3	3	0.380259	06
snp_sb04206038521		1349436		9.35E-
1	3	1	0.496764	08
snp_sb04206043476		6570654		2.15E-
9	3	5	0.472492	08
snp_sb04206044648		7274264		2.67E-
6	3	4	0.343042	07
snp_sb04206044701		7301048		1.08E-
9	3	4	0.187702	05
snp_sb04206052317			3.40E-	-
9	4	4755657	0.158576	07
snp_sb04206052700		4933501		3.70E-
1	4	4	0.302589	07
snp_sb04206052559		5245990		1.44E-
1	4	1	0.478964	05
snp_sb04206052452		5404442		2.22E-
3	4	1	0.446602	13
snp_sb00100046972		5410880		3.37E-
2	4	6	0.18932	08
snp_sb04206052464		5416506		1.76E-
3	4	8	0.383495	09
snp_sb04206052682		6634300		2.07E-
5	4	2	0.496764	06
snp_sb04206053999			4.32E-	-
1	5	5752947	0.453074	08
snp_sb04206054108			9.84E-	-
2	5	6039745	0.346278	09
snp_sb04206058734		5799594		2.81E-
8	5	9	0.443366	11
snp_sb04206058747		5807849		6.82E-
8	5	9	0.365696	10
snp_sb04206058967		5977647		3.34E-
7	5	6	0.482201	06
snp_sb04206058986		5984424		4.54E-
2	5	3	0.415858	10
snp_sb04206061379		6976681		7.77E-
3	5	9	0.299353	06

snp_sb00100059184				4.97E-	-
1	6	1893544	0.067961	06	
snp_sb00100068530		3965053		4.84E-	-
8	6	7	0.433657	07	
snp_sb00100069964		4659326		1.52E-	-
2	6	1	0.067961	05	
snp_sb00100070214		4759975		9.67E-	-
1	6	7	0.355987	10	
snp_sb00100070220		4761431		1.83E-	-
4	6	2	0.415858	09	
snp_sb00100070265		4774713		2.63E-	-
5	6	4	0.389968	07	
snp_sb00100070306		4789724		1.61E-	-
8	6	7	0.423948	08	
snp_sb00100070337		4800750		3.89E-	-
3	6	8	0.126214	06	
snp_sb00100070339		4801901		1.50E-	-
7	6	5	0.386731	11	
snp_sb00100070343		4802233		1.39E-	-
5	6	7	0.326861	06	
snp_sb00100071003		5160405		1.49E-	-
6	6	8	0.391586	06	
snp_sb00100071078		5187793		1.99E-	-
5	6	3	0.404531	09	
snp_sb00100071912		5764704		4.25E-	-
3	6	3	0.393204	08	
snp_sb00100071912		5764728		8.49E-	-
7	6	7	0.380259	08	
snp_sb00100071925		5770411		6.61E-	-
4	6	0	0.31068	09	
snp_sb00100071960		5794769		1.40E-	-
6	6	0	0.393204	05	
snp_sb00100072011		5853746		2.82E-	-
1	6	5	0.202265	06	
snp_sb00100072275		6036907		9.03E-	-
7	6	8	0.050162	06	
snp_sb00100072373		6090884		8.88E-	-
9	6	2	0.300971	07	
snp_sb04206076008				3.49E-	-
1	7	2622240	0.100324	06	
snp_sb04206076009				5.02E-	-
8	7	2623348	0.10356	06	
snp_sb04206076009				4.78E-	-
9	7	2623635	0.098706	06	
snp_sb04206077074				8.44E-	-
2	7	8646573	0.360841	08	
snp_sb04206077074				1.17E-	-
8	7	8647644	0.415858	07	
snp_sb04206077125				5.59E-	-
7	7	8852228	0.346278	07	
snp_sb04206077498				3.83E-	-
5	7	1201877	0.430421	08	
		2			

snp_sb04206077729		1592654	1.70E-	-
7	7	3	0.456311	07
snp_sb04206077845		1713958	1.57E-	-
1	7	6	0.381877	06
snp_sb04206081074		3758784	2.36E-	-
9	7	8	0.286408	06
snp_sb04206081427		3976275	3.17E-	-
1	7	1	0.441748	08
snp_sb04206082908		4951314	9.34E-	-
3	7	8	0.300971	06
snp_sb04206084000		5777890	9.31E-	-
8	7	8	0.425566	06
snp_sb04206084497		6073737	1.46E-	-
8	7	9	0.331715	07
snp_sb04206084498		6073749	1.26E-	-
0	7	0	0.33657	08
snp_sb04206085037		6322742	1.77E-	-
3	7	5	0.456311	10
snp_sb04206085088		6338751	4.16E-	-
8	7	0	0.482201	06
snp_sb04206085155		6368759	9.21E-	-
9	7	9	0.242718	07
snp_sb04206085273		6431920	1.08E-	-
5	7	5	0.224919	05
snp_sb04206085643			1.09E-	-
6	8	606304	0.197411	05
snp_sb04206085770			6.59E-	-
1	8	1243863	0.080906	06
snp_sb04206085798			2.77E-	-
5	8	1398622	0.228155	07
snp_sb04206085806			6.98E-	-
4	8	1417507	0.436893	07
snp_sb04206085824			3.51E-	-
4	8	1459101	0.368932	07
snp_sb04206085824			2.15E-	-
6	8	1462792	0.367314	06
snp_sb04206086773			4.64E-	-
1	8	5247147	0.23301	06
snp_sb04206093554		5266927	1.27E-	-
6	8	2	0.377023	07
snp_sb04206093554		5266933	6.20E-	-
8	8	8	0.36246	08
snp_sb04206093570		5270838	3.18E-	-
0	8	9	0.349515	08
snp_sb04206093982		5461543	1.13E-	-
0	8	7	0.194175	05
snp_sb04206094458		5661725	8.10E-	-
4	8	6	0.440129	08
snp_sb04206094514		5684774	1.14E-	-
9	8	5	0.093851	05
snp_sb04206100517		4288932	1.89E-	-
7	9	4	0.360841	09

	snp_sb04206100532		4294117		6.97E-	-
	5	9	2	0.430421	07	
	snp_sb04206101655		5010124		2.71E-	-
	6	9	7	0.378641	06	
	snp_sb04206101655		5010137		5.49E-	-
	7	9	6	0.372168	06	
	snp_sb04206103270		5888081		6.21E-	-
	8	9	1	0.428803	08	
	snp_sb00100103994				1.38E-	-
	0	10	1485692	0.320388	05	
	snp_sb00100103997				1.46E-	-
	1	10	1488770	0.338188	05	
	snp_sb00100104916				1.23E-	-
	2	10	7201807	0.359223	09	
	snp_sb00100106618		1413776		2.53E-	-
	9	10	2	0.44822	07	
	snp_sb00100106771		1518366		4.61E-	-
	0	10	1	0.47411	07	
	snp_sb00100106802		1530589		1.23E-	-
	2	10	1	0.378641	05	
	snp_sb00100107548		1838816		1.03E-	-
	7	10	0	0.23301	07	
	snp_sb00100112574		4287279		8.92E-	-
	1	10	1	0.402913	09	
	snp_sb04206109207		5310811		3.14E-	-
	0	10	2	0.050162	06	
	snp_sb00100115014		5462960		1.02E-	-
	6	10	3	0.401295	05	
	snp_sb04206109532		5547785		2.49E-	-
	3	10	2	0.338188	06	
	snp_sb00100115140		5547874		1.33E-	-
	1	10	1	0.305825	05	
	snp_sb00100115140		5547922		5.54E-	-
	3	10	6	0.309061	06	
	snp_sb00100115320		5633953		4.37E-	-
	8	10	4	0.092233	06	
	snp_sb00100115437		5695377		4.74E-	-
	5	10	9	0.490291	07	
MLM	- ⁴	-	-	-	-	-
MLMM	- ⁵	-	-	-	-	-
CMLM	- ⁶	-	-	-	-	-
ECMLM	- ⁷	-	-	-	-	-
farmCP	snp_sb0010000253				1.45E-	
U	2	1	1495213	0.113269	05	27.4
	snp_sb04206037994		1083653		1.20E-	
	0	3	5	0.07767	05	0.11
	snp_sb04206038520		1349421		1.85E-	
	9	3	3	0.380259	06	8.23
	snp_sb00100046972		5410880		1.91E-	
	2	4	6	0.18932	07	0
	snp_sb00100070337		4800750		3.56E-	
	3	6	8	0.126214	06	0.65

BLINK	snp_sb00100071925		5770411		1.29E-12	5.50
	4	6	0	0.31068		
	snp_sb04206086716				2.56E-06	0
	2	8	5053406	0.085761		
	snp_sb04206102871		5660135		2.76E-07	0
	4	9	3	0.192557		
	snp_sb00100104590				7.46E-06	0
	3	10	5270775	0.11165		
	snp_sb00100104969				4.02E-08	0.96
	6	10	7303004	0.059871		
	snp_sb04206017673		4778713	0.404531	8.40E-06	2.38
	3	1				
	snp_sb04206037994		1083653		2.70E-10	10.4
	0	3	5	0.07767		
	snp_sb00100046972			5410880		
	2	4	6	0.18932	1.47E-06	7.34
	snp_sb04206058986		5984424		1.89E-06	8.19
	2	5	3	0.415858		
	snp_sb00100071925		5770411		1.77E-10	5.38
	4	6	0	0.31068		
	snp_sb04206084352		5999793		1.15E-06	15.3
	2	7	7	0.119741		
	snp_sb04206085045		6330034		2.46E-06	
	8	7	6	0.127832		5.29
	snp_sb04206086716				5.97E-07	
	2	8	5053406	0.085761		12.6

¹ MAF, minor allele frequency (>0.05).

² PVE, phenotypic variation (%).

³ PH, plant height (cm).

^{4,5,6,7} Non-significant SNP markers were identified by MLM, MLMM, CMLM, and ECMLM.

^a SNPs in bold were identified by two GWAS models (farmCPU and BLINK).

Conclusions

This study highlights the effectiveness of BLINK and farmCPU to identify significant SNP markers associated with plant height in 309 sorghum accessions, indicating that these models can be implemented for further GWAS analysis with other phenotypic traits. Both FarmCPU and BLINK identified four common SNP markers on chromosomes 3, 4, 6, and 8, with additional unique markers detected by each model. Notably, the SNPs with the largest effects on plant height were located in genes Sobic.001G017500 and Sobic.008G050800, which are involved in key metabolic and growth-related processes. Overall, these findings reinforce the importance of selecting robust GWAS models for trait association studies and provide valuable genetic insights that can aid in sorghum breeding programs aimed at improving plant height and overall crop performance.

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