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Genetic dissection of early flowering in cowpea (*vigna unguiculata* l.) Using genome -wide association studies

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Abstract

Cowpea is fascinating for its diverse flowering times, which can range from 30 to over 90 days after planting, depending on genotype, photoperiod, and environmental conditions. The primary objective of this study was to conduct genome-wide association studies (GWAS) to identify genomic regions associated with earliness in flowering in cowpea (*Vigna unguiculata* L. Walp.). The cowpea genotypes, DArT Panel Population, were made up of four distinct groups with different genetic backgrounds. These groups included elite breeding lines, germplasm accessions from the IITA Genetic Resources Centre, and multi- and bi-parental recombinant inbred, totalling 300 genotypes. Our research involved a genome-wide scan of these 300 cowpea genotypes to identify markers linked to early flowering. We phenotypically screened the population across two locations: Wudil and Minjibir in Kano state. Notably, we observed significant differences in the days to first flowering among the various populations. We conducted the GWAS using TASSEL v.5.2.79, applying a mixed linear model (MLM) with (Q + K) models, incorporating principal components and kinship matrices to correct for population structure. The statistical models from TASSEL generated Manhattan and quantile-quantile (QQ) plots. Results from genome-wide scan revealed three major regions on chromosomes Vu09, Vu03, and Vu011, along with three minor regions on chromosomes Vu07, Vu06, and Vu05, all significantly associated with early flowering. Among these regions, the gene Vigun09g063800 was found to be closest to the peak SNP positions and plays a crucial role in regulating flowering time, which is vital for transition of the plant from vegetative to reproductive phase. It is recommended that future studies focus on establishing a marker-assisted breeding platform and developing extra-early cowpea cultivars. In addition, the SNP markers associated with early flowering should be tested for consistent associations across different genetic backgrounds.

Key words: Cowpea, DArTag, Early Flowering, Markers, mid-density panel, SNP

INTRODUCTION

Cowpea (*Vigna unguiculata* (L.) Walp) is a vital grain legume widely cultivated in sub-Saharan Africa, Asia, and parts of Latin America. It plays a key role in food security, soil fertility improvement through nitrogen fixation, and serves as a source of income for millions of smallholder farmers. As a crop adapted to hot and drought-prone environments, cowpea is particularly important for low-input farming systems in regions with erratic rainfall and short growing seasons (Singh, *et al*., 1997). Cowpea is known for its wide variation in flowering time, ranging from 30 to over 90 days after planting, depending on genotype, photoperiod, and environmental conditions (Muchero *et al*., 2009). Understanding the genetic basis of flowering time is essential for developing improved varieties that are better suited to diverse agro-ecological zones. Among the critical traits influencing cowpea productivity and adaptability, early flowering has received considerable attention. Early flowering enables the crop to escape terminal drought, heat stress, and pest infestations that often intensify later in the growing season (Muchero et al., 2009). This trait is particularly beneficial in semi-arid and arid regions where the growing season is short and climatic variability is high.

Flowering time in cowpea is a complex quantitative trait controlled by multiple genes and influenced by environmental conditions such as photoperiod, temperature, and water availability(Ishiyaku et al., 2005). Most traditional cowpea varieties are photoperiod-sensitive and flower under short-day conditions, which limits their adaptability across diverse agro-ecological zones. However, breeding efforts have led to the development of photoperiod-insensitive and early-flowering genotypes, making it possible to grow cowpea in regions with longer or variable day lengths (Singh et al., 2003). With the advent of molecular tools and genomic resources, significant progress has been made in understanding the genetic control of flowering in cowpea. Quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have identified specific genomic regions associated with early flowering (Lo et al., 2019). These advances are enabling more precise and efficient selection of early-flowering lines through marker-assisted selection (MAS). The identification of such molecular markers offers great promise for marker-assisted selection (MAS) in breeding for early maturing varieties.

Early flowering not only helps in stress avoidance but also enables multiple cropping cycles within a year, contributing to increased productivity and food availability. Thus, improving our understanding of the genetics and physiology of flowering time in cowpea is a key priority for breeding programs targeting climate-resilient

agriculture. Early flowering in cowpea is advantageous in drought-prone or short-season environments, where terminal droughts or extreme heat can significantly reduce yields. Genotypes that flower early often escape late-season abiotic stresses, enabling them to complete their life cycles before the onset of unfavorable conditions (Fatokun et al., 2012). Consequently, early flowering is an important selection trait in breeding programs targeting climate resilience.

Furthermore, photoperiod sensitivity plays a significant role in determining flowering behavior in cowpea. Many landraces are photoperiod-sensitive and flower only under short-day conditions. However, the development of photoperiod-insensitive early-flowering lines allows for broader adaptability and double-cropping systems (Singh et al., 2003).

Traditional breeding approaches for improving flowering time are often slow and limited due to the polygenic nature of the trait and strong genotype × environment interactions. Genome-Wide Association Studies (GWAS) offer a powerful tool to dissect the genetic architecture of early flowering by identifying significant loci and allelic variants associated with the trait across diverse germplasm. The knowledge generated will accelerate marker-assisted selection and facilitate the development of climate-resilient, early-maturing cowpea varieties suitable for smallholder farmers**. The major objective was to identify genomic regions (loci) and single nucleotide polymorphisms (SNPs) significantly associated with early flowering in cowpea using GWAS and also to characterize the genetic architecture of flowering time, including major and minor effect genes, and their interaction with environmental factors.**

Materials and Methods

Plant genetic materials

The cowpea genotypes used in this study were constituted from groups of cowpea genotypes with different genetic backgrounds. The genetic groups included elite breeding lines, germplasm accessions from the IITA Genetic Resources Centre, multi- and bi-parental recombinant inbreeds, making a total of 376 genotypes.

The first group of cowpea genotypes used consisted of 123 elite breeding lines from IITA that are generally used as parents in several cowpea breeding programs. These lines are high yielding, drought tolerant, heat tolerant, striga resistant and have several seed quality traits demanded by farmers in SSA. The second category included 22 accessions which have been selected from the IITA cowpea mini-core population. The cowpea mini-core is a sub-set of a world cowpea germplasm collection maintained at IITA crop genetic resource gene bank and they are good sources for traits of economic importance in cowpea (Lonardi *et al*.,2019). The third group consisted of 100 cowpea multi-parent advanced generation inter-cross (MAGIC) inbred lines, here on referred to as multi-parental RILs. These recombinant inbred lines derived from eight diverse parents combine many abiotic and biotic stress resistances, seed quality and agronomic traits relevant to cowpea in sub-Saharan Africa. A fourth group was a random sample of 101 bi-parental RILs derived from a cross between aphid resistant wild relative TVNu1158 and elite IITA line IT99K-573-1-1.

Table 1: Cowpea genotype used in the Minjibir Experiment

Type of material	Size	Description
Breeding lines	116	Favourite breeding materials including released varieties and land races often used
Accessions	20	Favourite materials selected from the IITA mini-core which are part of a world Collection.
Multi-parental lines	98	Randomly sampled from the UCR cowpea MAGIC recombinant inbred lines.
Bi-parental lines	66	Randomly sampled from IITA recombinant inbred lines segregation for aphid resistance
Total	300	

Table 2: Cowpea genotype used in the Wudil Experiment

Type of material	Size	Description
Breeding lines	106	Favourite breeding materials including released varieties and land races often used
Accessions	12	Favourite materials selected from the IITA mini-core which are part of a world Collection.
Multi-parental lines	72	Randomly sampled from the UCR cowpea MAGIC recombinant inbred lines.
Bi-parental lines	48	Randomly sampled from IITA recombinant inbred lines segregation for aphid resistance
Total	238	

SNP Genotyping

Total genomic DNA of 300 genotypes was sampled at the Intertek Laboratory Australia and the samples were forwarded to Diversity Arrays Technology (DArT) facility for genotyping. Genotyping was done by employing DArTag technology, one of the targeted genotyping approaches which offer the capacity to genotype materials using specific or selected sets of SNP markers (https://www.diversityarrays.com/technology-and-resources/targeted-genotyping/). For the 300 leaf samples, a panel of 2,442 SNP markers regarded as the cowpea mid-density genotyping panel V1.0. was used. This marker platform has an average density of about 3 SNPs per cM (or 4 per Mbp) throughout the 11 cowpea chromosomes (Patrick Ongom. 2022)

Genome-wide association analysis

Genome-wide association analysis (GWAS) was conducted using pod sucking bug phenotypes. GWAS was conducted in Trait Analysis by association, Evolution and Linkage (TASSEL) v.5.2.79 by mixed linear model (MLM) with (Q + K) models PCs and Kinship (K) – matrix as correction for population structure. Model statistic from TASSEL v.5.2.79 was used to generate Manhattan and quantile-quantile (QQ) plots.

The GWAS significance threshold used in this study was determined by correcting for multiple testing through control of false discovery rate (FDR) (Verhoeven *et al*., 2005). The FDR approach aims at controlling the proportion of significant results that are in fact type I errors, and it has been praised to be more powerful in controlling the proportion of falsely rejected hypothesis than the conservative Bonferroni procedure (Verhoeven *et al*., 2005). We implemented FDR in R environment using the p.adjust function, with the method set to "FDR", which adjusts the GWAS p-values based on Benjamini and Hochberg ("BH") procedure (Verhoeven *et al*., 2005). An average FDR threshold was then computed from the adjusted p-values at 5% probability level as follows:

FDR = (α × 100)/ (p.adjust)

where FDR is the false discovery rate threshold, α is the acceptable level of type I error which was set at 0.05 in the present study, p.adjust is the sum of adjusted p-values for each SNP extracted from the R output; that is, p.adjust = 2,442 in our case. The −log10 (FDR) was then taken to establish the significant threshold for the GWAS results. Consequently, the FDR threshold in the present study was computed as:

FDR = [(0.05 × 100/2,442) = 5/2,442 = 0.00205; hence, −log10 (FDR) = 2.68

CANDIDATE GENE PREDICTION

To explore the likely genes responsible for the detected association signals, the positions of peak SNPs were searched along the annotated genome (v1.1) of elite IITA cowpea 218 variety IT97K499-35 (Lonardi *et al*.,2019). Using the genome browser (Browse) in Phytozome 13 (https://phytozome-next.jgi.doe.gov/info/Vunguiculata_v1_1). Predicted genes within the peak SNP regions were further explored for their annotated biological functions in relation to homologs in other crops, especially common bean (Phaseolus vulgaris), Soybean (Glycine max), Barrelclover (Medicago truncatula) and Arabidopsis thaliana, via both Phytozome and the Vigna unguiculata Gene expression atlas webserver (http://.noble.org) developed by (Yao *et al.* 2019,)

RESULTS

Histogram Distribution of phenotypic traits in location Wudil, Minjibir and Combined Location

The histograms and boxplot provide a clear picture of how days to first flowering (DFF) in cowpea varies across two locations—Wudil and Minjibir—as well as when you look at the combined data. The Wudil histogram (top left) reveals a fairly symmetrical distribution, with most genotypes blooming between 40 and 50 days. On the other hand, the Minjibir histogram (top right) shows a slight right skew, suggesting that there are more genotypes that flower earlier, around 40 to 45 days, with fewer that take longer. The combined histogram (bottom left) merges data from both sites, creating a nearly normal distribution that highlights the genetic and environmental factors at play in flowering time across these areas. The boxplot (bottom right) compares DFF between Minjibir and Wudil, showing that while the medians and interquartile ranges are quite similar, there are a few outliers in both locations. This visual summary indicates that although environmental influences are present, the flowering time tends to be fairly consistent across different sites, which supports the idea that this trait is stable and could be a good target for selection in cowpea breeding programs.

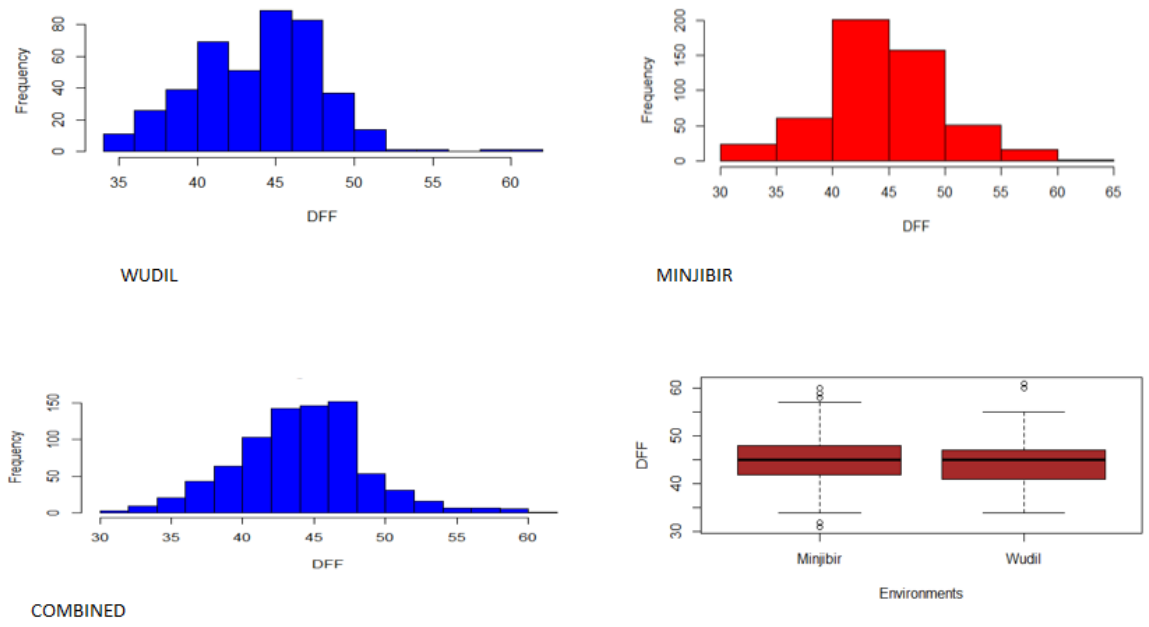

Figure 1: Histogram distribution of flowering traits in Minjibir, Wudil, and Combined Location

Table 3: Analysis of Variance for Early flowering captured in the cowpea DarT Panel population evaluated in two locations and combine location.

WUDIL LOCATION

SOV	Df	Sum of Squares	Mean Squares	F value	Pr(>F)
GENOTYPE	213	6297	29.562	8.21	<2e-16 ***
REP.NO	1	0	0.118	0.033	0.857
REP(Block)	32	79	2.47	0.649	0.925
Residuals	208	748	3.598		

MINJIBIR LOCATION

SOV	Df	Sum Sq	Mean Sq	F value	Pr(>F)
GENOTYPE	274	11428	41.71	4.614	<2e-16 ***
REP.NO	1	6	5.95	0.658	0.418
REP(Block)	38	400	10.53	1.165	0.25
Residuals	197	1781	9.04		

COMBINED LOCATION

SOV	Df	Sum Sq	Mean Sq	F value	Pr(>F)
GENOTYPE	212	11154	52.61	8.422	< 2e-16 ***
Environment	1	73	73.45	11.757	0.000686 ***
GENOTYPE: Environment	202	3551	17.58	2.814	< 2e-16 ***
Environment:REP_NO	2	5	2.40	0.385	0.680968
Environment:Block:REP_NO	70	471	6.73	1.077	0.329572
Residuals	316	1974	6.25		

ns P > 0.05; * P <= 0.05; ** P <= 0.01; *** P <=0.001

Table 4: Genetic Variability Statistics for Early Flowering in cowpea DarT Panel population evaluated in two locations and combine location.

Statistics	Wudil	Minjibir	Combined
Mean	44.3	45.0	44.6
Min.	34	31	31
Max.	61	61	61
SD	4.0	5.2	4.6
CV%	4.3	6.7	5.6
H^2	0.9	0.8	0.7

*Abbreviations: CV = coefficient of variation; SD = Standard Deviation,H^2 = heritability

3.2 GENOME-WIDE ASSOCIATION SIGNALS

A genome-wide scan based on the Blue from phenotypic data for early flowering depicted three major association signals on chromosomes 9,3 and 11 and three other minor regions in chromosome 7,6 and 5 (Figure 2). These six signals were identified using two data set in addition to the combined data. The three major effect regions on chromosomes 7,3, and 11 that displayed significant associations for early flowering were represented by peak SNPs 2_05951 [Log10(p) = 4.8], 2_10751[-Log10(p) = 4.0]and 2_10116[-Log10(p) = 3.9] respectively (Table 5).

Table 5: SNPs that were associated with Early Flowering in the cowpea DArT Panel Population

Location	SNP	Chr	Pos (Bp)	-Log10(P)	R^2(%)
Wudil	2_23113	5	4261655	2.8	6.6
	2_17516	6	19792983	2.7	4.8
	2_22464	9	481299	2.5	6.2
	2_08853	9	622403	3.1	8.4
	2_05951[a]	9	6720642	2.8	6.6
Minjibir	2_38761	3	35284356	3.0	5.6
	2_43455	3	38522983	2.6	4.9
	2_10751	3	54610377	4.0	7.9
	2_13013	3	58294530	3.5	6.7
	2_04680	3	58818791	3.7	7.1
	2_25694	3	61568396	3.0	5.8
	2_52577	3	63390471	3.6	7.3
	2_08433	7	36845505	3.7	7.8
	2_44371	9	5388535	3.1	6.5
	2_18645	9	5624880	2.7	5
	2_43409	9	6080373	3.3	6.3
	2_05951[a]	9	6720642	4.6	8.8
	2_10116	11	1476949	3.9	7.4
	2_47370	11	38661451	3.0	5.7
Combined	2_42229	2	12748462	2.9	7
	2_13013	3	58294530	2.8	6.9
	2_04680	3	58818791	2.9	7
	2_44371	9	5388535	3.5	9.3
	2_43409	9	6080373	3.3	8
	2_05951[a]	9	6720642	4.8	11.8

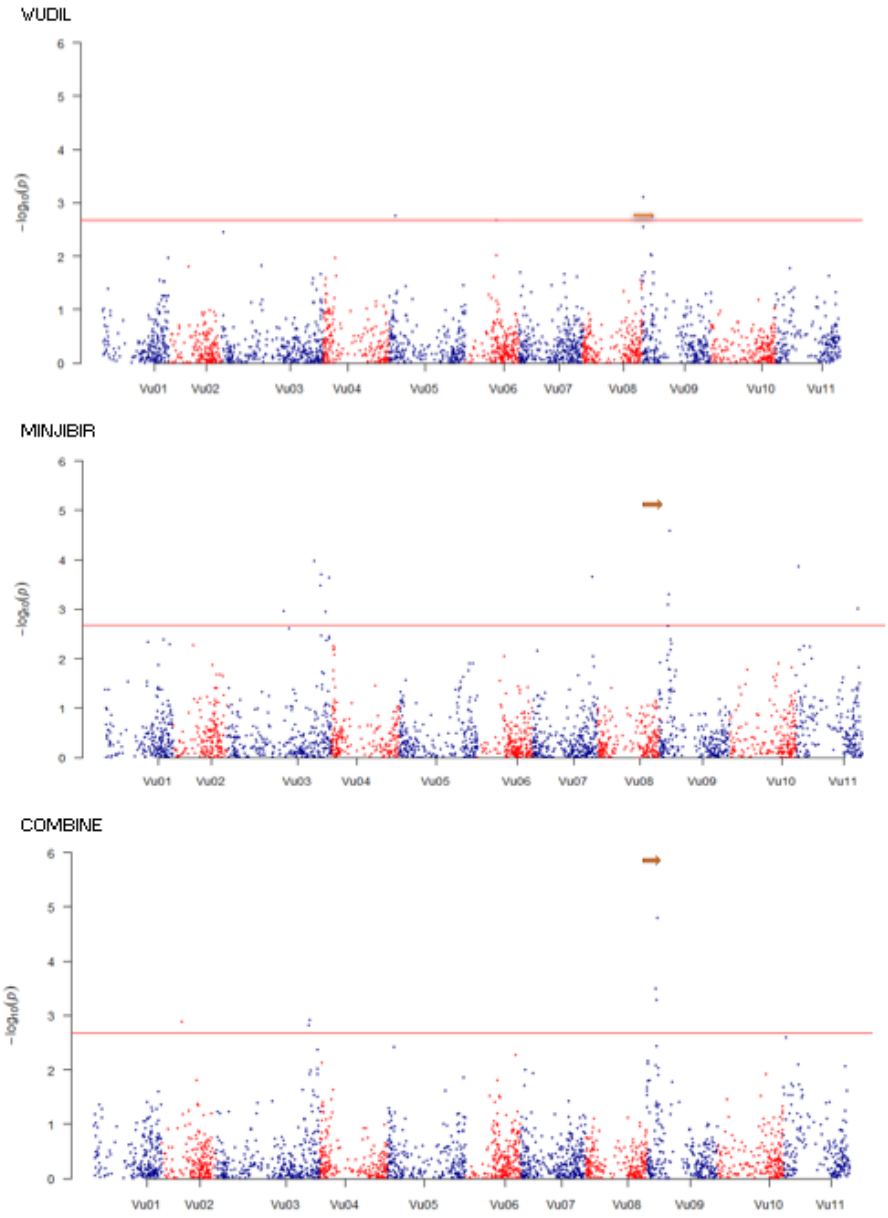

Figure 2: Manhattan plots of genome-wide association signals for early flowering in cowpea. The signals are based on SNP association with first flowering data collected from two locations and combined.

3.3 **Gene predictions and functions**

A Phytozome gene search identified a strong genes that is proximal to the position of representative peak SNPs. The genes uncovered within the one major regions that is associated with early flowering on chromosomes Vu9, Vigun09g063800 (PHYB ACTIVATION TAGGED SUPPRESSOR 1 (BAS1/CYP734A1)).it involved in regulating photomorphogenesis, the process by which plants adjust their development in response to light. Specifically, BAS1 is known to modulate the plant's response to various light signals, including those affecting hypocotyl elongation and cotyledon expansion. It also plays a role in flowering time, influencing when a plant transitions to reproductive growth. In essence, BAS1's role in BR inactivation and its interaction with PHYB contribute to the regulation of flowering time, making it an important factor in the plant's transition to reproductive development.

4 DISCUSSION

The latest genome-wide association study (GWAS) has pinpointed three major signals linked to early flowering on chromosomes 9, 3, and 11, along with three minor signals on chromosomes 7, 6, and 5. The peak SNPs—**2_05951**, **2_10751**, and **2_10116**—show impressive –Log10(p) values of **4.8**, **4.0**, and **3.9**, respectively. These results not only support but also expand upon previous research into the genetic factors influencing flowering time in cowpea and other leguminous crops. For instance, **Lo et al. (2018)** identified significant quantitative trait loci (QTLs) for days to flowering in cowpea on chromosomes Vu03 and Vu09, which closely align with the current findings on chromosomes 3 and 9. Their study highlighted the presence of orthologs of well-characterized flowering genes, such as **FLOWERING LOCUS T (FT)** and **CONSTANS (CO)**, within these genomic regions. Similarly, **Huynh et al. (2018)** reported notable associations on chromosome Vu11 with SNPs located near gene models involved in **photoperiodic flowering responses**, reinforcing the relevance of our observed signal on chromosome 11, particularly marked by SNP 2_10116. In addition, **Yao *et al.* (2016)** found SNPs linked to early flowering on chromosomes Vu07 and Vu05, suggesting that these may represent conserved minor loci influencing phenological traits across diverse cowpea germplasm. The identification of minor regions on chromosomes 7 and 5 in the present study, despite smaller effect sizes, reflects the **polygenic** and potentially **epistatic** nature of flowering time regulation. The consistency of these association signals across two datasets and the combined dataset strengthens their reliability and supports the idea proposed by **Herniter *et al.* (2020)** that multi-environment GWAS improves signal stability for complex traits like flowering.

Furthermore, the gene **Vigun09g063800**, identified as a homolog of **BAS1/CYP734A1**, lies near a major SNP peak on chromosome Vu09 and encodes a **cytochrome P450** enzyme involved in **brassinosteroid (BR) inactivation**. This gene plays a vital role in **photomorphogenesis** and the **regulation of flowering time**. In *Arabidopsis thaliana*, **BAS1** deactivates brassinosteroids, leading to reduced BR signaling, which influences plant development and flowering through interactions with **phytochrome B (PHYB),** a key photoreceptor that senses red/far-red light (Turk *et al.,* 2003; Neff *et al.,* 2005). The BAS1–PHYB interaction affects processes like **hypocotyl elongation** and the transition to reproductive growth, especially under variable light conditions. These functional roles are consistent with the findings of **Herniter et al. (2020)** and **Lo et al. (2018),** who identified flowering time QTLs in cowpea overlapping regions associated with light perception and hormone signaling pathways. Likewise, **Yao et al. (2016)** found that genomic regions linked to flowering contained genes involved in **hormone biosynthesis and signaling**, including brassinosteroids. **Zhang et al. (2014)** further demonstrated that BRs regulate flowering via multiple pathways, including repression of **FLOWERING LOCUS C (FLC)** and modulation of **PHYB-mediated photoperiod pathways**. The identification of **Vigun09g063800 (BAS1)** in cowpea highlights a **conserved regulatory mechanism** across species, where BR inactivation and light signal integration are crucial for floral initiation. Its co-localization with a major GWAS signal strengthens its candidacy as a key gene for **marker-assisted selection** in breeding early-flowering cowpea varieties.

CONCLUSION

In this study, genomic regions across two locations, Wudil and Minjibir were discovered. Among these, Vu09 stood out with the highest phenotypic variance explained (PVE) at 88%, while Vu03 followed with a PVE of 79%. The mapped regions contained a gene linked to functional annotations associated with plant hormones that encourage growth and regulate flowering time. This study also revealed new loci related to early flowering, enhancing our understanding of the genetic factors that control this trait in cowpea. The SNP markers identified in connection with early flowering could be valuable for consistent associations across different genetic backgrounds.

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