Indian J. Genet. Plant Breed., (2025); 85(1): 106-117
https://doi.org/10.31742/ISGPB.85.1.12
ISSN: 0975-6906
www.isgpb.org

RESEARCH ARTICLE

Deciphering genetics and mapping of early flowering and maturity in Indian soybean [*Glycine max* (L.) Merr.]

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Abstract

Soybean (*Glycine max* L.), a major oilseed crop of India, is predominantly cultivated during the *kharif* season under rainfed conditions. The development of early-maturing varieties is crucial due to the short growing season and the risks posed by terminal stresses like drought and high temperatures. To determine the genetics of photoperiod sensitivity, two soybean genotypes namely, SKAF148 (photoperiod insensitive) and DS9712 (photoperiod sensitive) were crossed. The F_1 hybrids of the cross SKAF148 × DS9712 indicated that early flowering is predominant under short-day conditions, while intermediate flowering occurred under long-day conditions. The F_2 plants on the other hand exhibited a continuous variation in photoperiod sensitivity indicating the trait to be controlled by polygenes. For trait mapping, 519 SSR markers were used, of which 258 were polymorphic. Analysis of 250 F_2 segregating population led to the identification of five QTLs for days to flowering; one QTL each on chromosome 10 (qDF10.1) and 11 (qDF11.1), and three QTLS on chromosome 19 (qDF19.1, qDF19.2, qDF19.3) explaining 44.34% of the phenotypic variance. Similarly, five QTLs were mapped for days-to-maturity; two QTLs on chromosomes 1 (qDM1.1 and qDM1.2) and one QTL each on chromosome 4 (qDM4.1), 5 (qDM5.1) and 11 (qDM11.1), accounting for 34.89% of the variance. Chromosome 19 was notably involved in flowering regulations these 3 QTLs have been validated. The proximity of some QTLs reflects their potential for yield improvement. The genetic insights and QTLs identified in the present study along with the linked SSR markers, offer valuable resources for breeding soybean varieties adapted to diverse agricultural conditions across India.

Keywords: E locus**,** *Glycine max,* inheritance, photoperiod sensitivity, QTL mapping, soybean

Introduction

Soybean [*Glycine max* (L.) Merr.] is a globally significant oilseed crop, widely recognized for its essential contributions to both nutrition and industry (Modgil et al. 2021; Anderson et al. 2019). Soybean is a legume crop belonging to the family Fabaceae and the genus *Glycine*, characterized by their ability to fix atmospheric nitrogen, enriching soil fertility (Sabagh et al. 2020). As one of the foremost sources of protein and oil, soybean is integral to meeting the dietary needs of people around the world and supports a wide range of industrial applications, including food products, animal feed, and biofuels, establishing its role as a cornerstone of modern agriculture (Song et al. 2004; Dwevedi et al. 2011; Baraibar et al. 2023; Barboza et al. 2024).

Globally, soybean production reached approximately 381 million metric tons in the 2023-24 crop year, with the United States, Brazil, and Argentina leading in output (USDA, 2024). In India, soybean is a crucial crop cultivated primarily in Madhya Pradesh, Maharashtra, Rajasthan, Karnataka, Telangana, and other states, contributing to a total production of around 11 million metric tons in

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How to cite this article: Rathod N.K.K., Taku M., Yadav R.R., Mujjassim N.E., Saini M., Kumar R., Reshma O., Yadav M., Mallikarjuna B.P., Rajendran R.A., Lal S.K. and Talukdar A. 2025. Deciphering genetics and mapping of early flowering and maturity in Indian soybean [*Glycine max* (L.) Merr.]. Indian J. Genet. Plant Breed., **85**(1): 106-117.
Source of support: Nil
Conflict of interest: None.
Received: June 2024 **Revised:** Dec. 2024 **Accepted:** Jan. 2025

2023 (Ministry of Agriculture and Farmers Welfare, 2023). The crop's diverse applications and benefits underscore its importance in Indian agriculture and food systems (Mishra et al. 2024). Despite its growing significance, India's soybean productivity remains lower compared to leading producers worldwide, averaging about 850 kg per hectare (Indian Council of Agricultural Research, 2023). This productivity gap highlights the urgent need for enhanced agronomic practices and targeted research to boost soybean farming efficiency in the country. Understanding the genetic underpinnings of key agronomic traits, such as flowering time and maturity, is vital for improving soybean productivity and adaptability across different environments (Fang et al. 2024; Vogel et al. 2021; Miranda et al. 2020).

Early flowering and maturity in soybeans are critically important due to the diverse and often challenging climatic conditions across the country (Choudhary et al. 2019). India's varying weather patterns, including regions with shorter growing seasons and unpredictable monsoon rains, make early-maturing soybean varieties essential for ensuring timely harvests and mitigating yield losses caused by adverse weather (Choudhary et al. 2019; Praharaj et al. 2023; Das 2024). These early varieties also enable farmers to optimize the cropping system by allowing planting of the subsequent crops, thereby enhancing land productivity, and improving economic returns (Shah et al. 2021). Additionally, early maturity can help manage pest and disease risks by reducing the exposure period, further contributing to stable and higher yields. Given these advantages, the development and adoption of early-maturing soybean cultivars is crucial to defend India's agricultural challenges and maximizing the benefits of soybean cultivation (Yadav et al. 2017; Singh et al. 2019; Bhartiya et al. 2024). In India, the importance of early maturity soybean can be understood from the fact that major indent (648 q/year) of breeder seeds contributing from photo insensitive class rather than photosensitive varieties (Tripathi et al. 2021).

The genetic regulation of flowering time and maturity in soybeans is governed by a complex network of genes influenced by environmental factors such as photoperiod and temperature. Central to this regulation are the E loci (E1 to E11), which play a significant role in determining the timing of flowering and maturation, especially under varying photoperiods. Recent Indian studies have highlighted the importance of photo-insensitive alleles and long juvenility traits in adapting soybean varieties to lower latitudes and short growing seasons (Tripathi et al. 2021; Gupta et al. 2022; Kumawat et al. 2021). These insights are critical for developing soybean varieties suited to diverse agro-climatic conditions. The J locus (Ray et al. 1995) and the *Flowering locus T (FT)* genes (Nan et al. 2014) also play significant roles in this regulatory network. Despite substantial advancements, the field remains dynamic, with ongoing research focused on discovering new genetic variants and their interactions with existing E loci. The E1, E2, E3 and E4 loci are particularly involved in the regulation of photoperiod sensitivity, significantly affecting flowering time and maturity (Xia et al. 2012; Raievska et al. 2024). Mapping and identifying quantitative trait loci (QTLs) associated with early maturity are essential for enabling marker-assisted selection (MAS) and accelerating the development of early-maturing soybean cultivars. Breeding efforts in soybeans have primarily focused on enhancing traits like early maturity, higher yield, wider adaptability, and waterlogging tolerance (Gill et al. 2023; Maranna et al. 2021). However, in Northern India, limited studies are addressing the inheritance patterns of early maturity or identifying molecular markers linked to this trait. To bridge this gap, this study aimed to understand the genetic basis of flowering and maturity to facilitate the development of early-maturing soybean varieties.

Materials and methods

Experimental material

The study utilized two soybean lines with distinct flowering and maturity characteristics: SKAF148, an extra-early maturing germplasm (68-70 days); and DS9712 a late-maturing line (110–120 days). These parental lines were crossed in both direct and reciprocal combinations to generate F_1 hybrids. The resulting hybrids, along with the parental lines, were evaluated under various growth conditions to assess their phenotypic traits. The experiment was carried out in a growth chamber, glasshouse (Fig. 1), and field environments to examine the effects of different conditions on flowering time and maturity. In the growth chamber, plants were exposed to short-day conditions with a 10-hour light period and 14-hour dark period, maintained at 25°C during the night and 30°C during the day, with 80% relative humidity. Glasshouse experiments were conducted during the *kharif* season and off-season of 2022, with natural day lengths and temperatures maintained at 25°C during night time and 32°C during day time, and 80% relative humidity as detailed in Table 1. Field trials took place at ICAR-IARI, New Delhi (29.1–29.5° N, 76.3–77.1° E, elevation 243 m above mean sea level) and IARI-RRS, Dharwad, Karnataka (32° N, 77° E, altitude 1900 m above mean sea level), with varying day lengths, temperatures, and humidity levels, as detailed in Table 1. The parental seeds and F_2 seeds were sown on January 6, 2023, with a spacing of 60 x 20 cm, and a basal application of 18 kg N and 46 kg P_2O_5 per hectare.

Observations recorded and statistical analysis

Observations were meticulously recorded on an individual plant basis for all parents and F_1 hybrids under different growth conditions. Similarly, data for the F_2 populations were collected on an individual plant basis under field conditions at IARI-RRS, Dharwad, Karnataka. Pre-harvest observations included days to flowering (DF), measured from sowing

Table 1. Growth conditions used to decipher photoperiod insensitivity of parental genotypes and Inheritance studies and mapping of early maturity

Growth condition	Average Day Length (in hours)		Temperature (°C) (min-max)	Humidity (%)	Genotypes/Population raised
Growth chamber	September-December	10:00	25-30	80	P1, P2 and F_1
Glasshouse *Kharif season-2022*	July	14:00	25-32	80	P1, P2, and F_1
	August	13:00–13:50			
	September	12:00–13:00			
	October	11:00–12:00			
Glasshouse *Off-season-2022*	August	13:00–13:50	25-32	80	P1, P2, and F_1
	September	12:00–13:00			
	October	11:00–12:00			
	November	10:00–11:00			
Field condition-2022 IARI, New Delhi	July	14:00	25-38	79	P1, P2, and F_1
	August	13:00–13:50	26-37	77	
	September	12:00–13:00	24-37	78	
	October	11:00–12:00	17-35	77	
Field condition-2023** ICAR-IARI-RRS	January	11:13–11.27	11-31	57	P1, P2, F_1 and F_2
	February	11:28–11:48	16-35	42	
	March	11:49–12:15	17-37	41	
	April	12:15–12:40	21-39	48	
	May	12:45–13:00	22-38	45	

** Growth condition in field at ICAR-IARI-RRS, Dharwad, for growing F_2 mapping population

to the appearance of the first fully opened flower and days to maturity (DM), noted when over 90% of pods had transitioned from green to brown color. Statistical analysis involved descriptive statistics, including mean, range, and standard error, computed using MS Excel. Additionally, a Chi-Square (χ^2) test was conducted to assess segregation patterns.

Construction of Genetic Linkage Map and QTL identification

To construct a genetic linkage map and identify quantitative trait loci (QTLs) for flowering and maturity, the 250 F_2 population derived from a cross between SKAF148 and DS9712 was subjected to genetic analysis. Fresh leaf tissue from 20-day-old seedlings of both parental lines and 250

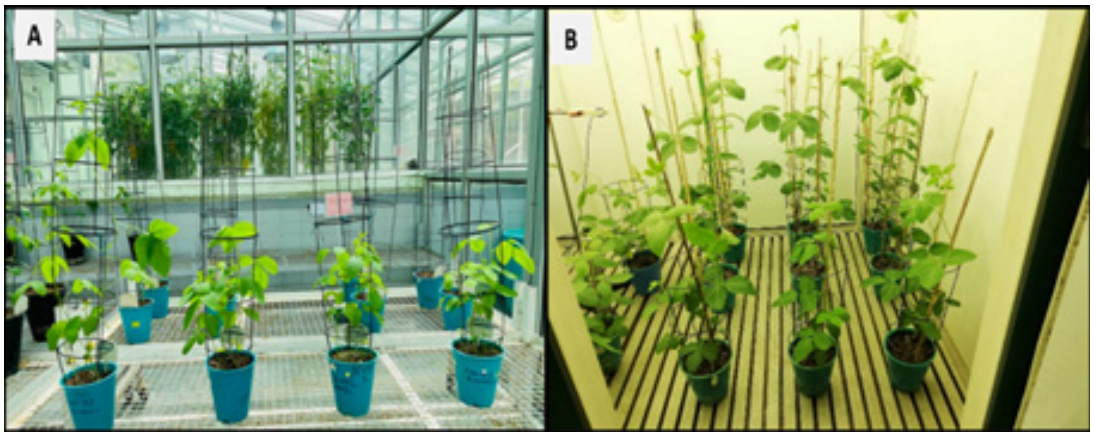

Fig. 1. Parental lines grown under different growth conditions A. Parental lines in glass house; B. parental lines in the growth chamber

F_2 plants was collected for DNA extraction. Genomic DNA was extracted using the CTAB method outlined by Doyle and Doyle (1990). The DNA quality was assessed through electrophoresis on a 0.8% agarose gel. PCR amplification was carried out with a reaction mixture consisting of 20 ng/µL DNA, 10x PCR buffer, dNTPs, Taq DNA polymerase, primers, and distilled water. The thermal cycling conditions included an initial denaturation at 94°C, followed by 35 cycles of denaturation, annealing at 52 to 55°C, and elongation at 72°C. The PCR products were separated on a 2.0% agarose gel, and SSR marker analysis was performed using 519 markers initially, with 142 polymorphic markers selected for genotyping. Linkage map construction and QTL detection were carried out using QTL IciMapping V4.2 (Wang et al. 2014), employing a minimum logarithm of odds (LOD) score of 3.0 and a genetic distance threshold of 50 centimorgans (cM). Inclusive Composite interval mapping (ICIM-ADD) was used for QTL analysis, with an LOD score threshold of 3.0 to verify the presence of QTLs in specific genomic regions.

Results

Understanding photoperiod-sensitivity in selected genotypes

The flowering and maturity periods of SKAF148 and DS9712 varied significantly under different growth conditions. SKAF148 consistently flowered in 26 to 28 days across all conditions, demonstrating insensitivity to photoperiod variations, while DS9712 exhibited delayed flowering, ranging from 28 to 30 days under short-day conditions to 42 to 45 days in the field (Fig. 2). SKAF148 matured in 68 to 70 days across all conditions, whereas DS9712 showed marked photoperiod sensitivity, with maturity delayed from 83 to 88 days under short-day conditions to 110to 120 days in the field. These results highlight the adaptability of SKAF148 and the greater photoperiod sensitivity of DS9712 (Table 2).

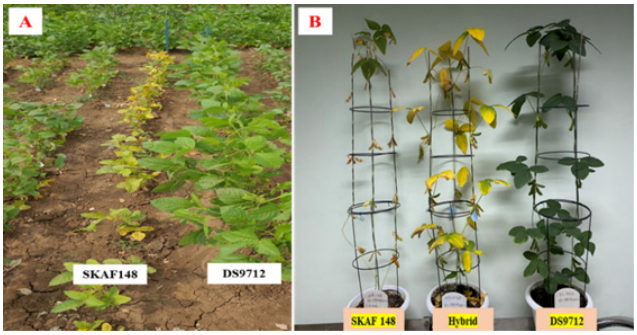

Fig. 2. Plant materials used in the experiment. A. Parental lines showing contrasting characters viz., plant height and maturity in the field and B. Maturity level of parental lines along with hybrids in glasshouse under *kharif* 2022

Inheritance of early flowering and maturity

Direct and reciprocal crosses were made between the early parent SKAF148 and the genotype DS9712. The F_1 seeds from these crosses were grown in a glasshouse and a growth chamber to test for true hybrids and data was collected on flowering and maturity times. SSR marker Satt 636 was used to verify the true hybrids (Fig. 3). Out of the direct crosses (SKAF148 × DS9712), 21 F_1 plants were confirmed as hybrids, while 13 F_1 plants from the reciprocal crosses (DS9712 × SKAF148) were identified as hybrids.

In the glasshouse during the *kharif* season, the early maturing parent SKAF148 began flowering in 28 days and matured in 70 days, while the late maturing parent DS9712 started flowering in 41 days and matured in 110 days. The F_1 plants from both direct and reciprocal crosses flowered in 33 days and matured in 98 days (Fig. 4). There was no significant difference between the reciprocal and direct crosses. The mid-parental values for days to flowering and days to maturity in the glasshouse under *kharif* season 2022 were 34.5 days and 90 days, respectively. Thus, the F_1 plants exhibited intermediate flowering and maturity times compared to the parents.

In the glasshouse during the off-season, the early maturing parent SKAF148 showed consistent flowering and maturity time began to flower in 28 days and matured in 70 days. In contrast, the late maturing parent DS9712 began flowering in 35 days (earlier than in the *kharif* season of 2022) and matured in 92 days. The hybrid plants from both direct and reciprocal crosses flowered in 29 days and matured in 82 days (Fig. 5). The mid-parental values for the off-season were 31.5 days to flowering and 81 days to maturity. This indicates that the hybrids exhibited dominance for early flowering and incomplete dominance for early maturity.

In the growth chamber under SD conditions, the early parent began flowering in 26 days and matured in 68 days. The late maturing parent DS9712 flowered in 30 days and matured in 87 days. Hybrid plants flowered in 27 days and matured in 75 days (Fig. 6). The mid-parental values for this condition were 28 days to flowering and 71.5 days to maturity. The hybrids showed dominance for early flowering and incomplete dominance for maturity, with a slight skew towards early maturity.

The F_2 mapping population was grown in the field at IARI-RRS, Dharwad, Karnataka (Fig. 7). The F_2 mapping population is not replicated because each individual in the population has a unique genetic makeup resulting from the segregation and recombination of alleles during the formation of gametes in the F_1 generation. The 690 F_2 plants exhibited continuous segregation for flowering and maturity (Figs 8 and 9). The early maturing genotype started flowering at 28 days after sowing (DAS), while DS9712 started flowering at 33 DAS. Days to flowering ranged from 33 to 52 days, with a mean of 38.86 days. The standard deviation was 2.44

Table 2. Deciphering photoperiod sensitivity of parental lines in different growth conditions

Character	Growth condition	Average day length (hrs/day)	SKAF148 (in days)	DS9712 (in days)
Days to flowering	Growth chamber (Short day condition)	10	26-28	28-30
	Glasshouse (*Kharif* season)	11-14	26-28	40-42
	Glasshouse (off-season)	10-13	26-28	34-36
	Field condition	11-14	26-28	42-45
Days to maturity	Growth chamber (Short day condition)	10	68-70	83-88
	Glasshouse (*Kharif* season)	11-14	68-70	100-105
	Glasshouse (off-season)	10-13	68-70	92-95
	Field condition	11-14	68-70	110-120
Photo-period sensitivity			Insensitive	Highly sensitive

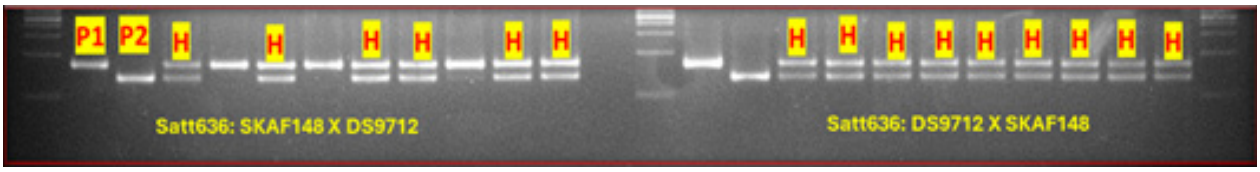

Fig. 3. Identification of true F_1 hybrids from crossed seeds through SSR markers P1=Early parent (SKAF148); P2 = Late parent (DS9712); H = Hybrids

days, reflecting low variability. The CV was 6.28%, indicating minimal variation. The skewness of 0.64 shows a moderate positive skew, and the kurtosis of 1.03 suggests a moderately leptokurtic distribution (Table 3). A total of 128 F_2 plants segregated transgressively towards early flowering, with one plant flowering at 24 DAS, four at 25 DAS, 37 at 26 DAS, and 86 at 27 DAS. Similarly, 50 plants were transgressively segregated towards late flowering, with 23 plants flowering at 34 DAS, 13 at 35 DAS, 9 at 36 DAS, and 2 at 37 DAS.

For maturity, the genotype SKAF148 matured at 70 DAS and DS9712 at 88 DAS. The days to maturity ranged from 70 to 106 days, with a mean of 80.39 days. The standard deviation was 4.99 days, indicating moderate variability. The CV was 6.21%, showing low variability. The skewness was 1.00, indicating a noticeable positive skew and the kurtosis of 2.63 suggests a leptokurtic distribution. A total of 44 F_2 plants showed transgressive segregation towards early maturity, with 2 plants maturing at 66 DAS, 9 at 67 DAS, 13 at 68 DAS, and 20 at 69 DAS. Similarly, 15 plants were transgressively segregated towards late maturity, with 3 plants maturing at 89 DAS, 3 at 93 DAS, and 1 plant each at 90, 95, and 97 DAS, with additional plants maturing at 91, 92, and 102 DAS. The continuous variation in days to flowering and maturity among the F_2 plants suggests that these traits are controlled by multiple genes.

QTL mapping for days to flowering

A total of 5 putative QTLs controlling days to flowering were identified on chromosomes, 10, 11, and 19 (Fig. 10). Chromosome 19 harboured 3 QTLs, while chromosomes 10 and 11 each contained one QTL. Among these, three were classified as major QTLs (explaining more than 10% of phenotypic variance), and two were minor QTLs (explaining less than 10% of phenotypic variance) (Table 4). On chromosome 10, a QTL (qDF10.1) located at 31.18 cM between markers satt581 and satt331 had a LOD score of 7.46, explaining 4.23% of the phenotypic variance (PVE). The additive effect was -1.18, and the dominance effect was -0.60. Chromosome 11 revealed a QTL (qDF11.1) at 62.00 cM between markers satt484 and sat_149 with a LOD score of 8.33, accounting for 6.97% of the PVE. This QTL had an additive effect of 1.65 and a dominance effect of -0.35. Chromosome 19 exhibited three QTLs at different positions. The first QTL (qDF19.1) at 245.00 cM between markers satt373 and satt664 had a LOD score of 5.40, explaining 10.20% of the PVE, with an additive effect of -1.50 and a dominance effect of -1.88. The second QTL (qDF19.2) at 343.00 cM, also between markers satt373 and satt664, had a LOD score of 7.07, accounting for 10.58% of the PVE, with an additive effect of -1.76 and a dominance effect of -1.26. The third QTL (qDF19.3) at 392.00 cM between markers satt664 and satt340

Fig. 4. Days to flowering and days to maturity of parents and their hybrids in glasshouse under *kharif* season-2022

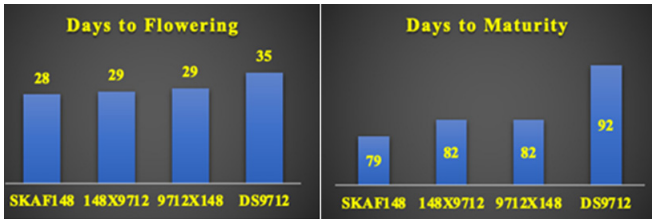

Fig. 5. Days to flowering and days to maturity of parents and their hybrids in glasshouse under off-season 2022

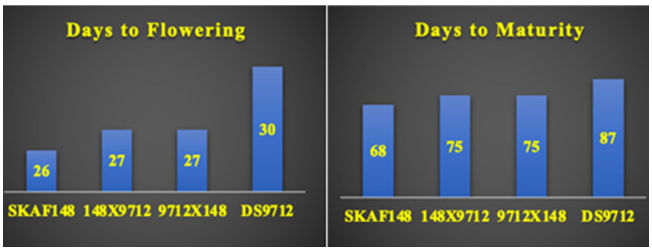

Fig. 6. Days to flower and days to maturity of parental and their hybrids in growth chamber under short day condition

had a LOD score of 6.99, explaining 10.54% of the PVE, with an additive effect of -1.76 and a dominance effect of -1.25.

QTL mapping for days to maturity

A total of 5 QTLs controlling days to maturity were identified (Fig. 10). Among these, two major QTLs were located on chromosome 1, and one minor QTL each was found on chromosomes 4, 5, and 11 (Table 5). On Chromosome 1, two QTLs were detected. The first QTL (qDM1.1) at 72.00 cM between markers satt408 and sat_201 had a LOD score of 7.44, explaining 12.73% of the phenotypic variance, with an additive effect of -4.18 and a dominance effect of -2.99. The second QTL (qDM1.2) on the same chromosome at 127.00 cM between markers sat_201 and sat_036 had a LOD score of 7.43, accounting for 12.97% of the PVE, with an additive effect of -4.27 and a dominance effect of -2.89. On Chromosome 4, a QTL (qDM4.1) was located at 80.00 cM between markers satt161 and sat_322, with a LOD score of 4.67, explaining 2.97% of the PVE. This QTL had an additive effect of -2.08 and a dominance effect of 0.53. Chromosome 5 exhibited a QTL (qDM5.1) at 0.00 cM between markers sat_271 and satt236 with a LOD score of 5.23, accounting for 3.38% of the PVE. The additive effect was 0.47, and the dominance effect was -3.58. On Chromosome 11, a QTL (qDM11.1) was found at

Fig. 7. F_2 mapping population in the field at IARI-RRS, Dharwad, Karnataka

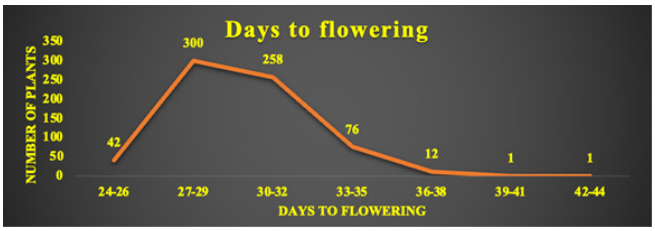

Fig. 8. The segregation pattern of days to flowering in F_2 mapping population

76.00 cM between markers satt484 and sat_149 with a LOD score of 3.11, explaining 2.84% of the PVE. This QTL had an additive effect of 1.76 and a dominance effect of -1.66.

Discussion

Soybean production faces significant yield reductions of over 40% due to terminal stresses like drought and high temperatures, particularly during the pod-filling stage (Marinho et al. 2022). In India, where soybeans are mainly grown during the rainfed *kharif* season, the risk of extreme weather is heightened by the short growing period (Rao et al. 2015). To address this, early-maturing soybean varieties

Table 3. Descriptive statistics for different traits in the F_2 mapping population

Parameters	Days to flowering	Days to maturity
Maximum	52.00	106.00
Minimum	33.00	70.00
Mean	38.86	80.39
STDEV	2.44	4.99
CV (%)	6.28	6.21
Skewness	0.64	1.00
Kurtosis	1.03	2.63

STDEV = Standard Deviation; CV = Coefficient of variation

Fig. 9. The segregation pattern of days to maturity in F_2 mapping population

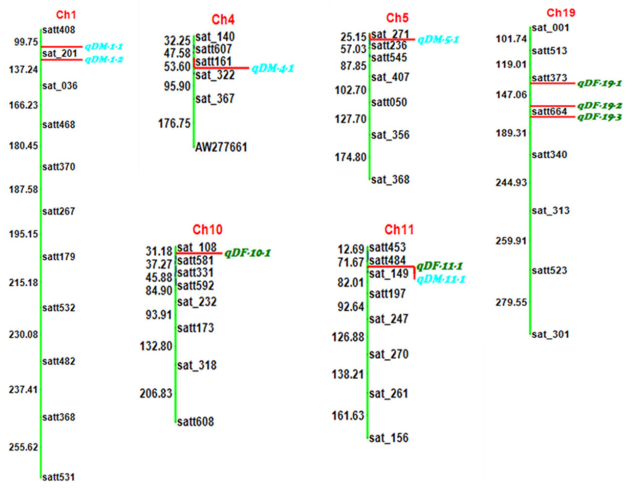

Fig. 10. Linkage map and Identified QTLs for days to flowering and maturity

are essential, as they can avoid severe weather by utilizing traits such as photoperiod insensitivity (Staniak et al. 2023; Dupare et al. 2020).

Photoperiod insensitivity is crucial for adapting crops to different environments (Hartwig, 1970; Hartwig & Kiihl, 1979). In this study, under short-day conditions, SKAF148 flowers in 26 to 28 days, while DS9712 takes 28 to 30 days. Conversely, in longer day lengths during the *kharif* season, DS9712 has a prolonged flowering time (40–42 days) compared to SKAF148 (26–28 days), indicating greater sensitivity to day length changes. Under off-season conditions with 10 to 13-hour day lengths, DS9712 shows moderate sensitivity, while SKAF148 remains relatively insensitive across conditions. Research confirms that photoperiod-insensitive varieties like SKAF148 exhibit consistent flowering times across varying day lengths (Verma and Sawaji, 1994). Gupta et al. (2017) identified six photoperiod-insensitive accessions among 2,071 screened under long-day conditions. In contrast, DS9712's high sensitivity makes it suitable for environments with stable day lengths but less adaptable to variable conditions. Similar patterns are seen in other crops like rice and wheat, where photoperiod sensitivity affects flowering times (Matsuoka et al. 2017; Lewis et al. 2019). SKAF148's consistent early flowering and maturity suggest its adaptability to regions with unpredictable day lengths.

In the present study, early flowering in F_1 hybrids was dominant under short-day conditions and in a glasshouse during the offseason. In this cross, the genes responsible for early flowering may have been expressed under short-day conditions, resulting in early flowering. However, initial long day conditions (August: 13:00–13:50 hours and September: 12:00–13:00 hours) in the glasshouse during the offseason of 2022 could have led to early initiation of flowering due to higher night temperatures, as reported in the studies of Cober, (2010) and Liu et al. (2011). Abrahao et al. (2018) and Cober et al. (2014) exposed soybeans to short photoperiods and high temperatures in low-latitude regions, resulting in early flowering, shorter periods of vegetative growth, shorter plant heights, and significant

Table 4. QTL mapping for days to flowering

Chr. No.	Position (cM)	Left marker	Right marker	LOD	PVE (%)	Add	Dom
10	31.18	satt581	satt331	7.46	4.23	-1.18	-0.60
11	62.00	satt484	sat_149	8.33	6.97	1.65	-0.35
19	245.00	satt373	satt664	5.40	10.20	-1.50	-1.88
19	343.00	satt373	satt664	7.07	10.58	-1.76	-1.26
19	392.00	satt664	satt340	6.99	10.54	-1.76	-1.25

Table 5. QTL mapping for days to maturity

Chr. No.	Position (cM)	Left marker	Right marker	LOD	PVE (%)	Add	Dom
1	72.00	satt408	sat_201	7.44	12.73	-4.18	-2.99
1	127.00	sat_201	sat_036	7.43	12.97	-4.27	-2.89
4	80.00	satt161	sat_322	4.67	2.97	-2.08	0.53
5	0.00	sat_271	satt236	5.23	3.38	0.47	-3.58
11	76.00	satt484	sat_149	3.11	2.84	1.76	-1.66

reductions in yield. Under long-day conditions, F_1 hybrids exhibited intermediate to days to flowering when grown in the *Kharif* season of 2022 (11–14 hours of day length) in the glasshouse. These observations confirm that the gene governing early flowering is completely dominant under short-day conditions and shows incomplete dominance under long-day conditions. The days to maturity of these hybrids showed incomplete dominance irrespective of growth conditions and were skewed towards earliness in short-day conditions and lateness in long-day conditions. These differential responses under different growth conditions may be due to interactions between different alleles and with the growth conditions. It is known that E1 to E4, E7, E8, and E10 alleles delay flowering under long-day conditions, while E6, E9, J, and E11 alleles promote flowering under long-day conditions (Samanfar et al. 2017; Watanabe et al. 2011; Xia et al. 2012; Zhao et al. 2016).

The F_2 population used in this study was derived from crosses between two contrasting parental lines. Therefore, different alleles of genes responsible for different traits must be present in these crosses and segregation can be clearly observed in the data distribution of the F_2 plants growing in an off-season environment. The analysis of the F_2 populations indicates that the continuous segregation of days to flowering and days to maturity are controlled by multiple genes, exhibiting polygenic inheritance. The observed positive skewness towards early flowering and maturity suggests that these traits are influenced by genes contributing to earliness, with the majority of plants in the F_2 populations showing traits similar to the early-flowering parent. In terms of statistical distribution, the kurtosis values for both days to flowering and days to maturity are positive, with values of 1.03 and 2.63 in the population. Positive kurtosis indicates a distribution with heavier tails and a sharper peak compared to a normal distribution, reinforcing the idea of skewness towards earliness. Earlier research indicated that dominant alleles at various loci (E1, E2, E3, E4, E5, E7, E8, E10) tend to delay flowering, while recessive alleles at other loci (E6, E9, E11, J) have varying effects on delaying flowering time (Samanfar et al. 2017; Watanabe et al. 2011; Xia et al. 2012; Zhao et al. 2016). The interaction of these alleles with environmental conditions and other loci can contribute to the observed variability. The transgressive segregation noted in these F_2 populations suggests that new gene combinations resulting from the cross, combined with spatial and temporal gene expression effects, contribute to the range of flowering and maturity times observed. This indicates a complex interplay between genetic factors and environmental influences shaping these traits, as discussed by Watanabe et al. (2012) and Kong et al. (2014).

QTL mapping is an effective method for identifying novel loci in soybean (Chen et al. 2021; Jun et al. 2014; Liu et al. 2017; Zhang et al. 2019; Fang et al. 2019; Ren et al. 2020). Despite the growing body of knowledge and ongoing identification of genes involved in soybean flowering, there is still a need for discovering new genes and QTLs for flowering and maturity. Currently, early-maturing soybean varieties have a maturity duration ranging from 85 to 95 days, while the germplasm line SKAF-148 matures in 68 to 70 days, containing novel QTLs as discussed in the following sections. As previously mentioned, days to flowering are influenced by photoperiod, temperature, and the genetic background of the cultivars. Thus, photoperiod insensitivity, flowering time, and plant maturity may be controlled by the same genes or closely clustered genes within the same chromosomal regions (Liu et al. 2011; Tasma et al. 2001). In the present study, five QTLs for days to flowering were identified on chromosomes 10, 11, and 19, collectively accounting for 44.34% of the phenotypic variance. Notably, three major QTLs on chromosome 19 explained more than 10% of the phenotypic variance. The region between the markers Satt373 and Satt664 was highly associated with days to flowering (Table 4). Mao et al. (2017) reported that the Satt664 marker was significantly associated with flowering time under long-day conditions. Watanabe *et al*. (2009) identified a QTL on chromosome 19 corresponding to the E3 locus, a finding corroborated by Wang et al. (2020). Liu et al. (2011) also identified a QTL in the Satt373 genomic region on chromosome 19. Kim et al. 2023 and found that markers in the same region as Satt664 were associated with flowering time, though different markers were identified. Watanabe et al. (2009) identified the marker Satt229 as being closely linked to the E3 locus, a critical regulator of photoperiod sensitivity and flowering time in soybeans. According to the Soymap3 resource from the soybean lab at IARI, Satt229 (93.89 cM) is in close proximity to markers Satt664 (92.66 cM) and Satt373 (107.24 cM). This suggests that the identified QTLs, qDF19.1, qDF19.2, and qDF19.3 on chromosome 19 are likely associated with the E3 locus. The clustering of these markers and QTLs in the vicinity of the E3 locus reinforces its significance in controlling flowering time and provides strong genetic evidence for their association with the E3 locus. Furthermore, the identification of multiple QTLs in the E3 locus region suggests the presence of a complex genetic architecture influencing flowering time, potentially involving interactions between multiple alleles or genes. This linkage is particularly valuable for marker-assisted selection programs, as it allows for precise identification and manipulation of flowering-related traits. The E2 locus is located on chromosome 10 between the Satt 581 and sat_307 markers (Fedorina et al. 2022) and is an ortholog of the *Arabidopsis GIGANTEA* gene (Watanabe et al. 2011). Initial studies proposed the presence of an E5 locus affecting maturity, but subsequent research has questioned its uniqueness, suggesting that the effects attributed to E5 might overlap with those of E2 (Dissanayaka et al. 2016). The

identified minor QTL, qDF 10.1 is mapped on chromosome 10, located between the markers Satt 581 and Sat_108. This positioning places it in close proximity to the E2 locus, suggesting a possible genetic interaction. Given the known role of E2 in flowering time regulation, qDF 10.1 may either be influenced by E2 or represent a region with additional genetic factors contributing to flowering and maturity.

For days to maturity, five QTLs were identified, including two major QTLs on chromosome 1 and one minor QTL each on chromosomes 4, 5, and 11 (Table 5). These QTLs collectively explain 34.89% of the phenotypic variation. The presence of two major QTLs on chromosome 1 (qDM1.1 and qDM1.2) suggests that this chromosome plays a significant role in controlling maturity timing. These QTLs exhibited high LOD scores (7.44 and 7.43) and explained substantial portions of the phenotypic variance (12.73 and 12.97%, respectively), indicating their strong influence. The minor QTLs identified on chromosomes 4 (qDM4.1), 5 (qDM5.1), and 11 (qDM11.1) might contribute to fine-tuning maturity duration but are likely to be influenced by environmental factors or interactions with other genetic elements. The region between Satt484 and Sat_149 on chromosome 11 harbors QTLs for both days to flowering and days to maturity. Single marker analysis revealed that four markers (Satt664, Satt513, Satt380, Sat_108) are commonly associated with both traits flowering and maturity. Kong et al. (2018) and Lee et al. (2015) reported overlapping QTLs for flowering and maturity on chromosome 11, indicating a conserved region across studies. Li et al. (2019) and Wang et al. (2018) identified a major QTL for flowering on chromosome 11, though the specific markers differed. Several studies have associated Tof11 and Tof12 loci on chromosome 11 with photoperiod sensitivity and extended vegetative growth (Li et al. 2020; Lu et al. 2020). The presence of maturity-related QTLs in this region supports the hypothesis that genes influencing the time of flowering may co-localize with these QTLs. This alignment reinforces the role of chromosome 11 in governing soybean adaptation to diverse latitudes and planting conditions. Comparing these findings with previous studies, similar QTLs for maturity have been mapped in soybean populations (Dissanayaka et al. 2016; Kong et al. 2018; Lee et al. 2015). The fact that different populations reveal distinct but overlapping QTLs suggests a complex genetic architecture underlying soybean maturity, influenced by multiple loci interacting across different genomic regions. Additionally, known maturity-related genes such as E1, E2, and E3 have been implicated in previous QTL mapping studies (Watanabe et al. 2009; Watanabe et al. 2011; Wang et al. 2020; Liu et al. 2011; Kim et al. 2023; Fedorina et al. 2022; Dissanayaka et al. 2016). The co-localization of some QTLs with these genes highlights their potential functional relevance in regulating maturity through photoperiod sensitivity and hormonal pathways.

Overall, this research underscores the importance of integrating genetic insights into breeding programs to enhance soybean resilience and productivity. The novel QTLs identified here offer promising targets for further investigation and could significantly advance efforts to develop soybean varieties that thrive under increasingly variable climatic conditions.

Authors' contribution

Conceptualization of research (AT, SKL); Designing of the experiments (AT, NKKR); Contribution of experimental materials (AT), Execution of field/lab experiments and data collection (NKKR, MT, BPM, RRY, MS, RK, OR, MY, AT); Analysis of data and interpretation (NKKR, NEM, RAR); Preparation of the manuscript (NKKR, AT).

Acknowledgments

The authors express their gratitude to the National Phytotron Facility, Division of Genetics, IARI, New Delhi, and IARI-RRS, Dharwad, for providing the necessary facilities for the successful execution of this research. This research is part of the first author's Ph.D. thesis submitted at ICAR-IARI, New Delhi, India.

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