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Genetic analysis of yield and physiological traits in soybean [*Glycine max* (L.) Merr.] under drought stress

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Abstract

The present investigation on soybean [*Glycine max* (L.) Merr.] was conducted at the Post Graduate Research Farm, Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri, during the academic years 2023–25. Under drought conditions, P_1 flowered and matured significantly earlier, F_1 showed superior yield traits, P_2 and F_1 excelled in plant height (PH) and number of pods per cluster (NPC), while F_2 and F_3 displayed only intermediate performance across traits. P_1 generally performed best for earliness and chlorophyll content (CC), P_2 for leaf area (LA) and relative water content (RWC) related traits and F_1 consistently excelled in canopy temperature depression (CTD) and harvest index (HI). F_2 and F_3 showed mostly average or desirable leaf senescence performance, depending on the cross. All four crosses showed additive gene action for flowering and maturity, while Crosses I, II and III showed the same pattern for number of pods per plant (NPP) and Cross I alone for PH. Dominance and dominance × dominance effects were expressed for multiple traits across crosses, with Cross I showing them for 3 traits, Cross II for four, Cross III for four and Cross IV for six yield traits. Duplicate epistasis was observed for seed index (SI) (Crosses I and IV), DF (Crosses II and III) and NPP (Crosses II and IV). However, complementary epistasis was observed for maturity (Crosses I and IV), PH (Crosses II and IV) and NPP and yield per plant (YPP) (Cross III).

Keywords: epistasis; gene action; gene interaction; generation mean; soybean; variation

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1. Introduction

Oilseed crops have played a vital role in strengthening the global and national economies since ancient times (1). Among them, soybean [*Glycine max* (L.) Merr.] is the most important legume crop worldwide, serving as a major source of both edible oil and protein. It contributes approximately 25 % of global edible oil production and provides nearly two-thirds of the protein concentrate used in livestock and poultry feed. Soybean is a self-pollinated species (2n = 40) belonging to the family Leguminosae (syn. Fabaceae) and subfamily Papilionoideae (2).

Soybean is recognised as the leading oilseed crop globally due to its high productivity, profitability and contribution to soil fertility through biological nitrogen fixation. Commercial soybean varieties typically contain about 40 % protein, rich in essential amino acids and 20 % oil, largely composed of polyunsaturated fatty acids such as omega-6 and omega-3. The crop also provides approximately 6–7 % minerals and 5–6 % fibre. The nutritional quality of soybean protein is comparable to that of animal-derived proteins from meat, milk and eggs (1). In addition to its use in human nutrition, soybean serves as a critical component in fish and poultry feed formulations (3).

Globally, soybean production during 2024–25 is estimated at 420.8 million metric tonnes (4). Brazil leads the world with 169.0 million tonnes (MT), followed by the United States (118.84 MT), Argentina (50.9 MT) and China (20.65 MT), while India ranks fifth, contributing about 3 % of global production (15.13 MT) (4). In terms of cultivated area, soybean occupies 146.3 million hectares (Mha) worldwide, with Brazil (47.4 Mha) and the United States (34.64 Mha) leading, followed by Argentina (17.3 Mha), India (13.5 Mha) and China (10.5 Mha) (4). Within India, Maharashtra ranks first in production (7.27 MT), followed by Madhya Pradesh (5.35 MT) and Rajasthan (1.17 MT). In terms of area, Madhya Pradesh contributes the largest share (5.35 Mha), followed by Maharashtra (5.13 Mha) and Rajasthan (1.12 Mha) (4).

Global climate variability, particularly in terms of irregular rainfall and temperature extremes, has intensified the frequency and severity of abiotic stresses, posing major challenges to crop productivity. Such fluctuations hinder normal plant growth and reproductive development, leading to substantial yield

reductions. Plants must constantly regulate their physiological and metabolic functions to adapt to these dynamic environmental conditions. Therefore, identifying genetic and physiological traits associated with resilience to climatic stresses is critical for ensuring sustainable productivity (5, 6).

In India, more than 90 % of soybean cultivation occurs under rainfed conditions during the monsoon season, primarily in vertisols and related clay-rich soils (1). However, the high dependency on inconsistent and erratic monsoon rainfall often results in drought stress at various growth stages, severely affecting soybean productivity. Drought adversely impacts yield from germination through flowering and seed development, with terminal-stage droughts, especially during seed-filling and maturity, causing irreversible yield losses (5, 6). Maximum yield losses due to drought can reach up to 40 % (7). Drought during the vegetative stage leads to leaf wilting, curling and abscission, reducing photosynthetic capacity, whereas reproductive-stage stress causes flower and pod abortion and seed shrinkage.

To mitigate these losses, several strategies have been developed, including improved agronomic practices and genetic enhancement of drought-tolerant cultivars (8). However, despite progress in optimising water use efficiency, the adoption of advanced irrigation technologies such as micro-irrigation remains limited and costly in many regions (9). Consequently, developing drought-tolerant soybean genotypes remains a key breeding objective to sustain yield under water-limited environments (10, 11). Improving drought tolerance in soybean should not only focus on survival under stress but also on stabilising yield through enhanced physiological efficiency and water-use optimisation throughout the crop's life cycle (8, 11–13).

Enhancing drought resistance remains a strategic yet complex objective in modern plant breeding programmes aimed at developing climate-resilient crops. In this context, the present study focuses on elucidating the gene action governing various yield-associated and physiological traits in soybean under drought stress conditions. Specifically, it aims to dissect the genetic architecture underlying these traits to better understand their contribution to drought resilience and yield stability.

2. Materials and Methods

The experimental materials comprised segregating populations derived from four soybean [*Glycine max* (L.) Merr.] genotypes, namely JS 22 12, JS 22 16, EC 333901 and NRC 142, which served as parental lines for hybridisation. Among these, JS 22 12, JS 22 16 and EC 333901 were obtained from the soybean breeder, at the Agricultural Research Station, Kasbe Digraj, Sangli, while NRC 142 was procured from ICAR-Indian Institute of Soybean Research (IISR), Indore. The selected genotypes represented a diverse genetic background, with variation in yield potential and physiological traits relevant to the study objectives.

Hybridisation was carried out among these four genotypes to generate four distinct crosses (Table 1). The resulting F_1 seeds were selfed to advance the generations and obtain F_2 and F_3 segregating populations. The true hybrids were identified and confirmed using the distinctness, uniformity and stability (DUS) test by employing diagnostic marker traits characteristic of the respective male and female parents, such as flower colour, plant height, leaf shape, leaf colour, pod and stem pubescence colours. The resulting segregating generations were subsequently utilised for genetic analysis of yield-contributing and physiological traits.

Table 1. Arrangement of four crosses

Cross	**Female parent (P_1)**	×	**Male parent (P_2)**
Cross I	JS 22 12	×	EC 333 901
Cross II	JS 22 16	×	EC 333 901
Cross III	JS 22 12	×	NRC 142
Cross IV	JS 22 16	×	NRC 142

The experiment was conducted following a randomised block design (RBD) with 3 replications. All 5 generations (P_1, P_2, F_1, F_2 and F_3) of each cross were sown at a spacing of 45 × 10 cm. The plot size for each cross was 5 × 5 m and in each plot, nine rows, viz., one row each of P_1, P_2 and F_1 and three rows each of F_2 and F_3, were sown. Two irrigations were provided: one at sowing and the second 15 days after sowing (DAS) as life-saving measures. Drought conditions prevailed from the flowering stage, as clear-cut cracks in the soil were observed during this period. The total average rainfall during whole drought trial (February–May 2025) was estimated as 0.10 mm; therefore, a rainout shelter was not used. The maximum temperature was of 34.5 ºC, as recorded by the Meteorological Department of Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri, Ahilyanagar. Standard agronomic practices, including timely intercultural operations and fertiliser applications, were adopted to ensure uniform crop growth.

Observations were recorded under drought stress conditions on eight yield-contributing and six physiological traits. Data were collected from 30 randomly selected plants each from the parents (P_1 and P_2) and F_1 generations and from 300 randomly selected plants each from the F_2 and F_3 generations across all four crosses. In each replication, 10 plants of each parent, 10 plants of F_1, 100 plants of F_2 and 100 plants of F_3 were randomly selected for recording observations. The statistical analysis was performed using WINDOW STAT software, a facility provided by MPKV, Rahuri.

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Canopy temperature depression

Canopy temperature was measured using an infrared thermometer (model FLUKE 64 MAX) between 11.00 am and 12.00 pm in degrees Celsius (ºC) at the pod-filling stage. The infrared thermometer was kept at a height of 50 cm from the plant and 1 m away from the plot and the angle was kept constant throughout the observations. If the canopy was low, the angle was adjusted accordingly to avoid capturing the ground. Canopy temperature depression (CTD) was calculated in degrees Celsius (ºC) using the following formula (14).

CTD = Air temperature (ºC) - Canopy temperature (ºC)

Chlorophyll content

Chlorophyll content was recorded in bright sunshine using a SPAD meter at the pod-filling stage and expressed as a percentage (15). Observations were recorded at three levels, viz., upper, middle and bottom leaves and the average was then calculated.

Delayed leaf senescence (DLS) /wilting score at seed-filling stage (1–5 scale)

Delayed leaf senescence/wilting score was recorded at the seed-filling stage by observing individual plants morphologically. The following scale was used to score the plants (16).

No wilting = 0

Few top leaves showed wilting = 2

Half of the leaves showed wilting = 3

Severe wilting (up to 75 % of leaves shows wilting) = 4

Severely wilted = 5

Relative leaf water content (RLWC)

Relative leaf water content was calculated as a percentage (%) using the following formula (17):

Leaf area

Leaf area (LA) was measured using a leaf area meter through image analysis and expressed in square millimetre (mm^2). Leaves were collected from the plants, placed on the leaf area meter and the LA was recorded.

Harvest index

Harvest index was estimated as a percentage (%) using the following formula (18):

3. Results and Discussion

The visualized picture of final evaluation trial of soybean plot 45 and 75 days after sowing depicted in Fig. 1 and Fig. 2.

Analysis of variance

The ANOVA for eight yield and yield-contributing traits revealed a significant amount of variation for these characters among the five generations of the four crosses studied under drought conditions, as indicated in Table 2.

The ANOVA revealed a considerable amount of variation in ten physiological traits contributing to drought tolerance among the five generations of the four crosses studied under drought conditions, as shown in Table 2.



Fig. 1. Evaluation trial at 45 days after sowing (DAS) under drought conditions during summer 2025.

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Fig. 2. Evaluation trial at 75 days after sowing (DAS) under drought conditions during summer 2025.

Table 2. Analysis of variance (ANOVA) for yield, yield-contributing and physiological characters of four soybean crosses under drought conditions

Characters	Cross I		Cross II		Cross III		Cross IV	
	Generations	Error	Generations	Error	Generations	Error	Generations	Error
	4	8	4	8	4	8	4	8
Days to 50 % flowering (DF)	41.32**	0.15	49.79**	0.11	51.08**	0.22	52.39**	0.23
Days to physiological maturity (DM)	196.74**	0.53	203.72**	1.23	175.31**	0.55	172.54**	0.19
Plant height (PH)	901.80**	0.17	780.98**	0.19	1176.8**	0.21	1050.72**	0.18
Primary branches/plant (PBP)	9.61**	0.01	10.52**	0.02	6.07**	0.01	5.94**	0.01
No. of pods/plant (NPP)	90.33**	0.11	67.75**	0.09	1860.85**	0.49	1786.11**	0.52
No. of pods/cluster (NPC)	0.64**	0.01	0.86**	0.01	1.19**	0.03	1.46**	0.02
Seed index (SI)	8.63**	0.00	8.06**	0.01	8.37**	0.01	16.88*	3.23
Yield/plant (YPP)	13.33**	0.01	13.10**	0.03	9.02**	0.01	8.84**	0.02
Canopy temperature depression (CTD)	3.67**	0.00	4.03**	0.01	0.09**	0.01	0.30**	0.01
Chlorophyll content (CC)	116.65*	0.83	2.38**	0.10	2.12**	0.05	2.10**	0.01
Delayed leaf senescence (DLS)	5.85**	0.01	5.03**	0.02	0.08*	0.01	0.18**	0.01
Relative water content (RWC)	40.04**	0.28	49.98**	0.12	4.58**	0.60	3.59*	0.59
Leaf area (LA)	12046.20**	126.9	11181.31	486.8	88082.22**	212.5	62262.7**	386.7
Harvest index (HI)	79.28**	0.04	88.25**	0.06	64.59**	0.03	74.84**	0.04

Note: * and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Mean performance analysis

The current investigation presents the mean performance of each yield and yield-associated trait and physiological trait for five generations, viz., P_1, P_2, F_1, F_2 and F_3, for four crosses under drought conditions. The results of the mean performance are presented in Tables 3–10.

Mean performance analysis for yield and yield-associated traits under drought conditions

The current investigation exhibits the mean performance of each yield and yield-associated trait for five generations, viz., P_1, P_2, F_1, F_2 and F_3 for four crosses under drought conditions. The results of the mean performance are presented in Tables 3–6.

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Table 3. Mean performance of different generations for yield and yield-contributing characters in Cross I (JS 22 12 × EC 333 901) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Days to 50 % flowering (DF)	30.8 ± 0.14	39.7 ± 0.18	39.1 ± 0.17	36.1 ± 0.24	37.3 ± 0.23
Days to physiological maturity (DM)	81.6 ± 0.21	101.9 ± 0.27	100.8 ± 0.15	94.0 ± 0.53	96.5 ± 0.40
Plant height (PH)	11.0 ± 0.04	52.9 ± 0.05	52.9 ± 0.05	43.7 ± 0.91	42.3 ± 0.91
Primary branches/plant (PBP)	2.5 ± 0.09	6.7 ± 0.09	6.9 ± 0.08	5.4 ± 0.10	4.9 ± 0.10
No. of pods/plant (NPP)	22.1 ± 0.16	35.4 ± 0.11	36.2 ± 0.14	28.6 ± 0.28	28.6 ± 0.28
No. of pods/cluster (NPC)	2.7 ± 0.13	3.6 ± 0.09	3.2 ± 0.10	3.0 ± 0.06	3.3 ± 0.06
Seed index (SI)	3.8 ± 0.03	7.7 ± 0.03	7.9 ± 0.02	5.6 ± 0.09	5.0 ± 0.09
Yield/plant (YPP)	5.9 ± 0.04	10.8 ± 0.06	11.2 ± 0.09	8.8 ± 0.13	8.8 ± 0.13

Table 4. Mean performance of different generations for yield and yield-contributing characters in Cross II (JS 22 16 × EC 333 901) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Days to 50 % flowering (DF)	30.8 ± 0.17	40.7 ± 0.14	40.1 ± 0.18	37.1 ± 0.26	36.6 ± 0.26
Days to physiological maturity (DM)	81.0 ± 0.18	101.7 ± 0.23	100.6 ± 0.12	93.7 ± 0.44	94.0 ± 0.42
Plant height (PH)	14.1 ± 0.04	53.0 ± 0.04	53.5 ± 0.04	36.6 ± 0.83	35.9 ± 0.81
Primary branches/plant (PBP)	2.4 ± 0.11	6.8 ± 0.09	6.2 ± 0.09	4.5 ± 0.10	4.5 ± 0.10
No. of pods/plant (NPP)	24.1 ± 0.15	35.2 ± 0.14	36.3 ± 0.14	29.4 ± 0.25	28.9 ± 0.26
No. of pods/cluster (NPC)	2.4 ± 0.09	3.7 ± 0.12	3.2 ± 0.11	3.0 ± 0.06	3.1 ± 0.06
Seed index (SI)	4.0 ± 0.04	7.8 ± 0.03	8.0 ± 0.02	5.7 ± 0.08	5.1 ± 0.09
Yield/plant (YPP)	6.0 ± 0.05	10.5 ± 0.05	10.0 ± 0.09	8.8 ± 0.13	8.2 ± 0.12

Table 5. Mean performance of different generations for yield and yield-contributing characters in Cross III (JS 22 12 × NRC 142) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Days to 50 % flowering (DF)	30.0 ± 0.13	40.0 ± 0.15	40.3 ± 0.16	36.3 ± 0.27	36.3 ± 0.29
Days to physiological maturity (DM)	80.8 ± 0.16	99.5 ± 0.19	99.1 ± 0.12	92.2 ± 0.45	91.5 ± 0.47
Plant height (PH)	11.0 ± 0.05	58.9 ± 0.05	59.0 ± 0.05	37.7 ± 1.08	39.2 ± 0.99
Primary branches/plant (PBP)	2.4 ± 0.09	5.9 ± 0.12	5.6 ± 0.10	4.0 ± 0.09	3.7 ± 0.09
No. of pods/plant (NPP)	22.2 ± 0.20	38.2 ± 0.14	38.9 ± 0.23	33.7 ± 1.30	32.8 ± 1.31
No. of pods/cluster (NPC)	2.6 ± 0.11	4.0 ± 0.11	4.2 ± 0.09	3.5 ± 0.06	3.5 ± 0.06
Seed index (SI)	3.8 ± 0.03	7.8 ± 0.03	7.6 ± 0.02	5.6 ± 0.08	5.1 ± 0.09
Yield/plant (YPP)	5.9 ± 0.03	9.9 ± 0.06	10.2 ± 0.10	8.2 ± 0.12	8.0 ± 0.11

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Table 6. Mean performance of different generations for yield and yield-contributing characters in Cross IV (JS 22 16 × NRC 142) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Days to 50 % flowering (DF)	30.2 ± 0.14	40.1 ± 0.17	40.7 ± 0.20	37.1 ± 0.28	36.4 ± 0.29
Days to physiological maturity (DM)	81.1 ± 0.20	99.7 ± 0.19	99.1 ± 0.14	91.2 ± 0.45	91.9 ± 0.47
Plant height (PH)	14.0 ± 0.04	59.0 ± 0.05	59.5 ± 0.04	38.5 ± 0.99	37.5 ± 0.97
Primary branches/plant (PBP)	2.3 ± 0.11	5.7 ± 0.11	5.9 ± 0.10	4.1 ± 0.09	4.0 ± 0.09
No. of pods/plant (NPP)	24.2 ± 0.15	38.3 ± 0.13	38.5 ± 0.10	33.2 ± 1.47	32.5 ± 1.32
No. of pods/cluster (NPC)	2.03 ± 0.09	4.0 ± 0.11	3.9 ± 0.12	3.6 ± 0.06	3.8 ± 0.06
Seed index (SI)	3.9 ± 0.04	7.6 ± 0.03	8.0 ± 0.04	5.5 ± 0.08	5.5 ± 0.08
Yield/plant (YPP)	6.0 ± 0.05	9.9 ± 0.06	9.5 ± 0.11	8.3 ± 0.10	8.3 ± 0.10

Table 7. Mean performance of different generations for physiological traits in Cross I (JS 22 12 × EC 333 901) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Canopy temperature depression (CTD)	1.6 ± 0.06	4.2 ± 0.06	4.0 ± 0.05	3.0 ± 0.07	2.5 ± 0.07
Chlorophyll content (CC)	37.6 ± 0.08	35.9 ± 0.08	35.7 ± 0.09	37.8 ± 0.08	37.2 ± 0.09
Delayed leaf senescence (DLS)	4.6 ± 0.09	1.2 ± 0.08	1.5 ± 0.08	2.9 ± 0.08	3.2 ± 0.08
Relative water content (RWC)	71.9 ± 0.07	80.8 ± 0.08	81.2 ± 0.09	77.6 ± 0.23	76.4 ± 0.23
Leaf area (LA)	2500.1 ± 1.46	7399.5 ± 1.50	7108.2 ± 7.86	5692.5 ± 119.14	5805.0 ± 117.54
Harvest index (HI)	13.6 ± 0.04	25.6 ± 0.05	25.1 ± 0.05	19.0 ± 0.26	19.4 ± 0.25

Table 8. Mean performance of different generations for physiological traits in Cross II (JS 22 16 × EC 333 901) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Canopy temperature depression (CTD)	1.5 ± 0.04	4.2 ± 0.06	4.4 ± 0.06	3.1 ± 0.06	3.4 ± 0.07
Chlorophyll content (CC)	37.8 ± 0.08	35.7 ± 0.07	35.8 ± 0.09	36.8 ± 0.24	37.1 ± 0.07
Delayed leaf senescence (DLS)	4.4 ± 0.11	1.3 ± 0.08	1.4 ± 0.11	2.9 ± 0.08	2.2 ± 0.08
Relative water content (RWC)	70.9 ± 0.06	80.8 ± 0.08	81.0 ± 0.07	77.4 ± 0.24	77.9 ± 0.22
Leaf area (LA)	2690.5 ± 0.36	7400 ± 1.52	7199.5 ± 1.53	5715.3 ± 278.18	5482.1 ± 114.21
Harvest index (HI)	12.7 ± 0.03	25.7 ± 0.05	25.2 ± 0.05	19.0 ± 0.26	19.6 ± 0.29

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Table 9. Mean performance of different generations for physiological traits in Cross III (JS 22 12 × NRC 142) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Canopy temperature depression (CTD)	1.7 ± 0.04	2.0 ± 0.04	2.1 ± 0.05	1.5 ± 0.03	1.8 ± 0.03
Chlorophyll content (CC)	38.7 ± 0.09	36.2 ± 0.07	36.7 ± 0.08	37.9 ± 0.08	37.1 ± 0.08
Delayed leaf senescence (DLS)	4.4 ± 0.11	4.3 ± 0.13	4.4 ± 0.13	4.1 ± 0.05	4.1 ± 0.05
Relative water content (RWC)	70.9 ± 0.99	73.7 ± 0.13	74.0 ± 0.04	73.8 ± 0.09	73.4 ± 0.12
Leaf area (LA)	2502 ± 1.52	3805.1 ± 2.04	3795.3 ± 2.16	3389.1 ± 36.72	3164.2 ± 36.26
Harvest index (HI)	13.6 ± 0.03	24.5 ± 0.04	24.9 ± 0.05	19.6 ± 0.25	18.8 ± 0.24

Table 10. Mean performance of different generations for physiological traits in Cross IV (JS 22 16 × NRC 142) under drought conditions

Generations	P_1	P_2	F_1	F_2	F_3
Canopy temperature depression (CTD)	1.8 ± 0.04	2.0 ± 0.04	2.2 ± 0.04	1.6 ± 0.01	1.4 ± 0.01
Chlorophyll content (CC)	38.8 ± 0.07	36.8 ± 0.07	36.1 ± 0.08	37.8 ± 0.08	37.1 ± 0.07
Delayed leaf senescence (DLS)	4.6 ± 0.09	4.2 ± 0.14	4.2 ± 0.15	4.0 ± 0.05	3.9 ± 0.04
Relative water content (RWC)	71.0 ± 0.05	73.9 ± 0.04	73.0 ± 1.01	72.2 ± 0.14	72.8 ± 0.11
Leaf area (LA)	2702.7 ± 2.10	3805.4 ± 2.15	3504.8 ± 2.30	3318.1 ± 41.05	3180.2 ± 32.39
Harvest index (HI)	12.7 ± 0.04	24.4 ± 0.05	24.9 ± 0.05	19.4 ± 0.24	20.0 ± 0.23

Days to 50 % flowering (DF): The P_1 (30–30.8 days) parental line consistently exhibited the shortest time to flowering when compared to all other crosses or parental lines involved in the study. In contrast to P_1, the P_2 (40.7 days and 40 days) parent line showed a delayed flowering time, specifically when it was involved in Crosses I and II, while F_1 flowered late (40.3 days and 40.7 days) in Crosses III and IV.

Days to physiological maturity (DM): The P_1 parent (80.8 –81.6 days), consistently showing early maturity across all crosses, suggests that it possesses genetic factors that confer this trait. Conversely, the P_2 parent (101.7–101.9 days for Crosses I and II and 99.5–99.7 days for Crosses III and IV), consistently exhibiting late maturity across all studied crosses, indicates that it carries genetic determinants for delayed development. There is no drought escape mechanism, as it is only related to maturity.

Plant height (PH): In all crosses, only P_1 (11–14.1 cm) was consistently shorter across all generations. Specifically, Cross I recorded P_2 (52.9 cm) and F_1 (52.9 cm) as taller, while Crosses II, III and IV exhibited taller F_1 plants (53.5 cm, 59 cm and 59.5 cm respectively).

Primary branches per plant (PBP): Among all parental lines and filial generations, P_1 (2.3–2.5) had fewer branches than the others in all crosses. Meanwhile, the F_1 (6.9 and 5.9) generation exhibited the highest number of branches in Crosses I and IV, whereas P_2 (6.8 and 5.9) had the highest number of branches in Crosses II and III.

Number of pods per plant (NPP): The P_1 (22.2–24.2) parent exhibited a lower NPP across all crosses, while the F_1 (35.2–38.3) generation recorded the highest NPP among the four crosses. However, the F_2 and F_3 generations were found to be intermediate due to segregation and environmental effects.

Number of pods per cluster (NPC): P_2 (3.6, 3.7 and 4.0) exhibited a higher NPC in Crosses I, II and IV, whereas the F_1 (4.2) generation showed this trait in Cross III. P_1 (2.3–2.7) displayed the fewest pods and the segregating generations were intermediate (3.0–3.8).

Seed index (SI): The P_1 (3.8–4.0 g/100 seeds) generation recorded the lowest SI, while the F_1 (7.9, 8.0 and 8.0 g/100 seeds) generation had higher SI values for Crosses I, II and IV and the P_2 (7.8 g/100 seeds) generation showed higher values for Cross III.

Yield per plant (YPP): Across all crosses, P_1 (5.9–6.0 g/plant) consistently exhibited low yields. The F_1 (11.2 g/plant and 10.2 g/plant) generation showed high yields in Crosses I and III, whereas P_2 (10.5 g/plant and 9.9 g/plant) demonstrated high yields in Crosses II and IV.

Mean performance analysis for physiological traits under drought conditions

The current investigation evaluated the mean performance of each physiological trait for five generations, viz., P_1, P_2, F_1, F_2 and F_3, for four crosses under drought conditions. The results of the mean performance are presented in Tables 7–10.

Canopy temperature depression : The highest CTD was recorded for P_2 (4.2 ºC) in Cross I and for the F_1 generation (4.4 ºC, 2.1 ºC and 2.2 ºC) in Crosses II, III

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and IV. Conversely, the lower CTD was recorded for P_1 (1.6 ºC and 1.5 ºC) in Crosses I and II, while the lowest values were observed in the F_2 generation (1.5 ºC) for Cross III and the F_3 generation (1.4 ºC) for Cross IV. Higher CTD indicates lower canopy temperature and vice versa; hence, a high CTD value is beneficial and indicative of drought tolerance.

Chlorophyll content : Lower chlorophyll content values were estimated for the F_1 generation (35.7 % and 36.1 %) in Crosses I and IV, while low amounts were recorded for P_2 (35.7 % and 36.2 %) in Crosses II and III. Conversely, higher amounts of chlorophyll were recorded for P_1 (37.8 %, 38.7 % and 38.8 %) in Crosses II, III and IV and for the F_2 generation (37.8 %) in Cross I.

Delayed leaf senescence

The lowest scores for a particular trait were recorded for P_2 (1.2 and 1.3) in Crosses I and II, for the F_2 (4.1) and F_3 (4.1) generations in Cross III and for the F_3 generation (3.9) in Cross IV. All individuals with these low scores demonstrated a strong capacity for thriving under drought conditions. Conversely, higher scores were attained by the P_1 (4.4–4.6) across all crosses, including the F_1 generation (4.4) in Cross III. All individuals exhibiting these higher scores shed their leaves prematurely, up to maturity.

Relative water content : Higher relative water content was recorded for the F_1 generation (81.2 %, 81 % and 74 %) in Crosses I, II and III, while P_2 (73.9 %) exhibited the highest RWC in Cross IV. Conversely, the lowest RWC was observed in P_1 (70.9–71.9 %) across all crosses.

Leaf area : The lowest LA was recorded for P_1 (2500.1–2702.7 mm^2) across all crosses, while the largest was recorded for P_2 (3805.1–7400 mm^2) in every instance. A larger LA likely led to the interception of more radiation, which in turn resulted in higher photosynthesis.

Harvest index (HI): A high HI was recorded for P_2 (25.6 % and 25.7 %) in Crosses I and II and for the F_1 generation (24.9 %) in Crosses III and IV, suggesting a good convergent ability of biomass into seeds. The lowest HI was recorded for P_1 (12.7–13.6 %) across all crosses.

Estimation of scaling tests and chi-square (χ^2) tests for yield, yield-associated and physiological traits in four soybean crosses under drought conditions

The results of yield, yield-contributing and physiological traits studied under drought conditions are presented in Table 11 and 12 respectively.

If either scaling test C or D is found to be significant, along with a significant chi-square (χ^2) test, then it is considered that epistasis is present.

In the context of yield-related traits, Cross I indicated that all traits were found significant for individual and joint scaling tests, except NPC. Cross II showed non-significance for PBP and YPP. Cross III indicated non-significance for NPC and SI while Cross IV gave non-significance for PBP and NPC. However, all remaining yield-related traits were found significant for the scaling tests in each cross.

In the case of physiological traits, Cross I demonstrated non-significance of the scaling test for CC and LA, Cross II for CC, Cross III for CTD and DLS, while Cross IV demonstrated non-significance for RWC. However, all remaining traits in the respective crosses represented significance in the scaling test.

Those traits that showed significance in the scaling test were studied using the five-parameter model, as they confirmed the presence of epistasis, while those that exhibited non-significance in the scaling test were studied using three-parameter model, as they lacked epistasis.

Table 11. Estimation of scaling tests and chi-square (χ2) tests for yield and yield-contributing characters in four soybean crosses under drought conditions

Characters	Cross I JS 22 12 × EC 333 901			Cross II JS 22 16 × EC 333 901			Cross III JS 22 12 × NRC 142			Cross IV JS 22 16 × NRC 142		
	C	D	χ^2	C	D	χ^2	C	D	χ^2	C	D	χ^2
DF	−5.67**	3.86**	32.38*	−4.76**	2.65*	17.97*	−5.33**	2.98*	22.48*	−5.35**	2.49*	19.30*
DM	−9.09**	6.32**	19.49*	−9.28**	4.39**	27.16*	−10.23**	1.24^{ns}	34.67*	−14.24**	3.72*	62.21*
PH	−34.95**	1.73^{ns}	110.95*	−30.89**	5.79^{ns}	95.83*	−37.09**	11.38**	77.42*	−41.01**	5.87^{ns}	121.92*
PBP	−5.00**	−0.21^{ns}	138.95*	−4.85^{ns}	−0.04^{ns}	120.37^{ns}	−3.54**	−0.30^{ns}	72.62*	−3.15^{ns}	−0.41^{ns}	56.98^{ns}
NPP	−12.34**	−0.02^{ns}	132.14*	−13.90**	−1.47^{ns}	211.56*	−53.50**	−4.50^{ns}	139.18*	−59.48**	1.32^{ns}	130.15*
NPC	−1.86^{ns}	−0.30^{ns}	29.79^{ns}	−1.36**	0.08^{ns}	15.08*	−0.59^{ns}	0.54^{ns}	14.5^{ns}	0.38^{ns}	1.75^{ns}	34.05^{ns}
SI	−5.02**	−0.63^{ns}	255.07*	−4.67**	−0.17^{ns}	232.05*	−4.56^{ns}	−0.04^{ns}	216.96^{ns}	−9.43*	−0.62*	312.8*
YPP	−3.77**	1.24*	49.60*	−4.16^{ns}	0.85^{ns}	61.42^{ns}	−3.36**	−0.41^{ns}	57.20*	−3.72**	0.79*	61.12*

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively. ns = not significant DF = days to 50 % flowering, DM = days to physiological maturity, PH = plant height, PBP = primary branches/plant, NPP = number of pods/plant, NPC = number of pods/cluster, SI = seed index, YPP = yield/plant.

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Table 12. Estimation of scaling tests and chi-square (χ2) tests for physiological traits in different soybean crosses under drought conditions

Characters	Cross I JS 22 12 × EC 333 901			Cross II JS 22 16 × EC 333 901			Cross III JS 22 12 × NRC 142			Cross IV JS 22 16 × NRC 142		
	C	D	χ^2	C	D	χ^2	C	D	χ^2	C	D	χ^2
CTD	−1.72**	−0.56**	84.14*	−1.06**	0.02^{ns}	19.69*	0.61^{ns}	−0.10^{ns}	9.81^{ns}	1.25**	0.38*	41.90*
CC	2.77^{ns}	−0.65^{ns}	18.31^{ns}	1.90^{ns}	−0.97^{ns}	15.20^{ns}	2.63**	0.92^{ns}	44.43*	1.89**	−0.59^{ns}	20.36*
DLS	2.96**	0.14^{ns}	77.70*	2.46**	0.35^{ns}	69.88*	−0.86^{ns}	−0.44^{ns}	6.20^{ns}	−0.71*	−0.37^{ns}	4.95*
RWC	−7.71**	−1.19**	376.53*	−7.65**	−1.39**	374.17*	−0.31*	0.24*	0.61*	−0.74^{ns}	0.25^{ns}	2.79^{ns}
LA	-2599.25^{ns}	1524.52^{ns}	20.02^{ns}	−5191.79**	−87.43^{ns}	100.66*	−232.06**	1280.22**	101.2*	−595.27 **	97.79**	103.5*
HI	−11.38**	−0.97^{ns}	276.37*	−13.58**	−0.78^{ns}	350.77*	−16.21**	−3.33**	452.85*	−21.65 **	−7.88^{ns}	67.11*

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively. ns = not significant, CTD = canopy temperature depression, CC = chlorophyll content, DLS = delayed leaf senescence, RWC = relative water content, LA = leaf area, HI = harvest index.

Estimation of gene action and genetic parameters

The knowledge of gene action behind any trait is a prerequisite for deciding the selection pattern and breeding method. Hence, to determine the gene action, the five-parameter model was used. It gave estimates of five genetic parameters, viz., mean (*m*), additive (*d*), dominance (*h*), additive × additive (*i*) and dominance × dominance (*l*). When *h* and *l* have opposite signs with significant values, duplicate epistasis is present, while when *h* and *l* have similar signs with significant values, complementary epistasis is present.

The findings of the genetic parameters for all four crosses under drought conditions for yield-contributing and physiological traits are presented in Tables 13–20.

Estimation of gene action and genetic parameters for yield and yield-associated traits under drought conditions

The results for a total of eight yield and yield-attributing characters studied in five generations of four crosses under drought conditions are presented in Tables 13–16 respectively.

Days to 50 % flowering (DF): In the case of Crosses I and IV, a significant mean (*m*) effect of high magnitude was observed. The additive (*d*) main effect and the additive × additive (*i*) interaction effect were found to be significantly negative in the desirable direction. This indicated the predominance of additive gene action under drought conditions. A previous study reported a similar type of epistasis in soybean for the flowering trait (19).

In the case of Crosses II and III, this trait exhibited a significant mean (*m*) of high magnitude. Additive effects (*d*) and additive × additive interactions (*i*) were significantly negative in the desirable direction, whereas dominance × dominance interactions (*l*) were significantly positive but in an undesirable direction. Therefore, the flowering character demonstrated the predominance of additive gene action alongside duplicate epistasis.

Table 13. Estimation of gene effects for yield and yield-contributing characters in Cross I (JS 22 12 × EC 333 901) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	l	
Days to 50 % flowering (DF)	36.13**	−4.45**	1.14	−12.42**	12.71**	-
Days to physiological maturity (DM)	94.01**	−10.17**	3.31*	−26.06**	20.54**	Complementary
Plant height (PH)	33.69**	20.93**	−13.98	48.84**	−48.90**	-
Primary branches/plant (PBP)	4.42**	−2.08**	1.49	−4.86**	6.39**	-
No. of pods/plant (NPP)	28.47**	6.74**	−6.31**	-	-	-
No. of pods/cluster (NPC)	2.98**	−0.47**	0.53	−1.04**	2.08**	-
Seed index (SI)	5.55**	−1.95**	1.68**	−4.31**	−5.86**	Duplicate
Yield/plant (YPP)	8.79**	2.48**	1.32	6.42**	−6.68**	-

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

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Table 14. Estimation of gene effects for yield and yield-contributing characters in Cross II (JS 22 16 × EC 333 901) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	l	
Days to 50 % flowering (DF)	37.05**	−4.98**	−2.42**	−12.53**	9.88**	Duplicate
Days to physiological maturity (DM)	93.67**	−10.35**	4.75	−25.17**	18.22**	-
Plant height (PH)	35.55**	−19.51**	10.55**	−48.03**	48.91**	Complementary
Primary branches/plant (PBP)	4.27**	−2.28**	2.24**	-	-	-
No. of pods/plant (NPP)	28.99**	5.53**	4.33**	12.40**	−16.56**	Duplicate
No. of pods/cluster (NPC)	3.04**	−0.65**	0.30	−1.58**	1.92**	-
Seed index (SI)	5.73**	1.90**	1.34	4.46**	−5.99**	-
Yield/plant (YPP)	8.35**	−2.43**	2.60**	-	-	-

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Table 15. Estimation of gene effects for yield and yield-contributing characters in Cross III (JS 22 12 × NRC 142) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	l	
Days to 50 % flowering (DF)	36.30**	−4.97**	−2.39**	−12.81**	11.09*	Duplicate
Days to physiological maturity (DM)	92.17**	−9.35**	6.69**	−21.23**	15.28	-
Plant height (PH)	37.69**	−23.95**	10.22	−61.66**	64.62**	-
Primary branches/plant (PBP)	4.01**	−1.75**	1.10	−3.89**	4.32**	-
No. of pods/plant (NPP)	53.68**	30.02**	−23.77**	65.95**	−65.32**	Complementary
No. of pods/cluster (NPC)	3.29**	−0.72**	0.84**	-	-	-
Seed index (SI)	5.66**	−1.92**	2.14**	-	-	-
Yield/plant (YPP)	8.22**	1.99**	−2.08**	4.27**	−3.94**	Complementary

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Table 16. Estimation of gene effects for yield and yield-contributing characters in Cross IV (JS 22 16 × NRC 142) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	l	
Days to 50 % flowering (DF)	36.57**	−4.92**	3.10	−12.38**	10.45**	-
Days to physiological maturity (DM)	91.19**	−9.30**	3.91**	−23.46**	23.96**	Complementary
Plant height (PH)	37.48**	−22.48**	11.72**	−55.71**	62.50**	Complementary
Primary branches/plant (PBP)	3.75**	−1.71**	1.52**	-	-	-
No. of pods/plant (NPP)	53.0**	−29.08**	−18.46**	−68.96**	81.07**	Duplicate
No. of pods/cluster (NPC)	3.32**	−0.86**	0.80**	-	-	-
Seed index (SI)	5.60**	−1.85**	−3.17**	−4.85**	11.75**	Duplicate
Yield/plant (YPP)	8.21**	−1.94**	1.29	−5.02**	6.01**	-

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

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Table 17. Estimation of gene effects for physiological traits in Cross I (JS 22 12 × EC 333 901) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	H	i	l	
Canopy temperature depression (CTD)	3.03**	−1.29**	1.12	−2.92**	3.02**	-
Chlorophyll content (CC)	37.80**	7.34**	−1.02	21.17**	−6.33*	-
Delayed leaf senescence (DLS)	2.87**	1.68**	−1.30**	3.72**	3.80**	Duplicate
Relative water content (RWC)	76.35 **	−4.45**	4.47**	-	-	-
Leaf area (LA)	4949.79**	−2449.70**	2457.59**	-	-	-
Harvest index (HI)	19.12**	−6.00**	−3.66**	−14.55**	19.41**	Duplicate

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Table 18. Estimation of gene effects for physiological traits in Cross II (JS 22 16 × EC 333 901) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	l	
Canopy temperature depression (CTD)	3.09**	−1.39**	0.02	−4.16**	4.56**	-
Chlorophyll content (CC)	36.82**	1.03**	−1.57**	1.49**	−1.06	-
Delayed leaf senescence (DLS)	2.56**	1.58**	−1.07	3.55**	−3.69**	-
Relative water content (RWC)	77.42**	−4.96**	2.31**	−12.71**	−9.55**	Duplicate
Leaf area (LA)	5044.92**	−2355.08**	2354.56**	-	-	-
Harvest index (HI)	18.98**	−6.51**	−3.53**	−15.80**	18.97**	Duplicate

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Table 19. Estimation of gene effects for physiological traits in Cross III (JS 22 12 × NRC 142) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	L	
Canopy temperature depression (CTD)	1.76**	−0.19**	0.15	−0.41**	0.77**	-
Chlorophyll content (CC)	37.93**	0.95**	−0.97	1.94**	−2.82**	-
Delayed leaf senescence (DLS)	4.12**	0.09	−0.40*	-	-	-
Relative water content (RWC)	73.26**	−1.43*	0.25	−4.27**	2.38**	-
Leaf area (LA)	3189.09**	−651.56**	477.94**	−1477.89**	1512.76	-
Harvest index (HI)	19.59**	−5.54**	−3.73**	−13.11**	13.79*	Duplicate

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

Table 20. Estimation of gene effects for physiological traits in Cross IV (JS 22 16 × NRC 142) under drought conditions

Characters	Genetic parameters					Type of epistasis
	m	d	h	i	L	
Canopy temperature depression (CTD)	2.02**	−0.30**	0.12**	−1.02**	−0.64**	Duplicate
Chlorophyll content (CC)	37.80**	0.98**	−0.42	2.56**	−3.31**	-
Delayed leaf senescence (DLS)	4.14**	0.28**	−0.32*	-	-	-
Relative water content (RWC)	72.46**	−1.48**	1.41**	-	-	-
Leaf area (LA)	3318.07**	−551.33**	425.40**	−1228.04**	1096.14**	Complementary
Harvest index (HI)	19.37**	−5.99**	−3.51**	−14.67**	15.16**	Duplicate

* and ** indicate significance at $p \leq 0.05$ and $p \leq 0.01$ respectively.

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A preponderance of additive gene action has also been reported for soybean (20, 21). Similar results were previously observed for the same trait in the cross JS 2034 × TGX 709–50E (19).

Days to physiological maturity

Under drought conditions, Cross I indicated significant mean (*m*) of high magnitude. All the genetic parameters were significant; however, the additive (*d*) main effect and additive × additive (*i*) interaction effect were significantly positive in the desirable direction. This indicated the preponderance of additive gene action with complementary epistasis, based on the similar signs of h and l. Earlier, additive gene action in soybean was reported for the cross Monetta × MACS 450 and for the cross JS 2034 × TGX 709–50E (19, 20).

In Crosses II, III and IV, the mean (*m*) effect was found to be significant for this trait under drought conditions. The additive (*d*) and additive × additive (*i*) effects were significantly negative in the desirable direction, whereas *h* and *l* effects were significantly positive but in the undesirable direction. These results indicate a preponderance of additive gene action. A predominance of additive gene effects in the cross combination Monetta × MACS 450 has been reported previously (20).

Plant height

In the restricted irrigation trial, a significantly high mean (*m*) effect was recorded for this trait. All genetic parameters were significant, but the additive (*d*), additive × additive (*i*) and dominance × dominance (*l*) effects were significantly positive. Therefore, both additive and non-additive gene actions played a role, with a duplicate type of non-allelic interaction in Cross I. A previous finding indicated that both additive and dominance gene effects were significant for PH (20).

A significant mean (*m*) effect was observed under drought conditions for Cross II. All genetic components were found to be significant; however, only the dominance (*h*) main effect and the dominance × dominance (*l*) interaction effect were significantly positive, while the others were negative. This indicates that the trait was primarily governed by dominance gene action and exhibited complementary epistasis under drought conditions for Crosses II and IV. Dominance gene action for this trait has been reported previously, whereas complementary epistasis has also been documented (19, 20).

A significant mean (*m*) effect of high magnitude was recorded under drought conditions. The additive (*d*) effect and additive × additive (*i*) interaction effect were found to be significantly negative, whereas the dominance × dominance (*l*) effect was significantly positive, indicating the preponderance of dominance gene action for Cross III.

Primary branches per plant

Under drought conditions, a significant mean (*m*) effect of high magnitude was recorded. The additive (*d*) main effect and additive × additive (*i*) interaction effect were found to be significantly negative, while the dominance × dominance (*l*) interaction effect was significantly positive for Cross I. Hence, dominance gene action was prevalent for this trait and selection was suggested to be delayed until later generations.

Under drought conditions, a significant mean (*m*) effect of high magnitude was observed. The additive (*d*) main effect was significantly negative, whereas the dominance (*h*) main effect was significantly positive, indicating that the trait was predominantly governed by dominant gene action for Cross II. A similar finding has been reported previously for the cross Monetta × MACS 450 (20).

In the scenario of Cross III, the dominance × dominance (*l*) interaction effect was significantly positive, indicating the predominance of dominance gene action. A previous finding reported the predominance of dominance gene action in the cross Monetta × MACS 450, indicating the importance of non-additive genetic effects in the inheritance of the trait (20).

In the case of Cross IV, both the additive (*d*) main effect and the dominance (*h*) main effect were found to be significant, while no interaction effects were present. Hence, both additive and dominance gene actions played a role in governing this trait. Therefore, a population improvement approach was considered the appropriate choice for its improvement. Previous findings indicate that both additive and non-additive gene actions influence branching in soybean (2).

Number of pods per plant : The mean (*m*) effect was significantly high in magnitude for Cross I. The additive (*d*) component was recorded significantly positive with a high magnitude, with no interaction effects. Additive gene action was predominant for this trait under the drought trial. Similar results have been reported previously, indicating consistency across different soybean cross combinations (20, 22).

The drought study concluded that the mean (*m*) effect was of high magnitude and statistically significant. All genetic components were significant; however, only the additive (*d*) main effect and the additive × additive (*i*) interaction component were significantly positive with high magnitude. Therefore, additive gene action, along with duplicate epistasis, played a crucial role in governing this trait for Cross II. Previous findings indicated that dominance gene action plays a crucial role in controlling NPP (20, 21).

In the case of Cross III, the additive (*d*) main effect and additive × additive (*i*) components were significantly positive. This indicated the presence of additive gene action and the similar signs of *h* and *l*

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reflected complementary epistasis under drought conditions. Previous findings indicate that additive gene action plays a crucial role in controlling this trait (22, 23).

In case of Cross IV, only the dominance × dominance (*l*) interaction effect was significant, while the others were significant but in an undesirable direction. Therefore, dominance gene action made the major contribution to this trait and duplicate epistasis was recorded, so delayed selection was considered rewarding for Cross IV. A previous finding indicated that both additive and dominance gene effects were significantly positive for this trait, with duplicate epistasis also playing an important role in its genetic control (20).

Number of pods per cluster : The drought trial recorded a significant mean (*m*) effect. The additive (*d*) main effect and additive × additive (*i*) interaction effect were significantly negative, while the dominance × dominance (*l*) component was significantly positive, suggesting that dominance gene action played a key role in this trait; therefore, selection was postponed in the case of Cross I. A previous finding indicated the preponderance of dominance gene action in controlling this trait (24).

In the context of Crosses II and III, a significant mean (*m*) effect of high magnitude was observed under the drought trial. The additive (*d*) main effect and additive × additive (*i*) interaction component were significantly negative, whereas the dominance × dominance (*l*) component was significantly positive. These results indicate that dominance gene action played a major role.

The dominance (*h*) main effect was significantly positive, indicating that the trait was predominantly governed by dominance gene action, while epistasis was absent in the case of Cross IV. Previous findings indicate that NPC are predominantly governed by dominance gene action, suggesting the importance of heterozygosity in the expression of this trait (22, 24, 25).

Seed index : In the case of Cross I, a significant mean (*m*) effect of high magnitude was recorded. All genetic parameters were significant; however, only the dominance (*h*) main effect was significantly positive under drought conditions. It indicated the major role of dominance effect along with duplicate epistasis. A major role of dominance gene action for this trait has been reported previously, indicating the importance of non-additive genetic effects in its inheritance (22, 23).

A highly significant mean (*m*) effect was observed for this trait. The additive (*d*) main effect and the additive × additive (*i*) interaction component were significantly positive, while the dominance × dominance (*l*) component was also significantly positive. This indicated that dominance gene action primarily governed the expression of the trait for Crosses II and III. A role of dominance gene action has also been reported in previous findings (22, 23).

In the scenario of Cross IV, the dominance × dominance (*l*) interaction effect was significantly positive. Hence, the trait was predominantly governed by dominance gene action with duplicate epistasis. A similar dominance × dominance (*l*) interaction for SI has been reported previously (2, 22, 23).

Yield per plant (YPP): A significant mean (*m*) effect of high magnitude was observed. The additive (*d*) main effect and additive × additive (*i*) interaction were significantly positive, while the dominance × dominance (*l*) interaction was significantly negative under drought conditions. The predominance of additive gene action was observed for this trait for Cross I. Additive gene action was found to be major in soybean yield as identified by previous researchers (2, 22).

A highly significant mean (*m*) effect with a large magnitude was observed for the trait under drought conditions. The additive (*d*) main component was found to be significantly negative, whereas the dominance (*h*) main effect was significantly positive, indicating that the trait was primarily influenced by dominance gene action for Cross II. A similar trend for yield-related traits has been reported previously (20, 25).

In the case of Cross III, the same trait was predominantly governed by additive gene action. Complementary epistasis was also observed, as indicated by the same signs of *h* and *l*.

The dominance × dominance (*l*) component was significantly positive, while the other components were negative. Therefore, the trait was predominantly governed by dominance gene action in Cross IV. A similar pattern of gene action for yield-related traits has been reported in previous findings (20, 23, 25).

Estimation of gene action and genetic parameters for physiological traits under drought conditions

The results for a total of six physiological characters in five generations of four crosses studied under drought conditions are presented in Tables 17–20 respectively.

Canopy temperature depression : Under drought conditions, the trait exhibited a significant mean (*m*) effect of high magnitude. The additive (*d*) and additive × additive (*i*) components were significantly negative, whereas the dominance × dominance (*l*) interaction component was significantly positive, indicating the presence of dominance gene action in Crosses I, II and III. A similar finding has been previously reported at the flowering and seed-filling stages in soybean (26). The dominance (*h*) main effect was significantly positive, indicating that dominance gene action played a vital role along with duplicate epistasis for Cross IV. Dominance gene action is crucial because many physiological traits controlling water use are governed by genes showing dominance effects.

Chlorophyll content : A highly significant mean (*m*) effect of large magnitude was observed under the drought trial.

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Both the additive (*d*) main effect and the additive × additive (*i*) interaction effect were significantly positive, indicating that additive gene action was predominant in the case of Crosses I and II. The additive (*d*) component and the additive × additive (*i*) interaction were significantly positive. Therefore, additive gene action was found to be prevalent in Crosses III and IV.

Delayed leaf senescence : The mean effect of the trait was found to be highly significant under drought conditions. All the genetic components were significant; however, only the dominance (*d*) main effect was significantly negative, but in a desirable direction. Therefore, DLS was primarily governed by dominance gene action. Selection in later generations was helpful in improving this trait for Crosses I, II, III and IV because such gene action makes it difficult to fix superior genotypes, so the breeding cycle takes time to fix that gene effect from interacting alleles.

Relative water content : Under drought conditions, a significant mean (*m*) effect of high magnitude was recorded. The additive (*d*) main effect was significantly negative, whereas the dominance (*h*) main component was significantly positive. This indicates that the trait was primarily governed by dominance gene action; therefore, selection should be practised accordingly, as no interaction effects were observed for Cross I.

However, dominance gene action also predominated in the case of Cross II along with duplicate epistasis. A same gene action has been previously reported for RWC in soybean (19).

In Cross III, the additive (*d*) component and the additive × additive (*i*) interaction were significantly negative, whereas the dominance × dominance (*l*) interaction effect was significantly positive, while in Cross IV the dominance main effect was significant. Hence, the trait was predominantly governed by dominance gene action.

Leaf area : A significant mean (*m*) effect of high magnitude was observed. The dominance (*h*) main effect was significantly positive under drought conditions. This indicated that dominance gene action played a vital role in controlling this trait and no interaction effects were detected in the case of Crosses I, II and III. For Cross IV, the dominance (*h*) main effect and the dominance × dominance (*l*) interaction effect were significantly positive, indicating that dominance gene action, along with complementary epistasis, was predominant.

Harvest index : A significant mean (*m*) effect of high magnitude was recorded under restricted irrigation conditions. All genetic parameters were found to be significantly negative, except for the dominance × dominance (*l*) interaction effect, which was significantly positive. Therefore, the trait was primarily governed by dominance gene action, while duplicate non-allelic interaction was also present for Crosses I, II, III and IV. Comparable results were previously reported in soybean, indicating consistency of the present findings with earlier studies and suggesting that similar genetic mechanisms may govern this trait across different genetic backgrounds and environmental conditions (27, 28).

4. Conclusion

Analysis of variance (ANOVA) revealed that all the traits evaluated in this investigation exhibited highly significant variation across four crosses under drought conditions. The yield and yield-contributing as well as physiological traits predominantly governed by additive gene action are heritable and fixable so they can be improved by selection in early generations, while those governed by dominance gene action are heritable but non-fixable in nature. Therefore, for the improvement of these traits, effective selection should be performed in the later segregating generations. Traits expressed under drought conditions that are governed by duplicate type gene interactions can be enhanced through biparental mating, whereas traits controlled by complementary epistasis, which is favourable for genetic improvement, can be effectively improved through simple selection, particularly in the later generations.

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Authors' contributions

SCS handled the entire experiment and manuscript preparation. CVP contributed to the planning of the experiment. SSD performed the statistical analysis. AVR was responsible for setting up the physiological observations. DMP provided the genotypes for the experiment. SGC contributed to the planning of the experiment and interpretation of the results. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

The authors do not have any conflict of interests to declare.

Ethical issues

None

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