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DISSECTING GENETIC VARIATION AND FREQUENCY DISTRIBUTION OF AGRONOMIC AND PHYSIOLOGICAL TRAITS IN WATERLOGGED SOYBEAN F₂ POPULATIONS: IMPLICATIONS FOR EARLY GENERATION SELECTION

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ABSTRACT

Waterlogging is a major abiotic constraint limiting soybean [*Glycine max* (L.) Merr.] productivity in rainfed systems. This study investigated phenotypic and physiological trait variability in an F₂ population derived from JS 335 (susceptible) × NRC 186 (tolerant) under waterlogged and control conditions. Evaluation was performed using 17 agro-morphological and physiological traits across 150 F₂ individuals and identify key indicators of waterlogging tolerance. Significant reductions in yield and biomass under stress were observed, notably for yield per plant (5.02 g vs. 9.31 g) and 100-seed weight (6.64 g vs. 13.63 g).

Substantial variability was observed across all traits, with wide ranges, moderate to high coefficients of variation and notable skewness and kurtosis traits such as yield per plant (YPP), number of pods per plant (NPC) and days to flowering (DFF). Distribution analyses revealed that traits such as plant height, NDVI, and shoot dry weight / duration ratio followed near-normal distributions under control, indicating additive gene action. However, under waterlogging, key traits like pods per plant, yield per plant, and foliar damage score showed positive skewness and leptokurtosis, supported by significant Kolmogorov–Smirnov (K–S) values—indicating dominance, epistasis, or gene × environment interaction. The presence of transgressive segregants in both favorable and stress environments highlights the potential for genetic improvement. SPAD chlorophyll content and shoot dry weight exhibited transgressive segregation, offering prospects for selection under stress.

Findings underscore the utility of early-generation selection for additive traits and delayed selection for traits under complex inheritance. This study provides a robust phenotypic foundation to advance waterlogging-tolerant soybean breeding through targeted selection strategies.

Key words : Soybean (*Glycine max*), Waterlogging stress, Genetic variability, Frequency distribution, Skewness and kurtosis, Non-additive gene action, Early generation selection, Abiotic stress tolerance.

Introduction

Soybean (*Glycine max* L.) ranks among the most vital leguminous crops worldwide, producing nearly 360 million tonnes of grain during the 2021–22 season. It serves as a major dietary component, offering around 40% protein and 20% vegetable oil, essential for both human and animal consumption (Sharmin *et al.*, 2024). In India, soybean remains integral to rainfed agricultural

systems in central and western regions, significantly impacting rural economies. Its role in biological nitrogen fixation further contributes to sustainable farming by improving soil fertility and reducing reliance on chemical fertilizers (Mannan *et al.*, 2022).

Despite these benefits, soybean production is often hampered by abiotic stresses, particularly waterlogging. Excessive soil moisture leads to oxygen depletion in the

root zone, impeding respiration, nodulation, and nutrient uptake, and ultimately restricting photosynthesis (Mustroph, 2018; Rajendran *et al.*, 2025). Waterlogged conditions manifest through chlorosis, stunted development, reduced biomass, poor nodulation and substantial yield losses (Sharmin *et al.*, 2024). Depending on cultivar and growth stage, yield reductions from flooding can vary widely—from 17% up to 80%—with the reproductive phase being especially sensitive (Adegoye *et al.*, 2023).

To mitigate these challenges, breeding for waterlogging tolerance is a strategic priority. Segregating populations such as the F_2 generation offer abundant genetic diversity and often display transgressive segregation, making them suitable candidates for phenotypic screening under both flooded and non-flooded environments (Sharmin *et al.*, 2024; Malik *et al.*, 2015). Estimating parameters like genotypic variance, broad-sense heritability and genetic advance enables the identification of traits suitable for selection and genetic improvement.

Studying frequency distributions, including skewness and kurtosis, provides insights into the underlying genetic architecture of traits. A symmetrical, slightly platykurtic distribution often indicates additive gene action—suggesting higher selection potential—whereas skewness may imply dominance effects or epistatic interactions (Malik *et al.*, 2015; Mustroph, 2018).

In addition, trait correlation analysis in early generations like F_2 assists in identifying reliable secondary traits for indirect yield selection. This is particularly valuable under waterlogged conditions, where direct yield selection is confounded by environmental variation. Traits such as pod number, root-shoot balance, or nodulation characteristics can serve as reliable proxies (Sharmin *et al.*, 2024 and Lian *et al.*, 2023).

While molecular tools such as QTL mapping and transcriptome profiling are advancing the understanding of waterlogging tolerance, conventional breeding continues to play a fundamental role—especially in low-resource settings. Phenotypic selection within diverse segregating populations provides a cost-effective path for developing resilient cultivars suited to local agro-ecological conditions.

Materials and Methods

Experimental Site and Parental Material

The present investigation was conducted at the Department of Agricultural Botany, Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri, Maharashtra, during four

cropping seasons: *Kharif* 2022–2023, *Summer* 2022–2023, *Kharif* 2023–2024 and *Summer* 2023–2024. The experimental site is situated in the rain-shadow zone of Western Maharashtra under semi-arid conditions.

Two contrasting soybean genotypes were selected based on their differential responses to waterlogging stress. JS 335, a waterlogging-susceptible variety, was used as the female parent, and NRC 186, a waterlogging-tolerant genotype, served as the male parent for the crossing programme.

Hybridization and Generation advancement

Experiment I: Hybridization programme

A cross was made between JS 335 (a waterlogging-sensitive genotype) and NRC 186 (a waterlogging-tolerant genotype) through manual hand emasculature and pollination across three seasons—*Kharif* 2022–2023, *Summer* 2022–2023 and *Kharif* 2023–2024—to ensure sufficient F_1 seed production. The crossing was conducted under field conditions, using designated male and female parental rows.

Experiment II: Generation advancement

The F_1 generation was raised and advanced during *Summer* 2022–2023 and *Kharif* 2023–2024. Selfed F_1 plants were used to develop the F_2 generation, which was evaluated during *Summer* 2023–2024. Generation advancement was facilitated using off-season fields, ensuring genetic purity and continuity of segregating material.

Experiment III: Evaluation under Waterlogging and control conditions

The evaluation of parents (P_1 , P_2), F_1 and F_2 generations was conducted during *Kharif* 2023–2024 under two contrasting pot-based environments: Control: Well-drained pots & Waterlogged: Standing water maintained continuously for 14–15 days at R1 (beginning bloom) and R4 (full pod) stages. The experiment was laid out in a Randomized Block Design (RBD) with three replications, each consisting of 30 pots. Each pot accommodated 3–4 plants. Around 150 F_2 plants were evaluated. Separate sets of pots were maintained for destructive sampling at specific growth stages to record physiological traits.

Data collection

Data on agronomic and yield-related traits were recorded across all generations (P_1 , P_2 , F_1 and F_2), including: Days to 50% flowering, Days to physiological maturity, Plant height (cm), Number of primary branches per plant, Number of clusters per plant, Number of pods

per cluster, Number of pods per plant, Number of seeds per pod, 100-seed weight (g), Grain yield per plant (g), Harvest index (%). In addition, 4 key physiological traits were assessed from selected pots at two critical reproductive stages (R₁ and R₄) to evaluate waterlogging tolerance: Shoot dry weight (g), Shoot leaf area (cm²), Chlorophyll content (SPAD values), Foliar damage score (1–9 visual scale). All observations were taken from randomly selected and tagged plants. Data were averaged and subjected to statistical analysis for interpretation of genetic variability under stress and control environments.

Statistical analysis

The collected data were subjected to statistical analysis to assess variability and identify significant differences among generations under both control and waterlogged conditions. Analysis of variance (ANOVA) was performed using the Randomized Block Design (RBD) layout to test the significance of differences for each trait. Descriptive statistics such as mean, range, standard deviation and coefficient of variation (CV) were computed for all recorded traits using SPSS v22.0.

Frequency distribution patterns were illustrated using histograms to assess the distribution and variability of traits. To evaluate the normality and genetic behaviour of traits, skewness and kurtosis were estimated following the method of Snedecor and Cochran (1989). The Kolmogorov–Smirnov (K–S) test was employed to confirm the normality of trait distributions in the F₂ population.

Results and Discussion

Comparative performance of parents (P₁, P₂) and F₁

Analysis of Table 1 simplifies that under control conditions, the female parent (JS 335, P₁) outperformed the male parent (NRC 186, P₂) in traits related to yield and agronomy—such as yield per plant (14.10 g vs. 11.12/g), harvest index and pod number. Conversely, in the waterlogged environment, NRC 186 (P₂) showed greater resilience, yielding significantly higher values for yield per plant (6.12 g vs. 3.90 g), SPAD chlorophyll content, and shoot dry weight. The F₁ mean frequently aligned between the two parents, showing partial dominance of favorable traits from P₁ under control and from P₂ under stress conditions.

These results underscore the contrasting adaptive value of each parent under different environments. This pattern aligns with findings in soybean where tolerant genotypes retain physiological functioning under flooding better than sensitive types (Adegoye *et al.*, 2023 and

Sharmin *et al.*, 2024).

Variability, Skewness and Kurtosis in the F₂ population

Descriptive statistics of the F₂ progeny from the cross JS 335 × NRC 186 were assessed under two contrasting environments: Control (well-drained) and Waterlogged. Table 2 summarizes the trait-wise data, including variability parameters and distribution characteristics.

Plant Height (PH)

- **Control:** Mean = 34.29 cm (Range: 20.17–57.07), CV = moderate
- **Waterlogged:** Mean = 27.18 cm (Range: 11.87–44.67), CV = 30.56%
- **Skewness and Kurtosis:** Near-normal distribution under both conditions; skewness ≈ 0, kurtosis slightly platykurtic under control (−0.61), ~−0.94 under stress
- **Interpretation:** Waterlogging clearly suppresses vegetative growth. Higher CV and slight deviation from normality under stress indicate additive gene action and transgressive segregants (Bassuony *et al.*, 2021 and Viswabharathy *et al.*, 2023).

Pods per Plant (NPP) and Seeds per Pod (NSP)

- **Control:** NPP = 31.63, NSP = 2.71
- **Waterlogged:** NPP = 18.60, NSP = 1.63; CVs > 30%
- **Skewness & Kurtosis:** Positive skew (NPP skew ~1.34), leptokurtic (~1.27) under waterlogging; NSP also positively skewed
- **Interpretation:** Strong environmental impact on reproductive traits. Skewed, peaked distribution reflects dominance or epistasis for adaptive traits. Similar patterns were described in soybean and blackgram by Sharmin *et al.* (2024) and Vadivel *et al.* (2019)

Grain yield per plant (GY) and 100 seed weight (HSW)

- **Control:** GY = 9.31 g, HSW = 13.63 g
- **Waterlogged:** GY = 5.02 g, HSW = 6.64 g; CVs increased
- **Skewness & Kurtosis:** GY skew = 1.23; kurtosis = 1.17 (leptokurtic) under stress
- **Interpretation:** Yield and seed size drastically reduced under stress. Distribution shifts imply dominance × additive interaction or major gene effects. Skewed, high-peaked distributions align with findings in soybean by Adegoye *et al.* (2023)

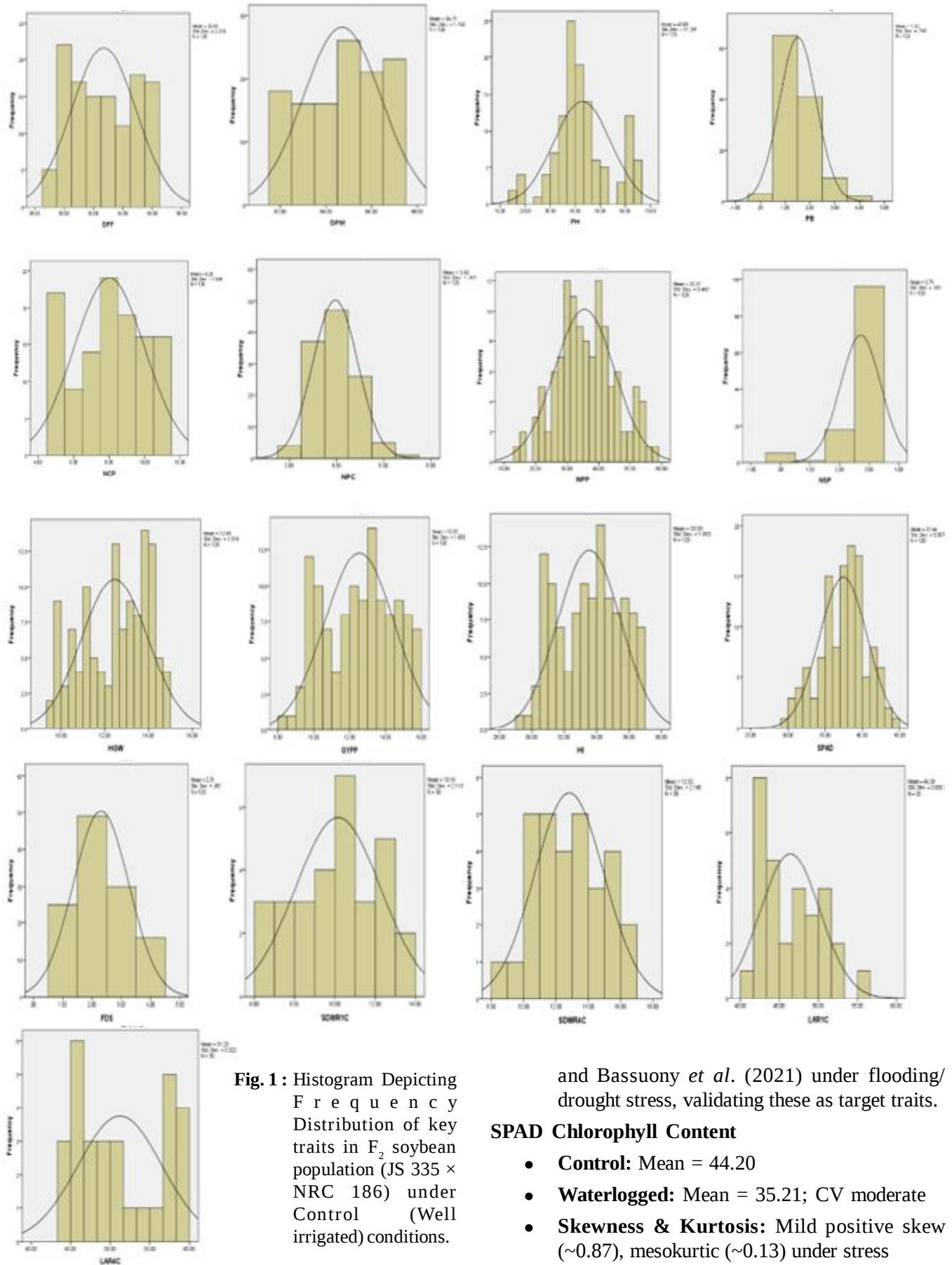


Table 1 : Mean values of parents and F₁ plants of the studied characters in Soybean cross JS335 × NRC 186.

S. no.	Characters	Stress Condition	P ₁ Mean	P ₂ Mean	t-value (P ₁ -P ₂)	F ₁ Mean
1.	Days to 50% flowering	Control	32.27	35.2	-19.71**	33.6
		Waterlogged	26.27	29.87	-11.27**	27.2
2.	Days to physiological maturity	Control	83.4	86.53	-17.02**	85.33
		Waterlogged	75.53	77.93	-4.66**	76.73
3.	Plant height (cm)	Control	35.43	40.93	-25.08**	38.09
		Waterlogged	26.06	37.13	-50.47**	30.51
4.	Number of primary branches per plant	Control	1.27	2	-3.33**	1.53
		Waterlogged	1.07	1.67	-4.47**	1.4
5.	Number of clusters per plant	Control	6.27	10.8	-8.72**	8.13
		Waterlogged	2.6	4.87	-12.16**	3.73
6.	Number of pods per cluster	Control	5.53	3.33	11.08**	4.13
		Waterlogged	2.73	3.73	-5.38**	3.33
7.	Number of pods per plant	Control	40.4	35.53	26.09**	37.33
		Waterlogged	15.07	20.33	-5.99**	18.47
8.	Number of seeds per pod	Control	3.8	2.33	9.41**	3.2
		Waterlogged	1.67	2.2	-2.58**	1.87
9.	Hundred seed weight	Control	12.23	14	-15.64**	13.36
		Waterlogged	5.75	7.35	-9.61**	6.91
10.	Yield per plant	Control	14.1	11.12	21.07**	12.65
		Waterlogged	3.9	6.12	-8.05**	5.47
11.	Harvest Index	Control	35.1	32.12	21.07**	33.65
		Waterlogged	24.9	32.12	-26.17**	31.47
12.	SPAD-Chlorophyll content	Control	35.43	40.93	-25.08**	38.09
		Waterlogged	26.23	36.88	-57.93**	35.14
13.	FDS-Foliar Damage Score (1-9)	Control	2.6	1.93	3.02**	2.47
		Waterlogged	7.47	2.47	27.20**	4.33
14.	Shoot dry weight at R1 stage	Control	10.42	12.85	-6.35**	11.27
		Waterlogged	1.24	2.48	-67.25**	2.12
15.	Shoot dry weight at R4stage	Control	14.04	15.77	-4.07**	14.1
		Waterlogged	0.88	1.87	-22.14**	1.21
16.	Leaf area at 30 days after sowing	Control	43.61	49.33	-27.84**	47.79
		Waterlogged	38.23	47.62	-20.75**	46.49
17.	Leaf area at 36 days after sowing	Control	49.14	55.93	-22.64**	53.92
		Waterlogged	42.14	50.98	-31.96**	46.97

- **Interpretation:** Water stress leads to pigment degradation. Moderate variation and distribution suggest quantitative control with possible physiological buffering. Retention of SPAD in tolerant lines (e.g., NRC 186) is crucial, as

supported by Mustroph (2018) and Sharmin *et al.* (2024)

Shoot Dry Weight (SDW) at R₁ and R₄ stages

- **Control:** R₁ = 2.32 g, R₄ = 3.24 g

Table 2 : Descriptive statistics for morphophysiological and yield traits under Control and Waterlogged conditions of F₂ population.

Characters	Stress condition	Mean	Std. Deviation	Skewness	Kurtosis	Range	Minimum	Maximum
Days to 50% flowering	Control	32.69	2.22	0.07	-1.32	7	29	36
	Waterlogged	26.45	2.44	1.78	5.13	15	22	37
Days to physiological maturity	Control	84.71	1.70	-0.21	-1.18	5	82	87
	Waterlogged	76.63	1.82	-0.11	-1.37	5	74	79
Plant height (cm)	Control	42.80	11.39	0.20	0.00	50.7	15.8	66.5
	Waterlogged	29.42	3.16	0.00	-1.24	10.78	24.09	34.87
Number of primary branches/plant	Control	1.52	0.74	0.94	1.02	4	0	4
	Waterlogged	1.38	0.87	0.48	-0.43	3	0	3
Number of clusters per plant	Control	8.01	2.00	-0.12	-1.13	6	5	11
	Waterlogged	3.48	1.00	-1.07	2.96	6	0	6
Number of pods per cluster	Control	3.95	0.95	0.40	0.10	5	2	7
	Waterlogged	3.05	0.77	-0.09	-0.66	4	1	5
Number of pods per plant	Control	35.51	9.44	0.10	-0.38	43	14	57
	Waterlogged	17.46	3.25	-0.07	-1.47	9	13	22
Number of seeds per pod	Control	2.71	0.69	-2.81	7.90	3	0	3
	Waterlogged	1.63	0.91	-0.23	-0.69	3	0	3
Hundred seed weight	Control	12.45	1.52	-0.33	-1.15	5.14	9.59	14.73
	Waterlogged	6.47	2.01	0.41	0.00	10.37	2.32	12.69
Yield per plant	Control	12.55	1.95	-0.16	-1.10	7.61	8.23	15.84
	Waterlogged	5.33	1.56	1.23	1.17	7.49	3.01	10.5
Harvest Index	Control	33.55	1.95	-0.16	-1.10	7.61	29.23	36.84
	Waterlogged	26.38	1.70	1.56	2.65	9	24.01	33.01
SPAD-Chlorophyll content	Control	37.44	3.21	-0.31	-0.27	15.68	29.27	44.95
	Waterlogged	34.53	2.56	0.04	-1.20	9	29.95	38.95
FDS-Foliar Damage Score (1-9)	Control	2.31	0.95	0.30	-0.79	3	1	4
	Waterlogged	4.28	1.93	0.02	-0.41	9	0	9
Shoot dry weight at R1 stage	Control	10.16	2.11	-0.24	-0.81	7.6	6.29	13.89
	Waterlogged	1.63	0.59	0.08	-0.88	2.08	0.63	2.71
Shoot dry weight at R4stage	Control	12.82	2.15	0.10	-0.83	8.17	8.56	16.73
	Waterlogged	1.04	0.39	0.50	-0.35	1.52	0.34	1.86
Leaf area at 30 days after sowing	Control	46.39	3.81	0.45	-0.74	14.63	40.7	55.33
	Waterlogged	43.00	4.81	0.24	-0.91	17.14	33.82	50.96
Leaf area at 36 days after sowing	Control	51.23	5.32	0.28	-1.53	15.72	43.85	59.57
	Waterlogged	45.71	6.18	0.40	-1.34	19.04	36.99	56.03

- **Waterlogged:** $R_1 = 1.71$ g, $R_4 = 1.21$ g; CVs increased
- **Skewness & Kurtosis:** Moderate positive skew (~ 0.74), platykurtic under stress

- **Interpretation:** Biomass decline at reproductive stages indicates compromised carbon allocation. Distribution suggests quantitative inheritance with environmental influence. Mustroph (2018)

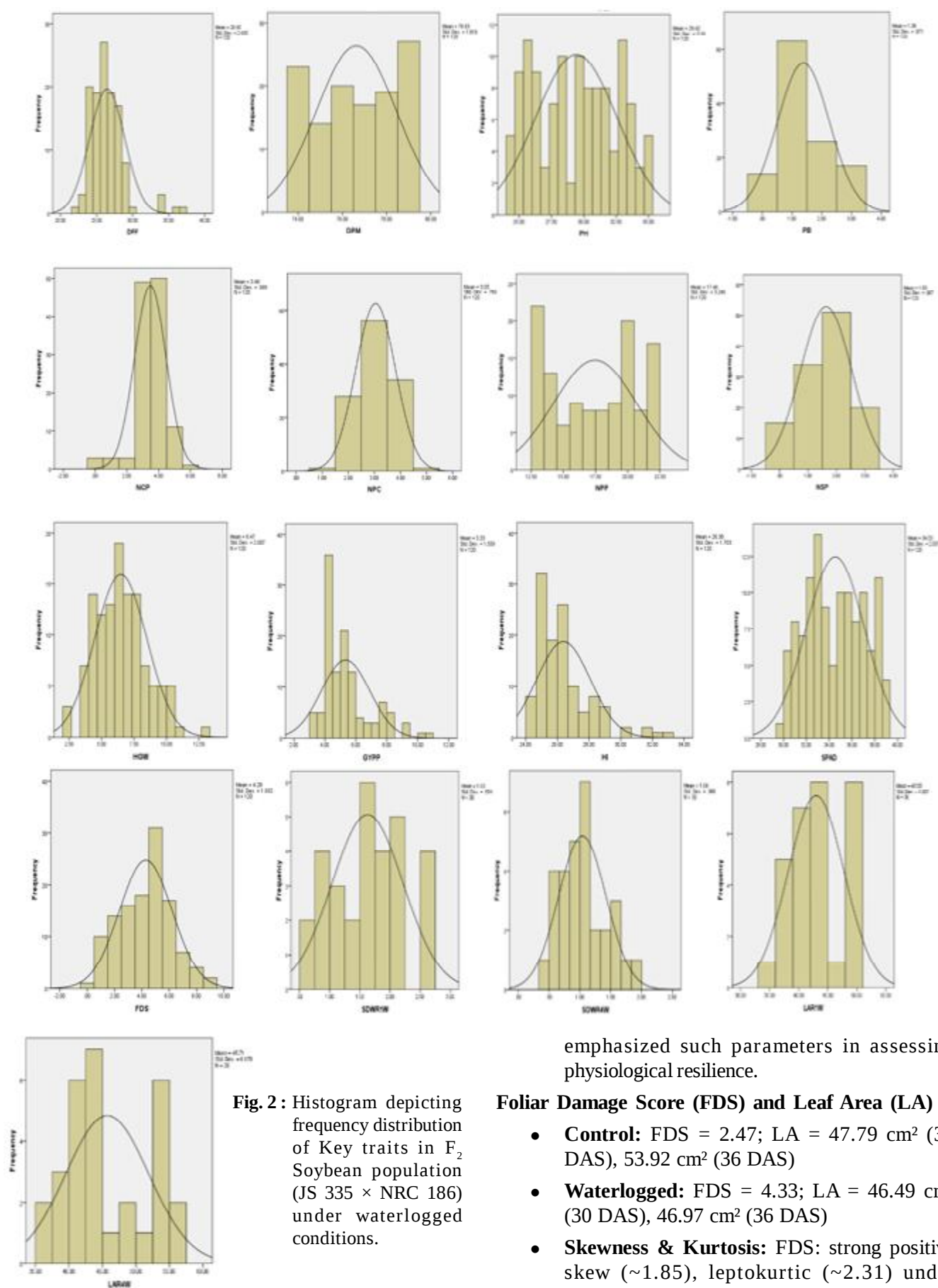


Fig. 2 : Histogram depicting frequency distribution of Key traits in F₂ Soybean population (JS 335 × NRC 186) under waterlogged conditions.

emphasized such parameters in assessing physiological resilience.

Foliar Damage Score (FDS) and Leaf Area (LA)

- **Control:** FDS = 2.47; LA = 47.79 cm² (30 DAS), 53.92 cm² (36 DAS)
- **Waterlogged:** FDS = 4.33; LA = 46.49 cm² (30 DAS), 46.97 cm² (36 DAS)
- **Skewness & Kurtosis:** FDS: strong positive skew (~1.85), leptokurtic (~2.31) under

waterlogging

- **Interpretation:** Visible foliar injury and reduced leaf expansion signal physiological stress. Strong skew and kurtosis in FDS suggest major gene effects or adaptive segregation (Adegoye *et al.*, 2023) support these findings.

Frequency Distribution Patterns and Genetic inference

The frequency distribution curves of F_2 progeny under control and waterlogged conditions revealed diverse segregation behaviors across traits, reflecting underlying gene action and environment-driven expression.

- Under control conditions, most traits such as plant height (PH), canopy temperature depression (CTD), NDVI and Shoot dry weight/duration followed near-normal distributions (skewness ≈ 0 ; kurtosis ≈ 0) and were statistically supported by non-significant Kolmogorov–Smirnov (K–S) values. This indicates additive gene effects and stable inheritance, making them suitable for early-generation selection. Similar findings were observed in F_2 populations of soybean and blackgram for traits with normal distribution patterns and low environmental distortion (Surendhar *et al.*, 2024; Rahmawati *et al.*, 2019; Reddy *et al.*, 2023).
- In contrast, under waterlogging stress, several traits including number of pods per plant (NPBP), yield per plant (YPP), days to 50% flowering (DFF), and number of primary branches (NPB) exhibited significant deviation from normality in the K–S test, combined with positive skewness and leptokurtosis. This suggests non-additive gene action, possibly due to epistasis, gene $\times$ environment interaction, or stress-induced segregation distortion (Tanksley, 1993; Mahendra, 2010). Similar patterns have been documented in blackgram and greengram under abiotic stress, where dominance and epistatic effects were evident in skewed distributions (Vadivel *et al.*, 2019; Kanavi *et al.*, 2020; Sri Subalakhshmi *et al.*, 2024).
- The presence of transgressive segregants in traits such as SPAD chlorophyll content, shoot dry weight, and 100 seed weight under stress indicates polygenic inheritance, and offers scope for selection of superior recombinants under adverse conditions. This phenomenon aligns with the findings of Manju Devi *et al.* (2021) and Silva

et al. (2015) in legume F_2 populations, where traits like biomass and seed weight under stress showed complex inheritance and greater selection potential.

- Traits showing highly skewed or peaked distributions under waterlogging (e.g., foliar damage score, pod number) may benefit from delayed selection in later segregating generations (F_2/F_4), due to potential dominance or epistatic effects. This approach is supported by studies in cowpea and cotton F_2 populations showing that skewed traits often require advanced generation stabilization (Hussainbi *et al.*, n.d.; Sri Subalakhshmi *et al.*, 2024).

Overall, the K–S test results, combined with visual distribution patterns and moment statistics (skewness, kurtosis), provide a quantitative foundation to infer genetic control. These results reinforce earlier reports in soybean and legumes under flooding stress (e.g., Sharmin *et al.*, 2024; Bassuony *et al.*, 2021), emphasizing that understanding trait-wise distribution behavior aids in optimizing generation-wise selection intensity and strategy.

Biological Significance and Breeding Implications

- **Contrast in Parental Performance:** JS 335 excels under control; NRC 186 performs better under waterlogging. F_1 hybrids follow parental trend with partial dominance effect.
- **High Variability Under Stress:** Elevated CV and wide range for key traits reflect potential presence of *transgressive segregants*—individuals outperforming parental lines ideal candidates for early-generation selection.
- **Indirect Selection Markers:** Traits such as GY, NPP, SPAD and SDW at R_4 stages serve as reliable indicators for tolerance breeding.

Distribution Patterns imply Mixed Gene Action:

Skewed, leptokurtic distributions for yield traits suggest both additive and non-additive genetic control, supporting a dual-phase breeding approach—early-generation screening followed by line stabilization.

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Conflict of interest

The authors declare no conflict of interest.

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