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YIELD PERFORMANCE OF TROPICAL SOYBEAN LINES CARRYING *pdh1* GENE UNDER DROUGHT STRESS DURING FLOWERING TO POD FORMATION

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SUMMARY

Soybean (*Glycine max* L.) production often experiences constraints from drought stress, which significantly reduces yield in tropical areas. The *pdh1* gene, known to support pod-shattering resistance, has shown significant potential for enhancing drought tolerance. Therefore, this study aimed to examine the performance of tropical soybean genotypes carrying the *pdh1* gene in response to drought stress during flowering to pod formation. A randomized complete block design with factorial arrangement had three replications. The factors included 25 genotypes and two water supply treatments. The water supply treatment consisted of D0=±80% and D1=±50% field capacity (FC), corresponding to soil water potentials of -0.47 and -1.42 MPa, respectively. The yield-related traits' analysis used 15 drought tolerance indices. The results showed AP21 and AP46 lines with the *pdh1* gene were considerably high-yielding and drought-tolerant genotypes. Substantial associations of yield in stress (Ys) and normal condition (Yn) were evident between genotypes with high geometric mean production (GMP), mean production (MP), stress tolerance index (STI), yield index (YI), and low stress susceptibility index (SSI). The results showed genotypes carrying the *pdh1* gene can potentially increase drought tolerance in soybeans. The high yield under drought primarily referred to better retention of pod numbers, seed numbers, and seed size.

Keywords: Soybean (*G. max* L.), water deficit conditions, long juvenile, seed yield, drought tolerance indices, reproductive stages

Key findings: Soybean (*G. max* L.) genotypes carrying the *pdh1* gene showed the highest potential for enhancing drought tolerance in soybeans. Principal component and biplot analyses confirmed that indices, such as high GMP, high MP, STI, and YI, and low SSI, emerged as effective measures for selecting high-performance genotypes under drought stress conditions.

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INTRODUCTION

Soybean (*Glycine max* [L.] Merrill) is a major global crop, with cultivation in tropical regions, such as Indonesia, expanding to meet the growing demand for food and feeds (Saryoko *et al*., 2017; Xu *et al*., 2022). However, productivity in these regions faces challenges from photoperiod sensitivity, as soybeans originally have an adaptation to temperate climates with longer day lengths (Gupta *et al*., 2021). The development of genotypes carrying the *long juvenile* (*lj*) gene has enabled soybeans to adapt to low-latitude environments by extending the vegetative phase, lengthening seed-filling periods, and increasing seed yield (dos Santos Silva *et al*., 2017; Tasma *et al*., 2018). Given the *lj* gene provides the foundation for tropical adaptation, productivity still encounters hindrances from environmental stresses, which require additional genetic improvement.

Soybean growth also entails high effects from environmental stress, including drought, which is becoming more frequent and severe due to climate change (Wibisono *et al*., 2024). Drought stress during reproductive growth stages, mainly at flowering to pod formation, can drastically reduce yield (Desclaux *et al*., 2000). Beyond reducing yield directly, drought stress also accelerates pod drying, which increases the risk of pod shattering and amplifies yield losses (Funatsuki *et al*., 2014). This indicates that drought and pod shattering are not separate problems but interconnected challenges that often occur simultaneously in tropical dryland environments.

Pod shattering resistance is an important trait in soybean improvement programs, particularly in dryland environments characterized by severe drought, low precipitation, high temperatures, and low humidity (Bara *et al*., 2013). The *pod dehiscence1* (*pdh1*) gene has succeeded in its identification as a key determinant of pod shattering resistance (Funatsuki *et al*., 2014; Tasma *et al*., 2021). Numerous studies have since reported advances in understanding pod indehiscence, including the role of pod morphology and lignin content (Bara *et al*., 2013; Madureira *et al*., 2023), QTL and marker-assisted selection strategies (Jia *et al*., 2022), and comparative investigations in related legumes (Murgia *et al*., 2017). Interestingly, the presence of *pdh1* not only reduces shattering risk but also has reports of being more frequent in soybeans grown in dry or low-precipitation regions (Yong *et al*., 2023). As the exact mechanism linking *pdh1* to drought response remains unclear, its occurrence in dryland environments suggests that pod indehiscence may provide indirect adaptive advantages in water-limited conditions (Funatsuki *et al*., 2014; Dou *et al*., 2023). This pattern proposes *pdh1* may confer adaptive advantages not only by preventing pod shattering but also by enhancing drought resilience.

Several studies have used yield-based methods under both optimal and stress conditions (Akbar *et al*., 2019) to assess drought tolerance. Indices for drought tolerance commonly served to identify stable and high-performing genotypes across conditions (Sarkar *et al*., 2025). The use of multiple indices has revealed an improvement in the accuracy of selection for drought tolerance, specifically when the basis of line screening was on yield performance (Hanume *et al*., 2024).

Based on the discussion above, this study aimed to examine the performance of tropical soybean genotypes carrying the *pdh1* gene under drought stress from flowering to pod formation. The specific objectives are to a) assess the effect of drought stress on yield and yield components, b) determine the appropriate tolerance indices for identifying drought-tolerant genotypes, and c) identify superior genotypes with enhanced drought tolerance.

MATERIALS AND METHODS

Genotypes and experimental procedure

The said experiment on soybeans (*G. max* L.) proceeded in a screenhouse at NRIA, Bogor, Indonesia, with controlled environmental conditions, from November 2023 to April 2024.

Table 1. Characteristics of soybean genotypes evaluated for flowering time, juvenility, pod-shattering resistance, and gene group classification.

No.	Genotypes	Genetic background[a]	Flowering time (days)	FTG[b]	Long juvenility trait[c]	Pod-shattering resistance[d]	GRP[e]
1	GRO	Gro	30.0	1	–	–	0
2	ANJ	Anj	38.0	2	–	+	0
3	DER	Der	36.5	2	–	–	0
4	MEL	Mel	38.5	2	+	+	0
5	AP17	Gro × Mel	42.0	3	+	–	2
6	AP21	Gro × Mel	41.5	3	+	+	1
7	AP16	Gro × Mel	40.0	3	+	–	2
8	AP19	Gro × Mel	42.5	3	+	–	2
9	AP33	Gro × Mel	42.5	3	+	–	2
10	AP38	Gro × Mel	41.0	3	+	–	2
11	AP28	Gro × Mel	40.0	3	+	+	1
12	AP32	Gro × Mel	41.0	3	+	–	2
13	AP35	Gro × Mel	42.0	3	+	–	2
14	AP18	Gro × Mel	41.5	3	+	+	1
15	AP26	Gro × Mel	42.0	3	+	+	1
16	AP3	Gro × Mel	41.0	3	+	–	2
17	AP29	Gro × Mel	47.0	4	+	+	1
18	AP30	Gro × Mel	47.0	4	+	–	2
19	AP46	Gro × Ver	48.0	4	+	+	1
20	AP49	Gro × Gly	49.0	4	+	–	2
21	AP24	Gro × Mel	49.5	4	+	–	2
22	AP9	Gro × Mel	49.5	4	+	–	2
23	VER	Ver	49.0	4	+	+	0
24	AP39	Gro × Mel	53.0	5	+	–	2
25	AP58	Gro × Par	54.0	5	+	–	2

[a]Gro = Grobogan, Anj = Anjasmoro, Der = Dering, Mel = Melrose, Ver = Vernal, Gly = Glycine H, Par = Paranagoiana, [b]FTG = flowering time groups, 28–30 days = group 1, 36.5–38.5 days = group 2, 40–42.5 days = group 3, 47–49.5 days = group 4, 53–55 days = group 5, [c]Long juvenility trait = has *long juvenile* gene (+) or absent (–), [d]*Pod-shattering resistance* = has *pod dehiscence 1* (*pdh1*) gene (+) or absent (–), [e]GRP = group gene, 0 = check varieties, 1 = *lj* and *pdh1* genes present, 2 = *pdh1* gene absent, *lj* gene present.

The study design used a randomized complete block design (RCBD) with three replications. The factorial arrangement consisted of two factors: soybean genotypes and water supply treatments. The first factor comprised 25 genotypes (20 soybean F_6 lines and five check varieties) (Table 1), while the second factor included a well-watered control (D0, ±80% FC) and drought stress treatment (D1, ±50% FC). Experimental units used totaled 150, and each unit consisted of three polybags containing fertile soil media.

Soybean genotypes' classification reached five groups (FTG1–FTG5) based on the flowering time similarities, namely, late, medium, or early flowering time. Late-flowering genotypes had the earliest planting, with early ones planted the latest to synchronize drought treatment stages together. Genotypes with flowering time group (FTG) 5 entailed planting first, followed by genotypes from FTG 4 (5 days after FTG 5), FTG 3 (11 days after FTG 5), FTG 2 (14 days after FTG 5), and FTG 1 (23 days after FTG 5). Planting four seeds per polybag before thinning them 10 days after planting (DAP) ensured the retention of only two healthy plants.

A planting media comprising topsoil, goat manure, and sand (1:1:1 w/w), prepared earlier, got filled into a polybag (20 cm diameter, 45 cm height), each weighing 10 kg. At planting time, fertilization comprised NPK 14-14-14 Osmocote (2.5 g per polybag) (Djanaguiraman *et al.,* 2012). Applying foliar fertilizer Gandasil D (1 g/L water) continued weekly, starting at 14 DAP for three weeks during the vegetative phase. After flowering, the treatment of foliar fertilizer Gandasil B (1 g/L water) ensued weekly for three weeks. Pest control implementation was weekly using Decis (1 mL/L water) and Caleb Tin (1 g/L water) (Dyah *et al*., 2024). Harvesting proceeded at the full maturity stage, when 90% of pods matured (Fehr and Caviness, 1977).

Drought stress evaluation and microclimatic conditions

Drought stress evaluation took place using nine polybags without plants, each containing 10 kg of fertile soil. A gravimetric method, as applied to the specified polybags, sought to determine soil weight at 80% and 50% FC. Soil water potential measurement at a 20 cm soil depth used a WP4 Dewpoint Potential Meter. The results of drought stress evaluation reached further usage in treatments. Applying drought stress on treated genotypes occurred, maintaining it from flowering to pod formation stages by adjusting watering based on daily monitoring results of the planting media weight. Microclimatic conditions in the screen house incurred recording every 15 minutes using a temperature and humidity data logger (BTH 81, BSide, China).

Yield and yield components

At the full maturity growth stage (Fehr and Caviness, 1977), seed yield, pod number, seed number, and seed size received measuring from three plants per experimental unit. Seed moisture content sustained adjustment to approximately 12% using the seed moisture meter (Jinan Precision, China).

Data analysis

All data organization and tabulation used Microsoft Excel 2019 (Microsoft, USA). Plant characteristic evaluation under control and drought treatments underwent the analysis of variance (ANOVA), followed by Tukey's test at a 0.05 significance level, using the SPSS 22 software. Responses to drought got expressed using the 15 drought-tolerance indices (El-Azeem *et al*., 2023). These include yield stability index (YSI), stress susceptibility index (SSI), tolerance index (TOL), stress tolerance index (STI), mean production (MP), geometric mean production (GMP), and harmonic mean (HM). Others were sensitivity drought index (SDI), drought resistance index (DI), relative drought index (RDI), stress susceptibility percentage index (SSPI), yield index (YI), drought tolerance efficiency (DTE), modified 1 stress tolerance index (K1STI), and modified 2 stress tolerance index (K2STI).

RESULTS AND DISCUSSION

Drought stress evaluation

In the soybean (*G. max* L.) experiment, the control treatment, maintained at approximately 80% FC, corresponded to a soil media weight of ±12.7 kg and a soil water potential of ± -0.47 MPa at 20 cm depth (Figure 1). Under drought stress (±50% FC), soil weight decreased to ±10.2 kg with a water potential of ± -1.42 MPa (Figure 1). The transition from -0.47 MPa to -1.42 MPa occurred over approximately 10 days without watering in the screenhouse, with an average daily water loss of ±200 mL.

The results are consistent with Lestari *et al*. (2023), who reported that a soil water potential of -1.46 MPa reflects drought stress conditions equivalent to 50% FC. Similarly, Desclaux *et al*. (2000) used soil water potential levels ranging from -0.05 MPa (control) to below -0.75 MPa (stress) to impose drought intensity in soybeans, supporting the relevance of soil water potential as a criterion for drought simulation.

Microclimatic conditions

Average daily air temperature and relative humidity (RH) during the experiment were 28.5 °C and 83.0%, respectively. Although there were differences in planting times among the groups, all genotypes encountered relatively similar air temperature and humidity throughout the growing season.

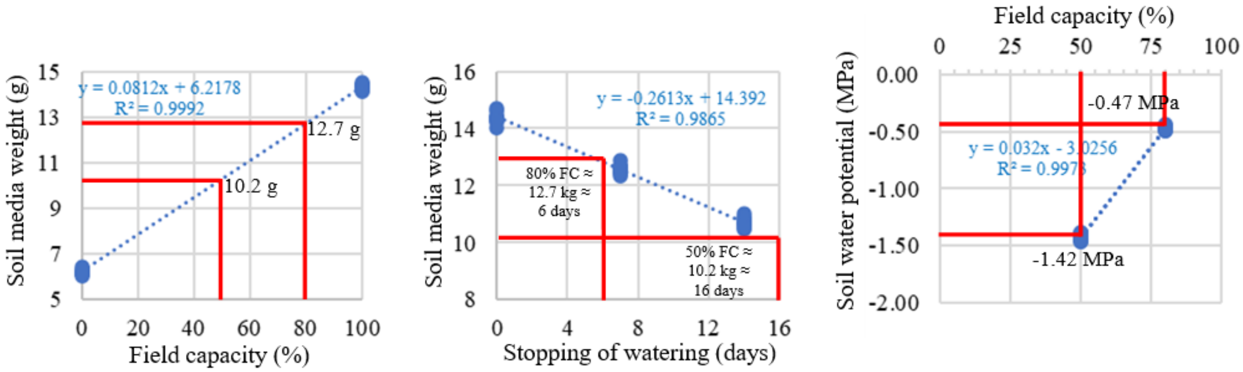

Figure 1. Validation of drought levels (50% and 80% field capacity) and corresponding soil water potential at a depth of 20 cm from the soil surface.

Table 2. ANOVA (mean square) for yield and yield components of 25 soybean genotypes under normal and drought stress treatments.

Characters	Genotype (G)	Environment (E)	G × E
Seed yield	55.088**	537.976**	3.534**
Pod number	695.825**	4962.096**	122.227**
Seed number	2188.113**	23754.982**	362.879**
Seed size	27.623**	142.838**	1.508**

*: significant at the 0.05 level, **: significant at the 0.01 level.

The temperature in tropical regions, such as Indonesia, remains stable year-round, ranging from an average of 27.7 °C to 27.9 °C in Banten Province (Saryoko *et al*., 2017). This study showed warmer growing conditions than those shown in subtropical regions. For example, in the U.S., the optimal soybean production period, June–October 2024, had an average temperature of 22.5 °C (NOAA, 2025).

Yield and yield components

Analysis of variance showed that genotype, environment (normal and drought stress), and their interaction (G × E) had highly significant effects ($p < 0.01$) on soybean yield and related components (Table 2). The significant environmental effect showed that drought stress substantially reduced plant performance, particularly for seed yield, pod number, and seed number. In addition, the significant G × E interaction demonstrated that genotypes responded differently across environments, highlighting the importance of evaluating lines under contrasting conditions to identify drought-tolerant soybean genotypes (Akbar *et al*., 2019; Mahadevaiah *et al*., 2021).

Seed yield of the 25 soybean genotypes varied significantly among the samples. The significant overall seed yield reductions appeared with those grown under a drought stress treatment (Figure 2). Varieties Melrose (MEL) and Dering (DER) showed stable yield performance under normal and drought stress treatments. However, the two genotypes (MEL and DER) displayed a relatively low yield average under drought conditions (7.45 and 7.5 g, respectively). The variety Grobogan (GRO), on the other hand, had a sharp yield decline (6.85 g), showing high susceptibility to drought stress. AP21 and AP46 lines, carrying the *pdh1* gene, exhibited least yield reductions under drought treatment (12.35 and 11.8 g, respectively), and outperformed seed yield of all other genotypes. This suggests the two genotypes (AP21 and AP46) have the potential as candidates for drought-tolerant genotypes.

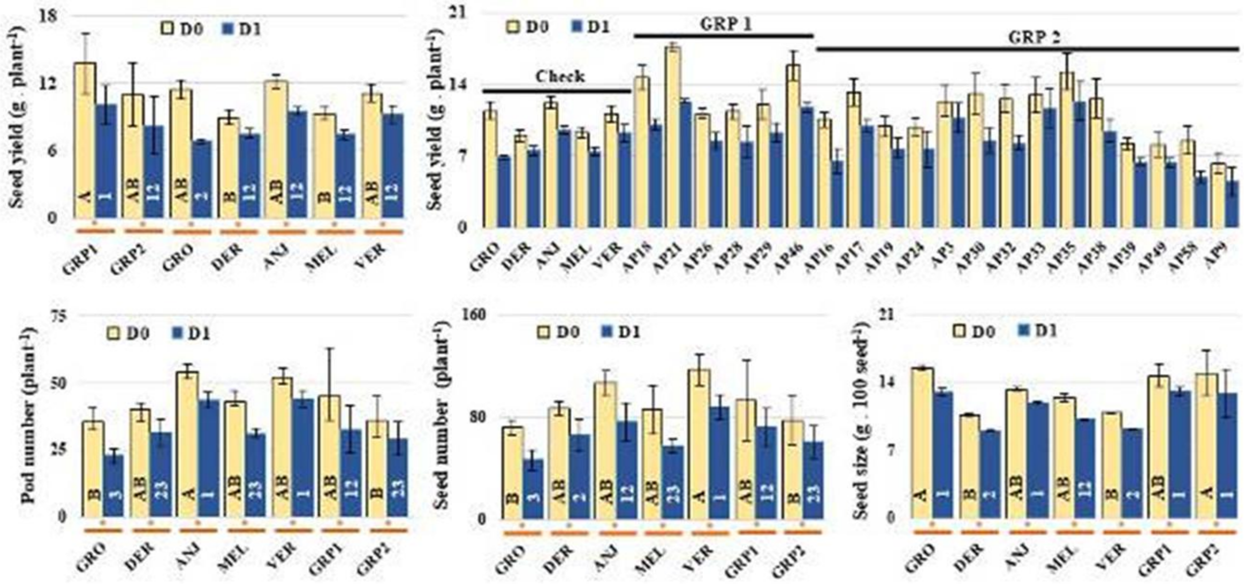

Figure 2. Yield and yield components of soybean genotypes grouped based on the presence or absence of the *pdh1* and *lj* genes, along with the check varieties. Values are presented as mean ± standard deviation. *: significant at the 0.05 level between treatment within the same genotype or genotype group. Different letters or numbers show significant differences between genotype and genotype group within the same treatment as determined by Tukey's test at the 5% significant level.

In general, genotypes carrying both *lj* and *pdh1* genes, grouped in GRP1 (Figure 2), exhibited a significantly higher average yield ($p < 0.05$) than genotypes carrying only the *lj* gene (GRP2) and the check varieties lacking both *lj* and *pdh1*. Nevertheless, since yield and drought tolerance are complex traits influenced by multiple genes (Saleem *et al*., 2022), not all genotypes carrying both *lj* and *pdh1* will necessarily achieve superior performance due to segregation and linkage during crossing (Mawasid *et al*., 2024). Thus, further studies are essential to test the tolerance performance of the two genotypes under drought in field conditions.

Jumrani and Bhatia (2019) reported that a genotype is potentially tolerant to drought stress when it can maintain both growth and yield in stress conditions at levels relatively comparable to those under optimal conditions. This tolerance phenotype received further support from specific biological or physiological mechanisms that sustain growth under drought stress, along with the presence of genes regulating adaptive traits (Desclaux *et al*., 2000).

Yield differences in this study signified a close correlation to yield components (Figure 2), particularly the pod number and seed number per plant, in which both characters showed declining performance under drought stress. High-yielding genotypes tended to maintain higher values for these traits, while more sensitive genotypes showed concurrent declines. These results suggest soybean genotypes having better pod retention, seed set, and seed size under drought stress have a higher tendency to maintain yield performance, becoming most likely classified as drought-tolerant genotypes.

The results are consistent with Xu *et al*. (2022), who reported soybean yield correlated with the pod number and seed number. Similarly, Desclaux *et al*. (2000) emphasized the importance of maintaining reproductive structures as a key trait associated with drought tolerance in soybeans. This suggests that selection for yield-related traits can indirectly improve soybean adaptation to drought stress.

Drought-tolerance indices based on yield

Drought tolerance indices based on yield under normal and drought stress conditions showed substantial variation among soybean genotypes tested (Table 3). This result enables the identification of both tolerant and susceptible soybean lines. AP21 and AP46 lines, carrying the *pdh1* gene, consistently gave high yields under drought stress, and this performance is consistent with that shown in Figure 2. Both lines steadily expressed the highest values for MP, GMP, STI, and YI, and the lowest SSI. In contrast, other genotypes, such as AP58, AP9, and GRO, constantly showed low MP, GMP, STI, and YI, with a high SSI, confirming their susceptibility to drought stress.

Pearson correlation analysis (Table 4) revealed that seed yield under drought stress (Ys) has a significant and positive correlation with several drought tolerance indices, including GMP, MP, STI, HM, YI, and K2STI. These strong associations confirm these indices are reliable for identifying high-yield potential and drought-tolerant genotypes. Conversely, Ys indicated a notably negative correlation with SSI and SDI, indicating that higher susceptibility implies an association with lower yield in stress. These findings align with Table 3, where genotypes, such as AP21 and AP46 (GRP1), consistently exhibited high values for MP, GMP, STI, and YI, along with a relatively low SSI, reinforcing their classification as drought-tolerant.

Poudel *et al*. (2021) reported a combination of high MP, GMP, and STI values with low SSI, showing strong drought tolerance indices in spring wheat. Kamrani *et al*. (2017) emphasized that SSI is useful for identifying durum wheat with stable yield under both drought stress and normal conditions. Similar findings came from Puri *et al*. (2020) in wheat under heat stress, supporting the effectiveness of using MP, GMP, and STI to identify genotypes with high-yield potential under optimal and stress conditions. The study also found that MP, GMP, and STI are reliable indices for selecting high-yielding and stress-tolerant genotypes across environments.

Principal component and biplot analyses

The research conducted principal component analysis (PCA) and biplot analysis to explore the relationships among drought tolerance indices and assist in identifying superior genotypes under contrasting water availability conditions. Based on eigenvalues > 1, PC1 and PC2 explained 60.17% and 39.20% of the total variation, respectively (Table 5). PC1 provided a strong correlation with Ys, Yn, MP, GMP, STI, and YI, representing yield potential and drought tolerance, with PC2 associated with SSI and TOL, showing stress susceptibility.

In the biplot analysis (Figure 3A), the relationships among drought tolerance indices appear by the angles between the vectors. Indices with angles less than 90° imply a positive correlation; those with angles > 90° suggest a negative correlation; and a right angle (90°) showed no correlation (Yan and Rajcan, 2002). The biplot analysis showed Ys and Yn signified a positive association with MP, GMP, STI, and YI, while Ys emerged as negatively associated with SSI and TOL.

These results agree with Nouri *et al*. (2011), who found in durum wheat, PC1 represented yield-related traits while PC2 reflected stress susceptibility, showing a similar trait structure to this study. Similarly, Yan and Rajcan (2002) showed biplot analysis effectively identifies favorable traits in soybeans. Traits consistent with yield vectors proved considerably ideal for selection. Consistently, the biplot grouped Ys and Yn with MP, GMP, STI, and YI, confirming these indices as reliable indicators of stable yield under both normal and drought conditions.

Genotypes with high PC1 and low PC2 (e.g., AP21 and AP46) were noticeably high-yielding and drought-tolerant genotypes, while those with low PC1 and high PC2 (e.g., AP58, AP9, and GRO) were drought-susceptible genotypes. Interestingly, no genotypes carrying the *pdh1* gene had positions in the quadrant characterized by high PC2 and low PC1 values (Figure 3B), showing a better yield under drought stress treatment.

Table 3. Seed yield of 25 soybean genotypes under normal and drought stress conditions and drought tolerance indices.

Genotype	Ys	Yn	YSI	SSI	TOL	STI	MP	GMP	HM	SDI	DI	RDI	SSPI	DTE	YI	K1STI	K2STI
ANJ	9.50	12.17	0.78	0.86	2.67	0.86	10.83	10.75	10.67	0.22	0.86	1.05	11.53	78.08	1.10	1.11	1.22
AP16	6.49	10.55	0.61	1.51	4.06	0.51	8.52	8.27	8.03	0.39	0.46	0.83	17.56	61.49	0.75	0.83	0.57
AP17	9.98	13.24	0.75	0.96	3.25	0.99	11.61	11.50	11.38	0.25	0.87	1.01	14.07	75.42	1.16	1.31	1.34
AP18	10.05	14.64	0.69	1.23	4.59	1.10	12.35	12.13	11.92	0.31	0.80	0.92	19.86	68.62	1.17	1.60	1.36
AP19	7.74	9.87	0.78	0.85	2.14	0.57	8.81	8.74	8.68	0.22	0.70	1.05	9.24	78.36	0.90	0.73	0.81
AP21	12.35	17.68	0.70	1.18	5.33	1.63	15.02	14.78	14.54	0.30	1.00	0.94	23.05	69.85	1.43	2.34	2.06
AP24	7.65	9.83	0.78	0.87	2.18	0.56	8.74	8.67	8.60	0.22	0.69	1.04	9.42	77.83	0.89	0.72	0.79
AP26	8.49	11.11	0.76	0.92	2.62	0.71	9.80	9.72	9.63	0.24	0.75	1.03	11.31	76.45	0.99	0.92	0.97
AP28	8.32	11.32	0.74	1.04	3.00	0.70	9.82	9.71	9.59	0.26	0.71	0.99	12.95	73.53	0.97	0.96	0.93
AP29	9.30	12.00	0.77	0.88	2.70	0.83	10.65	10.56	10.48	0.23	0.84	1.04	11.68	77.48	1.08	1.08	1.17
AP3	10.72	12.33	0.87	0.51	1.61	0.99	11.52	11.50	11.47	0.13	1.08	1.17	6.94	86.97	1.24	1.14	1.55
AP30	8.50	13.10	0.65	1.38	4.60	0.83	10.80	10.55	10.31	0.35	0.64	0.87	19.90	64.87	0.99	1.28	0.97
AP32	8.24	12.57	0.65	1.35	4.34	0.77	10.41	10.18	9.95	0.35	0.63	0.88	18.76	65.49	0.96	1.18	0.91
AP33	11.66	12.91	0.90	0.38	1.24	1.13	12.29	12.27	12.25	0.10	1.22	1.21	5.37	90.38	1.35	1.25	1.83
AP35	12.34	15.22	0.81	0.74	2.88	1.40	13.78	13.71	13.63	0.19	1.16	1.09	12.46	81.07	1.43	1.73	2.05
AP38	9.46	12.58	0.75	0.97	3.12	0.89	11.02	10.91	10.80	0.25	0.83	1.01	13.47	75.23	1.10	1.18	1.21
AP39	6.45	8.16	0.79	0.82	1.71	0.39	7.30	7.25	7.20	0.21	0.59	1.06	7.39	79.03	0.75	0.50	0.56
AP46	11.80	15.86	0.74	1.00	4.06	1.40	13.83	13.68	13.53	0.26	1.02	1.00	17.55	74.41	1.37	1.88	1.88
AP49	6.32	8.10	0.78	0.86	1.78	0.38	7.21	7.16	7.10	0.22	0.57	1.05	7.71	77.99	0.73	0.49	0.54
AP58	4.95	8.51	0.58	1.64	3.56	0.31	6.73	6.49	6.25	0.42	0.33	0.78	15.39	58.15	0.57	0.54	0.33
AP9	4.48	6.30	0.71	1.13	1.82	0.21	5.39	5.31	5.24	0.29	0.37	0.95	7.89	71.06	0.52	0.30	0.27
DER	7.50	8.96	0.84	0.64	1.46	0.50	8.23	8.20	8.16	0.16	0.73	1.12	6.30	83.73	0.87	0.60	0.76
GRO	6.85	11.42	0.60	1.57	4.56	0.58	9.14	8.85	8.57	0.40	0.48	0.81	19.72	60.05	0.80	0.97	0.63
MEL	7.45	9.29	0.80	0.78	1.84	0.52	8.37	8.32	8.27	0.20	0.69	1.08	7.94	80.21	0.86	0.64	0.75
VER	9.21	11.10	0.83	0.67	1.89	0.76	10.15	10.11	10.07	0.17	0.89	1.11	8.18	82.95	1.07	0.92	1.14
Mean	8.83	11.55	0.76	0.94	2.72	0.81	10.19	10.09	9.98	0.24	0.79	1.02	11.76	75.97	1.03	1.05	1.13
Range	10.47	11.38	0.32	1.26	3.36	1.76	10.92	10.94	10.96	0.32	1.13	0.43	14.53	32.24	1.22	2.04	2.74

Ys: yield under stress condition, Yn: yield under normal condition.

Table 4. Pearson correlation between seed yield (Yn and Ys) of soybean genotypes and drought tolerance indices.

Traits	Ys	Yn	YSI	SSI	TOL	STI	MP	GMP	HM	SDI	DI	RDI	SSPI	DTE	YI	K1STI	K2STI
Ys	1																
Yn	.90**	1															
YSI	.41*	-.02	1														
SSI	-.42*	.02	-.99**	1													
TOL	.20	.61**	-.79**	.79**	1												
STI	.96**	.97**	.20	-.20	.42*	1											
MP	.97**	.98**	.18	-.18	.44*	.99**	1										
GMP	.98**	.97**	.22	-.22	.41*	.99**	.99**	1									
HM	.98**	.96**	.25	-.25	.36	.99**	.99**	.99**	1								
SDI	-.41*	.02	-1.00**	.99**	.79**	-.2	-.18	-.22	-.25	1							
DI	.95**	.71**	.67**	-.68**	-.12	.84**	.84**	.86**	.87**	-.67**	1						
RDI	.42*	-.01	.99**	-1.00**	-.79**	.2	.19	.22	.26	-.99**	.68**	1					
SSPI	.20	.61**	-.79**	.79**	1.00**	.42*	.44*	.41*	.38	.79**	-.12	-.79**	1				
DTE	.42*	-.02	.99**	-1.00**	-.79**	.2	.18	.22	.25	-.99**	.68**	1.00**	-.79**	1			
YI	1.00**	.90**	.41*	-.41*	.21	.96**	.97**	.98**	.98**	-.41*	.95**	.42*	.21	.41*	1		
K1STI	.88**	.99**	-.03	.03	.62**	.97**	.97**	.96**	.95**	.03	.69**	-.03	.62**	-.03	.88**	1	
K2STI	.99**	.89**	.39	-.39	.21	.98**	.96**	.97**	.98**	-.39	.94**	.40*	.21	.39	.99**	.89**	1

Ys: yield under stress condition, Yn: yield under normal condition, *: correlation is significant at the 0.05 level (2-tailed), **: correlation is significant at the 0.01 level (2-tailed).

Table 5. Principal component analysis based on seed yield of 25 soybean genotypes and drought tolerance indices.

PC	Var (%)	Cum (%)	Ys	Yn	YSI	SSI	TOL	STI	MP	GMP	HM	SDI	DI	RDI	SSPI	DTE	YI	K1STI	K2STI
PC1	60.17	60.17	0.99	0.88	0.45	-0.46	0.17	0.96	0.96	0.97	0.98	-0.45	0.96	0.46	0.17	0.45	0.99	0.87	0.99
PC2	39.20	99.37	0.04	0.47	-0.89	0.89	0.98	0.27	0.29	0.25	0.22	0.89	-0.28	-0.89	0.98	-0.89	0.04	0.48	0.06

PC: principal component, Var: variance, Cum: cumulative, Ys: yield under stress condition, Yn: yield under normal condition.

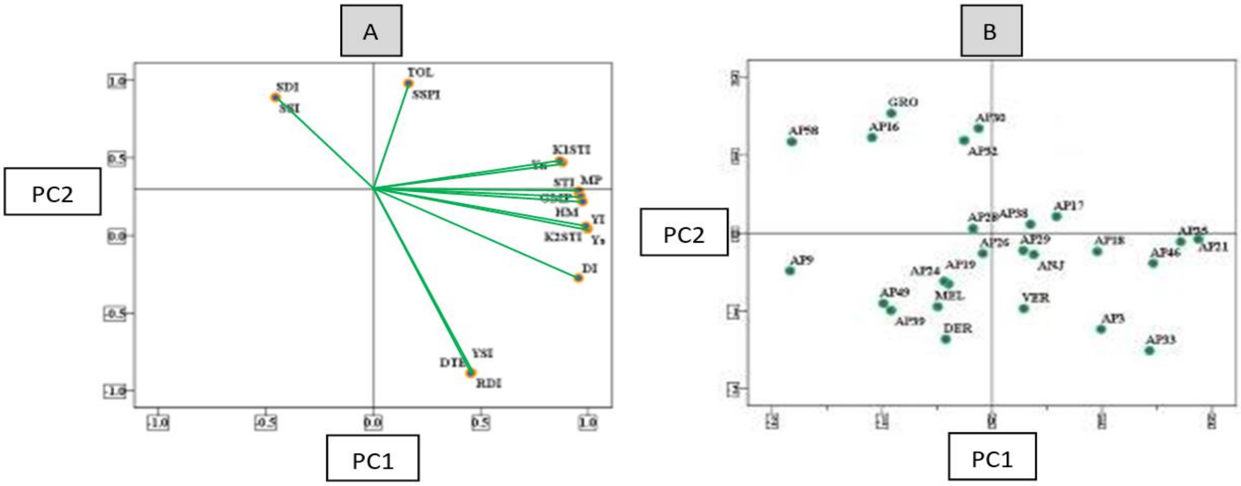

Figure 3. Biplot of principal component analysis (PCA) for drought tolerance indices (A) and soybean genotypes (B). PC1: first principal component, PC2: second principal component, Ys: yield under drought stress condition, Yn: yield under normal condition.

Yong *et al*. (2023) found that the *pdh1* gene with a premature stop codon, associated with pod indehiscence, became more frequent in low-precipitation regions. These results underscore the potential of genotypes carrying the *pdh1* gene for broader evaluation and use in dryland environments. Moreover, the observed variation in drought response suggests a complex polygenic mechanism. Saleem *et al*. (2022) identified 17 and 22 significant marker-trait associations under short- and long-duration drought, emphasizing the multifaceted genetic basis of drought-tolerant phenotypes. Building on these genetic insights, it is important to explore the underlying physiological and hormonal pathways that may link drought tolerance with pod shattering, particularly through the role of the *pdh1*.

Under drought stress, increased ABA (abscisic acid) levels can inhibit auxin biosynthesis and transport (Gupta *et al*., 2020). Insufficient auxin compromises lateral root formation and the elongation of primary roots, which are crucial for drought adaptation. It also affects pod structure by allowing increased activity of cell wall, modifying enzymes such as cellulase (CE) and polygalacturonase (PG), leading to degradation of the abscission layer (AL)—a key trigger of pod shattering—and promoting excessive lignin deposition in pod walls (Guo *et al*., 2022). As lignin normally provides mechanical strength, abnormal or uneven lignification can generate torsional forces during drying, thus accelerating pod rupture (Funatsuki *et al*., 2014). We further hypothesize that *PDH1* may directly or indirectly influence auxin biosynthesis through ABA–auxin crosstalk, thereby suppressing auxin levels that are critical for both root development and pod wall stability (Figure 4). In contrast, the loss of *PDH1* function (*pdh1*) prevents the suppression of auxin biosynthesis, consequently maintaining higher auxin levels that promote root elongation and enhance pod wall stability, ultimately conferring resistance to pod shattering under drought stress.

CONCLUSIONS

In conclusion, this study showed significant genotypic variation in drought tolerance during the flowering to pod formation in soybeans (*G. max* L.). The lines AP21 and AP46, carrying *lj* and *pdh1* genes, showed superior seed yield performance under drought stress in tropical regions, primarily due to better retention of pod number, seed number, and seed size.

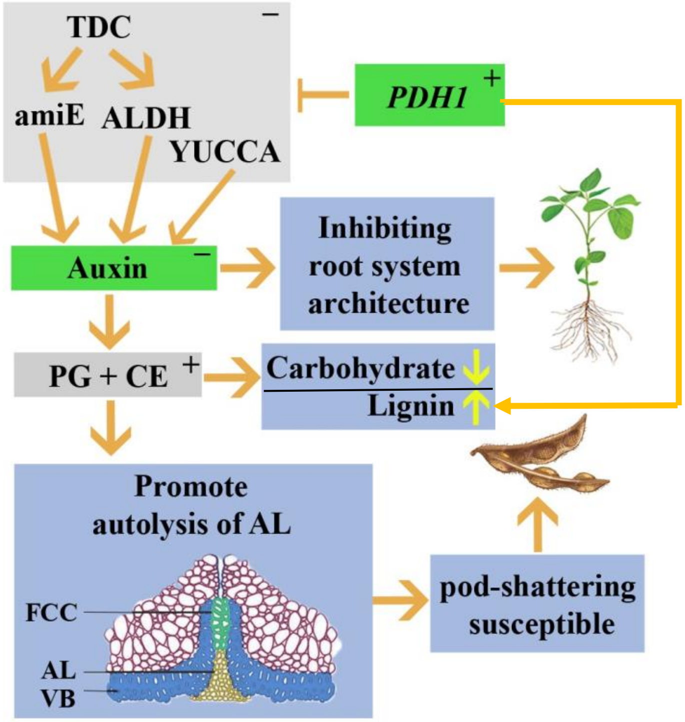

Figure 4. A proposed model for the role of the *PDH1* gene in regulating pod-shattering susceptibility and root architecture through auxin signaling pathways. TDC = L-tryptophan decarboxylase; YUCCA = indole-3-pyruvate monooxygenase; ALDH = aldehyde dehydrogenase; amiE = amidase; PG = polygalacturonase; CE = cellulase; AL = abscission layer; VB = vascular bundle; FCC = fiber cap cells.

Principal component and biplot analyses confirmed indices, such as high GMP, MP, STI, YI, and low SSI, effectively identified soybean drought-tolerant genotypes. More importantly, no *pdh1*-carrying genotypes reached a drought-sensitive classification, suggesting that the *pdh1* gene may contribute to adaptation, although further field validation and physiological characterization are necessary.

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