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Effects of Drought Stress During Branching and Pod Formation Stages on Morpho-Physiology and Yield in Soybean

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ABSTRACT

Background: Recurrent drought events in the Huaibei Plain of China pose a major constraint to soybean production. The peak drought period in July and September coincides with two critical stages of soybean, branching (B) and pod formation (PF), yet current research still focuses predominantly on the flowering-podding (FP) stage, leaving the physiological and yield response mechanisms to drought stress during these stages poorly understood. This study was designed to investigate the differential responses of soybean to varying intensities of drought stress during critical growth stages.

Methods: A pot experiment was conducted under drought conditions in the Huaibei Plain in 2024, with three limits of soil water content set at both the B and PF stages: light drought (LD, 55%), moderate drought (MD, 45%) and well-watered control (CK, 75%). Morphological, photosynthetic, yield and pod-related traits of soybean under varying drought levels were examined and Pearson correlation analysis was applied to assess their relationships with yield.

Result: The results indicated that, overall, drought stress during the B stage resulted in severe reductions in plant height (PH), root length (RL) and seed moisture content (MC) compared to the PF stage. In contrast, photosynthetic parameters (SPAD value, stomatal conductance (Gs), net photosynthetic rate (Pn), transpiration rate (Tr) and intercellular CO_2 concentration (Ci), yield, pod-related traits (total seed number (TSN), total pod number (TPN), filled pod number (FPN), empty pod number (EPN) and pod wall weight (PWW), as well as seed oil content (OC), exhibited an opposite trend. Furthermore, the magnitude of change in all aforementioned traits (except for EPN) relative to the CK followed the pattern MD > LD at the same growth stage. Correlation analysis showed that soybean yield was significantly and positively associated with TSN, TPN, FPN and PWW ($p<0.05$), while exhibiting negative correlations with EPN, Ci and MC.

Key words: Branching stage, Drought stress, Morphophysiological, Pod formation stage, Soybean, Yield traits.

INTRODUCTION

Amid the current trend of increasingly extreme global climate patterns, drought events are increasingly affecting agricultural production regions worldwide, characterized by their high frequency, prolonged duration and broad spatial extent (Mangena, 2020; Christian *et al*., 2023; Quat *et al*., 2025). In particular, it has resulted in a marked increase in drought risk and the extent of affected areas across varying regions in China (Song *et al*., 2021), imposing substantial economic losses on grain production. As one of the most important oil crops in China, soybean [*Glycine max* (L.) Merr.] is highly sensitive to water deficit during its growth stages, with severe drought potentially leading to yield losses of up to 40% (Zhou *et al*., 2022). However, China's domestic soybean production remains at approximately 20.65 million tons per year (2024 statistics), while import dependence remains as high as 80%, undoubtedly creating a critical bottleneck for national strategic food security (Jiang *et al*., 2025). Therefore, evaluating soybean adaptation under drought stress is critical to mitigating yield losses.

Drought stress substantially influences the growth and development of various soybean organs (Dietz *et al*., 2021). Notably, the responses of phenotypic traits to such stress can serve as valuable indicators for selecting drought-resistant soybean varieties (Kim *et al*., 2023). Studies have indicated that crop responses to drought follow a progressive sequence from physiological alterations to growth adjustments and ultimately yield reduction, with photosynthesis-a key physiological process-being among the first to be adversely affected (Chaves *et al*., 2009). Moreover, drought stress occurring at any growth stage of soybean can impair photosynthetic performance, primarily due to reduced chlorophyll content, which is widely recognized as a major cause of alterations in photosynthetic characteristics (Wijewardana *et al*., 2019; Elsalahy and

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Reckling, 2022). These physiological alterations can disrupt the synthesis and transport of assimilates in flowers and pods and also adversely affect morphological traits such as plant height and root architecture (da Silva *et al*., 2018; García-Rodríguez *et al*., 2024). Ultimately, this results in reduced yield and quality parameters such as protein and oil content in soybean (Gholamhoseini *et al*., 2018).

The Huaibei Plain in Anhui Province, China, a major soybean-producing region with an annual summer sowing area of 700,000-800,000 hectares, is frequently affected by droughts that significantly limit grain yield (Cui *et al*., 2021). Droughts frequently occur in July and September in the Huaihe River Basin of Anhui Province, which overlap with the branching and pod formation stages of soybean. In contrast to previous studies focusing on the flowering-podding stage, this study examines soybean responses to drought during these critical phases in the Huaibei Plain, to support breeding of drought-resistant varieties and development of targeted irrigation strategies.

MATERIALS AND METHODS

Experimental materials and crop management

The pot-based drought experiment on soybean was conducted from June to September 2024 at the Xinmaqiao Comprehensive Agricultural Water Experimental Station (33°09′N, 117°22′E), situated 25 km north of Bengbu City, Anhui Province, China. Meteorological records indicate that the experimental site is located within the warm temperate semi-humid monsoon climate region of the Huang-Huai-Hai Plain, where the long-term average annual precipitation and evaporation measure 917 mm and 916 mm, respectively. The pot experiment utilized a lime concretion black soil of heavy texture and low permeability, containing >95% silt and clay. Key soil properties are provided in Table 1.

Based on the long-term agronomic experience of the experimental station, the soybean growth period in this study was categorized into four stages: seedling (S, 19 June-14 July), branching (B, 15-29 July), flowering-podding (FP, 30 July-20 August) and pod formation (PF, 21 August-28 September). Pots measuring 33 cm in top diameter, 22 cm in bottom diameter and 28 cm in height were used for sowing soybean seeds of the cultivar ‘Zhonghuang 13’ at a density of 8-10 seeds per pot. Seven days after emergence, seedlings were thinned to three uniform plants per pot. All plants were uniformly managed-including fertilization, pest and weed control-throughout the growing season. All potted plants were placed on outdoor shelves and were equipped with a movable rain shelter to minimize interference from natural precipitation during the experiment.

Experimental design

The experiment included two factors: growth stages (B and PF) and drought intensity, the latter was implemented by maintaining specific limits of soil moisture content (SMC) in the pots. Based on the station’s long-term agronomic experience and established protocols (Cui *et al*., 2021), three SMC levels were applied: well-watered control (CK, 75%), light drought (LD, 55%) and moderate drought (MD, 45%). The experiment comprised one control group and four drought-treated groups, with three replicates each, resulting in a total of 15 pots. Table 2 for the complete experimental layout.

Morphological and yield traits measurement

At harvest, plant height (PH) and root length (RL) were measured using a 1-m standard ruler. The total pod number (TPN), filled pod number (FPN), empty pod number (EPN) and total seed number (TSN) were enumerated and recorded. Soybean grain yield and pod wall weight (PWW) were determined using an electronic balance.

SPAD and photosynthetic traits measurement

Measurements of relative chlorophyll content (SPAD) and photosynthetic traits-including intercellular CO_2 concentration (Ci), stomatal conductance (Gs), net photosynthetic rate (Pn) and transpiration rate (Tr)-were conducted from 9:00 to 12:00 on sunny days during the late B and late PF stages using a SPAD-502 Plus chlorophyll meter (Konica Minolta Inc., Japan) and a CIRAS-4 portable photosynthesis system (PP Systems International Inc., USA), respectively.

Quality traits measurement

Oil content (OC) and moisture content (MC) of soybean seeds were determined using an Infratec™ near-infrared grain analyzer (FOSS Analytical A/S, Denmark).

Data processing and analysis

Experimental data were organized using Microsoft Excel 2010, followed by one-way ANOVA performed with IBM Statistics SPSS 27.0 software. Visualization including column charts, vertical multi-panel line plots and correlation heatmaps was generated using Origin 2021 software.

RESULTS AND DISCUSSION

Effects of drought stress on PH and RL in soybean

As shown in Fig 1a, PH declined with increasing drought intensity at the same growth stage, though the reduction was less pronounced during the PF stage compared to the B stage. All treatment values were lower than those of

Table 1: Main physicochemical properties of the topsoil used in the experiment.

TN/g·kg^{-1}	TP/g·kg^{-1}	TK/g·kg^{-1}	pH	Particle size distribution/%			Bulk density/ g·cm^{-3}	Field capacity/ g·g^{-1}
				Sand	Silt	Clay		
0.73	0.44	6.06	6.75	3.40	70.70	26.00	1.45	0.28

Note: TN, TP and TK denote total nitrogen, total phosphorus and total potassium, respectively.

the CK, but no significant differences were detected ($p>0.05$). Specifically, PH in drought-stressed groups at the B stage (T1, T2) decreased by 9.97% and 15.03%, respectively, compared to CK, whereas at the PF stage (T3, T4), the reductions were about 5.55% and 6.04%. Greater drought intensity resulted in a more pronounced reduction in PH; however, as the PF stage coincides with limited vegetative growth in soybean, plants were less affected during this stage than at the B stage (Wei *et al*., 2018), consistent with our findings. Then, a similar response pattern was observed for RL under drought stress (Fig 1b). Compared with CK, RL in the B stage groups (T1, T2) declined by roughly 9.21% and 11.93%, whereas at the PF stage (T3, T4), the decreases were approximately 4.40% and 11.72%. No significant differences were found among any treatment groups ($p>0.05$). These results demonstrated that increasing drought severity exerts a more pronounced inhibitory effect on soybean root growth (García-Rodríguez *et al*., 2024). Ndlovu *et al*. (2025) observed a greater effect of drought stress on root length in sorghum seedlings at the early growth stage than at later stages, which aligns with the findings of this study. Therefore, MD was more inhibitory to PH and RL in soybean than LD. Since these traits were largely developed by the PF stage, drought stress during this phase had a much smaller effect compared to the B stage.

Table 2: Experimental design for drought stress at different growth stages of soybean.

Treatments	Lower limit of SMC for different soybean growth stages (%)			
	S	B	FP	PF
T1	75	55	75	75
T2	75	45	75	75
T3	75	75	75	55
T4	75	75	75	45
CK	75	75	75	75

Effects of drought stress on SPAD and photosynthetic traits in soybean

Drought stress impairs plant photosynthesis primarily by triggering stomatal closure, which subsequently leads to the degradation of chlorophyll and disruption of the electron transport chain in chloroplasts (El Amine *et al*., 2025). As shown in Table 3, SPAD and photosynthetic traits (Ci, Gs, Pn, Tr) were generally higher during the B than the PF stage across all treatments. These traits showed no significant differences during the B stage, but all except SPAD differed significantly ($p<0.05$) during the PF stage. Compared with CK, the SPAD values in T1 and T2 decreased by approximately 5.73% and 10.53%, respectively, during the B stage, while greater reductions of about 10.13% and 18.79% were observed in T3 and T4 at the PF stage. Previous studies have reported a marked decline in soybean SPAD values with progression of growth stages and intensification of drought stress (Elsalahy and Reckling, 2022), a trend consistent with the findings of the present study. In terms of photosynthetic traits, compared with CK, the treatment groups (T1, T2) at the B stage exhibited decreases in Gs, Pn and Tr of approximately (36.94%, 0.36%), (52.25%, 86.25%) and (-1.78%, 8.77%), respectively. In contrast, at the PF stage, the treatment groups (T3, T4) showed reductions in these parameters of about (21.90%, 73.20%), (52.43%, 91.94%) and (26.27%, 70.90%), respectively. Liu *et al*. (2019) reported that Gs, Pn and Tr in persimmon exhibited a decreasing trend with increasing intensity of PEG-6000-simulated drought stress, a response consistent with the observations in the present study. However, in both the B (T1, T2) and PF (T3, T4) stage treatment groups of soybean, the Ci increased rather than decreased with intensifying drought stress when compared to CK, with specific increases of (48.20%, 61.15%) and (11.47%, 29.07%), respectively. Fugate *et al*. (2018) observed a similar response pattern of the Ci to drought stress in sugar beet, as did Liu *et al*. (2024) in *Quercus acutissima*.

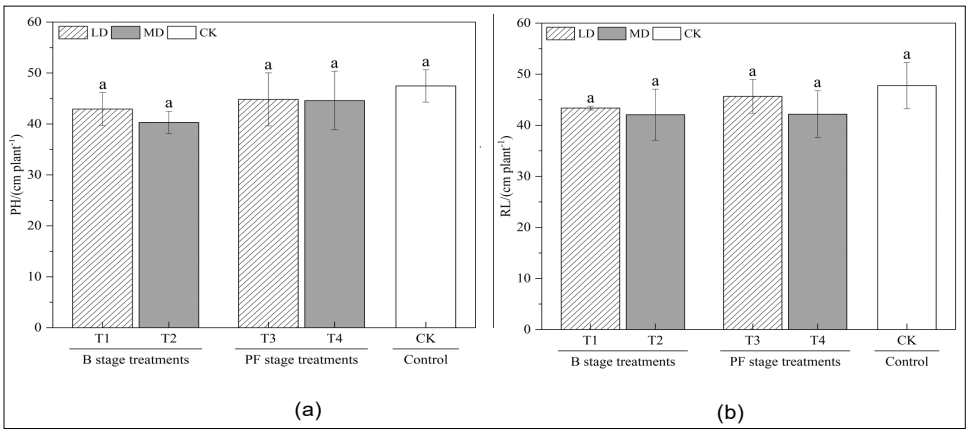


Fig 1: Effects of different drought treatments on PH and RL.

Effects of drought stress on yield and pod traits in soybean

Soybean pods and seeds, serving as the primary water-storing organs, critically influence grain yield through their size and number per plant (Desclaux *et al*., 2000). As shown in Table 4, with the progression of growth stages and the intensification of drought stress, soybean yield, TSN, TPN, FPN and PWW displayed a decreasing trend (*i.e*., T1 > T2 > T3 > T4). Compared to CK, all five traits showed reductions, with percentage decreases from T1 to T4 as follows: yield (7.09%, 16.48%, 42.59%, 44.36%), TSN (20.38%, 23.27%, 39.23%, 45.58%), TPN (9.69%, 14.96%, 28.03%, 31.08%), FPN (12.81%, 15.31%, 30.24%, 34.34%) and PWW (8.18%, 23.26%, 37.70%, 45.69%). Furthermore, these traits exhibited significant differences ($p<0.05$) from CK under drought stress at the PF stage. In contrast to other traits, the EPN in soybean showed an inverse trend under drought stress, with T1-T4 increasing by 100.00%, 12.36%, 174.16% and 83.15% compared to CK, though only T3 exhibited a significant difference ($p>0.05$). Previous studies (Wei *et al*., 2018; Cui *et al*., 2019; Kisman *et al*., 2025) have shown that drought stress significantly reduces soybean yield and pod traits, with water deficit during the reproductive stage having a greater impact than during the vegetative stage, consistent with our findings. Increasing drought intensity further amplified these effects, with the PF stage being more affected than the B stage.

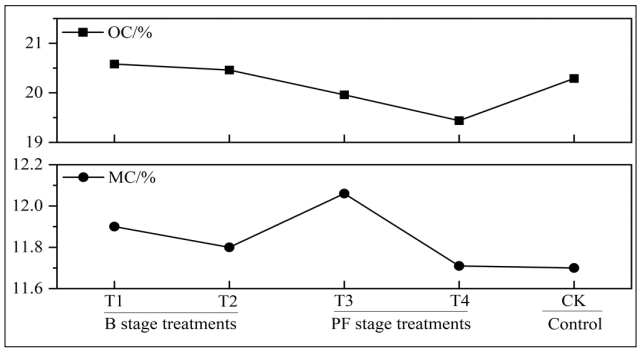


Fig 2: Effects of different drought treatments on OC and MC.

Effects of drought stress on quality in soybean

Within the same growth stage, both OC and MC of soybean seeds decreased with increasing drought stress intensity (Fig 2). Compared with CK, the OC in soybean kernels increased by approximately 1.43% and 0.84% under the T1 and T2 treatments at the B stage, respectively, but decreased by 1.63% and 4.19% under T3 and T4 at the PF stage. Meanwhile, the MC increased by 1.71%, 0.85%, 3.08% and 0.09% under T1-T4 across both the B and PF stages, respectively. Haghaninia *et al*. (2025) reported that severe drought stress leads to a reduction in OC compared with optimal irrigation conditions. In the present study, drought stress applied at the B stage increased the OC of soybean seeds, whereas a reduction was observed under drought at the PF stage. Furthermore, Kouighat *et al*. (2025) observed an increase in seed MC in sesame under drought stress conditions, which aligns with our results. Therefore, drought stress at the B stage enhanced the OC of soybean seeds, while that applied at the PF stage led to a reduction. In contrast, seed MC increased under drought stress regardless of the growth stage.

Table 3: Effects of different drought treatments on SPAD and photosynthetic traits.

Stage	Treatments	SPAD/value	Ci/μmol·mol^{-1}	Gs/mmol·m^{-2}·s^{-1}	Pn/μmol·m^{-2}·s^{-1}	Tr/mmol·m^{-2}·s^{-1}
B	T1	38.30±4.53a	488.02±205.32a	138.69±125.38a	5.73±18.65a	6.85±4.35a
	T2	36.35±1.63a	530.66±148.32a	219.16±157.27a	1.65±22.43a	6.14±1.65a
	T3	39.40±1.13a	447.71±53.10a	257.92±180.98a	-0.38±0.59a	7.14±2.57a
	T4	39.65±2.19a	353.03±9.69a	664.32±382.47a	14.57±1.56a	11.86±2.31a
	CK	40.63±6.39a	329.29±55.69a	219.95±18.58a	12.00±0.87a	6.73±0.00a
PF	T1	36.35±1.06a	334.61±37.15ab	50.94±6.54bc	2.17±1.09b	1.78±0.26bc
	T2	35.40±0.42a	344.92±15.83a	81.81±29.07ab	4.09±2.94b	2.43±0.69ab
	T3	35.05±7.42a	310.49±4.14ab	78.45±14.79ab	4.31±1.28ab	2.61±0.35ab
	T4	31.67±0.72a	359.50±25.05a	26.92±4.46c	0.73±0.49b	1.03±0.34c
	CK	39.00±0.28a	278.53±4.22b	100.45±35.07a	9.06±2.38a	3.54±0.99a

Table 4: Effects of different drought treatments on yield and pod traits.

Treatments	Yield/g	TSN	TPN	FPN	EPN	PWW/g
T1	29.76±1.66a	138.00±14.18b	29.00±4.85ab	27.22±5.19ab	1.78±1.20ab	14.37±0.82ab
T2	26.75±5.26a	133.00±12.53b	27.44±6.21ab	26.44±6.80ab	1.00±1.32b	12.01±2.16bc
T3	18.39±2.17b	105.33±13.61c	23.11±7.11b	21.78±7.29b	2.44±1.13a	9.75±0.95cd
T4	17.82±2.67b	94.33±5.03c	22.13±7.86b	20.50±7.54b	1.63±1.06ab	8.50±0.96d
CK	32.03±3.61a	173.33±15.14a	32.11±12.03a	31.22±11.30a	0.89±1.05b	15.65±1.40a

Note: All data presented in the table are expressed on a per-plant basis.

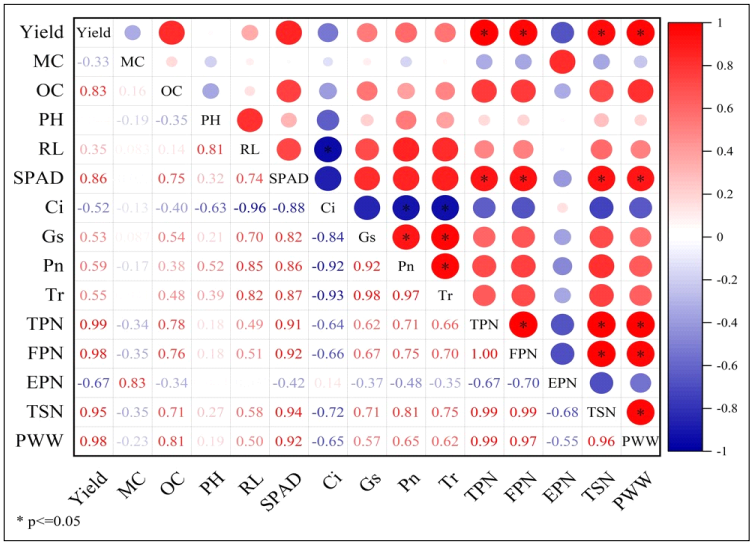


Fig 3: Correlation analysis among agronomic traits of soybean under drought stress.

Correlation analysis between soybean yield and agronomic traits

Pearson correlation analysis showed that yield was positively associated with most traits except MC, Ci and EPN (Fig 3). Strong significant correlations (r = 0.95-0.99, p<0.05) were observed with pod-related traits (TPN, FPN, TSN, PWW), while correlations with photosynthetic traits were positive but not significant, consistent with previous studies (Aminian *et al.,* 2007; Dou *et al*., 2023; Basavarajeshwari *et al*., 2025).

CONCLUSION

Pot experiments under drought stress in the Huaibei Plain showed that drought at the B stage mainly affected PH and RL, while at the PF stage it had greater impacts on photosynthetic traits, yield and pod-related traits. OC increased at B but declined at PF, whereas MC rose consistently. Moderate drought caused more severe effects than light drought. Yield correlated strongly with TPN, FPN, TSN and PWW, highlighting the importance of optimizing irrigation during the PF stage.

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Disclaimers

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Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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