



Effects of Drought Stress on Growth and Biomass Allocation of Soybean at the Seedling Stage

Xiaomei Li¹, Hongyu Li¹, Xuan Xia¹, Jing Yang¹, Zhifeng Hu¹, Jingxin Li¹

10.18805/LRF-952

ABSTRACT

Background: With the exacerbation of global climate change, drought has become one of the major abiotic stresses limiting soybean yield. The seedling stage is a critical period for root establishment and early growth in soybean, which is highly sensitive to water deficit. The morphological remodeling and biomass allocation characteristics during this stage directly affect subsequent plant growth and development.

Methods: In this study, a drought-tolerant genotype (HN-44) and a drought-sensitive genotype (HN-65) were used as materials. Drought stress was simulated using polyethylene glycol (PEG) at four concentration gradients (CK, 7.5%, 15% and 22.5%). By measuring plant height, leaf area and the dry mass of various organs (roots, stems, leaves and petioles) and constructing an allometric growth model, the effects of drought stress on the root-shoot growth relationship were investigated.

Result: The results showed that drought stress significantly inhibited morphogenesis and biomass accumulation in both genotypes and the inhibitory effects were exacerbated with increasing stress intensity and duration. Compared with HN-65, the drought-tolerant genotype HN-44 exhibited a stronger capacity for dry matter production and maintenance, particularly maintaining higher leaf area stability under severe stress. Regarding dry matter allocation, both genotypes exhibited assimilate translocation to the roots at the early stage of stress, resulting in a significant increase in the root mass fraction (RMF). As the stress duration prolonged, HN-44 adjusted its allocation strategy to gradually restore and maintain a relatively stable root-shoot balance, thereby achieving coordinated growth of the above and below-ground parts. Conversely, the severe inhibition of shoot growth in HN-65 led to a passive increase in its root-to-shoot ratio. Allometric analysis further confirmed that drought stress disrupted the inherent biomass allocation pattern of the plants. However, HN-44 demonstrated a more stable and moderate regulatory capacity, with a smaller reduction in the slope of the root-shoot allometric relationship (33.09%-50.36%).

Key words: Drought stress, Dry matter partitioning, Growth characteristics, Soybean.

INTRODUCTION

Soybean [*Glycine max* (L.) Merr.], as one of the world's most important sources of plant protein and edible oil, plays an irreplaceable role in ensuring global food security and sustainable agricultural development (Kumari *et al.*, 2025; Dilawari *et al.*, 2022). As a typical high-water-demanding crop, its growth and development are highly sensitive to soil moisture fluctuations (Shadakshari *et al.*, 2014; Huang *et al.*, 2026). With the exacerbation of global climate change, altered extreme precipitation patterns have led to frequent and severe drought events, which profoundly threaten global soybean yields (Christian *et al.*, 2023; Felisberto *et al.*, 2023; Xu *et al.*, 2019). The seedling stage is a critical period for root establishment and early vegetative growth; water deficit during this phase severely impedes plant development, causing irreversible negative impacts on subsequent reproductive stages and ultimate grain yield (Esan *et al.*, 2023; Kim *et al.*, 2023).

Under drought conditions, plants mitigate stress-induced damage primarily by remodeling their external morphology and optimizing internal resource allocation. Morphologically, drought directly inhibits cell elongation and division, leading to stunted plant growth, shortened internodes and reduced leaf area. Although this morphological adjustment comes at the cost of reduced

¹College of Agriculture, Heilongjiang Agricultural Engineering Vocational and Technical University, Harbin, Heilongjiang Province, 150029, China.

Corresponding Author: Xiaomei Li, College of Agriculture, Heilongjiang Agricultural Engineering Vocational and Technical University, Harbin, Heilongjiang Province, 150029, China.
Email: eileen828@126.com

How to cite this article: Li, X., Li, H., Xia, X., Yang, J., Hu, Z. and Li, J. (2026). Effects of Drought Stress on Growth and Biomass Allocation of Soybean at the Seedling Stage. *Legume Research*. **49(10)**: 1737-1745. doi: 10.18805/LRF-952.

Submitted: 25-03-2026 **Accepted:** 08-06-2026 **Online:** 23-06-2026

photosynthetic surface area, it effectively curtails transpirational water loss (Yavas *et al.*, 2024). Furthermore, under drought stress, plants alter the allocation of carbon assimilates and adjust source-sink relationships to coordinate resource distribution among various organs (Jaleh, 2017). Extensive research indicates that when water is limited, plants prioritize the translocation of limited assimilates to the below-ground parts. This sustains root development into deeper soil layers, thereby enhancing water acquisition capabilities (Kunert *et al.*, 2016; Guo *et al.*, 2024).

Despite these insights, current research often analyzes plant organs in isolation, leaving the dynamic coordination and whole-plant allometric growth trajectories of different genotypes under varying stress intensities poorly understood. Furthermore, in traditional soil-drying experiments, natural water depletion is often accompanied by continuous and uneven declines in soil moisture, making it difficult to precisely distinguish the effects of specific stress intensities on plant morphology (Poorter *et al.*, 2012). In contrast, utilizing polyethylene glycol (PEG) to simulate osmotic stress can effectively maintain a stable osmotic potential in the rhizosphere, providing a reliable and reproducible approach for evaluating plant responses to specific drought thresholds (Lawlor, 1970; Rajeswar and Narasimhan, 2021).

Therefore, in this study, two soybean genotypes with contrasting drought tolerance (HN-44, drought-tolerant; HN-65, drought-sensitive) were used as materials and varying concentrations of PEG-6000 were applied at the seedling stage to simulate precise levels of osmotic stress. We systematically analyzed the effects of different drought levels on morphological traits and biomass accumulation across various plant organs. By constructing log-log allometric growth models and performing three-way ANOVA, we integrated shoot and root indicators to quantitatively evaluate the dynamic biomass allocation strategies of the two genotypes. This study aims to elucidate the key morphological factors limiting soybean seedling growth under drought, thereby providing a theoretical basis for the screening of drought-tolerant soybean varieties and stress-resistant cultivation management.

MATERIALS AND METHODS

Materials and growth conditions

The experiment was conducted from May to October 2025 at the experimental station of Heilongjiang Agricultural Engineering Vocational and Technical University (Harbin, Heilongjiang, China). Two soybean cultivars with significantly different drought tolerances were used as the experimental materials: Heinong 44 (HN-44, drought-tolerant) and Heinong 65 (HN-65, drought-sensitive) (Wang *et al.*, 2012).

A sand culture pot was employed for the experiment. Plastic pots (0.3 m in diameter and 0.3 m in height) were used, with four 1 cm diameter drainage holes drilled at the bottom. A nylon mesh was placed over the holes to prevent substrate loss. The pots were filled with washed river sand up to 3 cm from the rim and watered thoroughly before sowing. Plump, uniform and disease-free soybean seeds were selected and sown at a rate of six seeds per pot, followed by covering with a 1 cm layer of dry sand. From sowing until the full expansion of the opposite true leaves (VC stage), the pots were irrigated daily with 500 mL of distilled water. Upon the expansion of the opposite true leaves, the seedlings were thinned to retain three uniform plants per pot. Subsequently, 500 mL of nutrient solution

was applied daily to each pot. The composition of the nutrient solution was as follows: 240 mg/L MgSO_4 , 136 mg/L KH_2PO_4 , 235.8 mg/L $(\text{NH}_4)_2\text{SO}_4$, 220 mg/L CaCl_2 , 0.03 mg/L $\text{Na}_2\text{MoO}_4 \cdot \text{H}_2\text{O}$, 0.08 mg/L $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 0.22 mg/L $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 4.90 mg/L $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$, 2.86 mg/L H_3BO_3 and Fe-EDTA. For the iron source (Fe-EDTA), stock solutions of 5.57 g/L $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ and 7.45 g/L $\text{Na}_2\text{-EDTA}$ were prepared separately and 1 mL of each stock solution was added per liter of the working nutrient solution.

When the soybean seedlings reached the V3 stage (three fully developed trifoliolate leaves), the drought stress treatment was initiated. Osmotic stress was simulated by adding different concentrations of polyethylene glycol 6000 (PEG-6000) to the nutrient solution. Four treatment groups were established: control (CK, normal nutrient solution without PEG-6000), 7.5% PEG-6000 (T1), 15% PEG-6000 (T2) and 22.5% PEG-6000 (T3). Each treatment group was irrigated daily with 500 mL of the respective stress-inducing nutrient solution.

Sampling was conducted at 3, 6, 9 and 12 days after treatment between 8:00 and 9:00 AM. For each treatment at each sampling point, three pots were randomly selected as three independent biological replicates (each pot served as an experimental unit). To ensure representative measurements and obtain sufficient biomass, the three seedlings within each pot were pooled and measured as a single biological replicate.

Measurement of morphological and biomass traits

Determination of plant height and leaf area

Plant height was measured immediately upon sampling as the distance from the cotyledonary node to the shoot apex using a measuring tape. Leaf area was determined using the leaf disc punch method. Specifically, leaf discs of a known area were punched and the total leaf area was calculated based on the ratio of the dry weight of the leaf discs to the total dry weight of the leaves.

Determination of dry matter accumulation

At each sampling point, the sampled plants were destructively harvested and separated into roots, stems, leaves and petioles. The root systems were carefully washed with clean water to remove adhering sand. Subsequently, the separated organs were placed into paper envelopes and heat-shocked in a forced-air oven at 105°C for 30 min to halt enzymatic activity. The samples were then dried at 65°C to a constant weight. The dry mass of each component was accurately weighed using an analytical balance.

Allometric growth analysis

To quantitatively evaluate the biomass allocation strategies between the roots and shoots of the two soybean cultivars under varying degrees of drought stress, allometric growth analysis was conducted. The relationship between root and shoot biomass was mathematically described using the classical allometric power equation:

$$Y=aX^b$$

Where

X= Shoot dry weight (g).

Y= Root dry weight (g).

The parameter a is the allometric coefficient (intercept) and b is the allometric scaling exponent (slope).

To achieve linearity, homogenize variances and facilitate the comparison of slopes among different treatments, the empirical data were $\log_{10}$ -transformed prior to regression analysis, yielding the following linear equation:

$$\log_{10}(Y)=\log_{10}(a)+b \log_{10}(X)$$

In this context, the slope (b) reflects the relative biomass accumulation rate of the roots compared to the shoots. A slope of $b=1$ indicates isometric growth (proportional allocation), whereas $b \neq 1$ indicates allometric growth. Specifically, a reduction in the b value under stress conditions implies a suppressed relative expansion capacity of the root system in tandem with shoot growth.

Statistical analysis

Data processing and table generation were performed using Microsoft Excel 2010. Statistical analyses were conducted using IBM SPSS Statistics (Version 21.0, IBM Corp., Armonk, NY, USA), with the significance level set at $\alpha=0.05$. Prior to the analysis of variance (ANOVA), the assumptions of ANOVA were validated: The normality of the data distribution was assessed using the Shapiro-

wilk test ($p>0.05$) and the homogeneity of variances was evaluated using Levene's test ($p>0.05$). Since the experimental design encompassed three independent variables-soybean genotype, PEG concentration and stress duration-a three-way ANOVA was employed to evaluate the main effects and their interactive effects on the measured parameters. All graphical representations were generated using Origin 9.0 (Origin Lab Corp., Northampton, MA, USA).

RESULTS AND DISCUSSION

Effects of drought stress on soybean plant height and leaf area

Drought stress significantly inhibited plant height and leaf area in both soybean cultivars and the inhibitory effects increased with increasing PEG concentration and prolonged treatment duration (Fig 1). Overall, HN-65 was more sensitive to drought stress, whereas HN-44 showed a stronger capacity to maintain growth under stress conditions. For plant height, no significant differences were observed among treatments in HN-44 at 3 d after treatment. In contrast, plant height in HN-65 was already significantly lower than that of the CK under the T2 and T3 treatments, indicating that HN-65 was markedly inhibited during the early stage of stress. By 12 d, plant height had significantly decreased in both cultivars; however, the reductions in HN-44 under the T1-T3 treatments ranged from 18.57% to 50.58%,

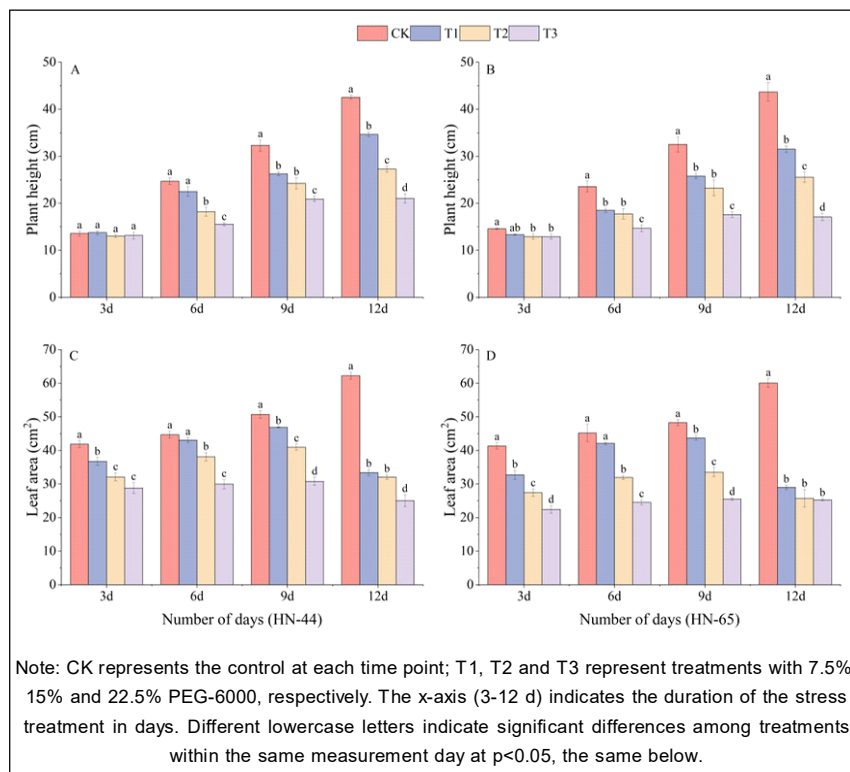


Fig 1: Effects of drought stress on the plant height and leaf area of soybean seedlings.

which were lower than those observed in HN-65, ranging from 27.82% to 60.92%.

Leaf area was more sensitive to drought stress than plant height. At 3 d, leaf area under the T1 treatment was already significantly lower than that of the CK in both cultivars and significant differences among treatments were observed in HN-65. By 12 d, leaf area decreased by 46.34%-59.78% in HN-44 and by 51.67%-57.85% in HN-65 under the T1-T3 treatments compared with the CK. In addition, no significant differences were observed among drought treatments in HN-65 at 12 d, suggesting that leaf expansion was severely restricted under prolonged stress. In contrast, HN-44 still maintained significant differences among treatments, indicating a stronger ability to sustain leaf area under drought conditions.

Effects of drought stress on dry matter accumulation in different organs

Drought stress significantly inhibited dry matter accumulation in leaves, stems, petioles and roots of both cultivars, with the inhibitory effect intensifying as PEG concentration increased (Fig 2). The most pronounced reductions were observed under the T2 and T3 treatments. Regarding shoot biomass, HN-44 exhibited greater resilience during the early stress stage. At 3 d, the leaf dry weight of HN-44 under T1 did not differ significantly from the CK, whereas HN-65 already showed a significant decline. By 12 d, dry weights of leaves, stems and petioles in HN-44 under T1-T3 decreased by 20.47%-59.21%, 35.69%-66.49% and 17.84%-59.46%, respectively, relative to the CK. In contrast, HN-65 experienced greater reductions (31.73%-67.96%, 40.22%-70.25% and 27.42%-71.51%, respectively), indicating that HN-44 maintains a stronger capacity for shoot biomass accumulation under drought.

Root dry weight followed a similar pattern. At 3 d, low-concentration PEG had minimal inhibitory effects, with root dry weights under T1 slightly exceeding those of the CK in both cultivars. However, prolonged stress led to significant suppression. By 12 d, root dry weights of HN-44 under T1, T2 and T3 decreased by 36.12%, 46.92% and 59.47%, respectively, compared to the CK. HN-65 showed slightly greater reductions under the same treatments (39.49%, 53.04% and 56.78%, respectively). Notably, under mild to moderate stress (T1 and T2), HN-44 exhibited a smaller decline in root biomass than HN-65, demonstrating a superior ability to sustain belowground growth under water deficit.

Drought stress on the root-to-shoot ratio

As illustrated in Fig 3, drought stress significantly altered the root-to-shoot ratio of both soybean cultivars and cultivars with varying drought tolerances exhibited distinct resource allocation capacities. Overall, the PEG treatments promoted an increase in the root-to-shoot ratio to a certain extent, reflecting the stress response of the plants under water-limited conditions. During the initial stress period (3 d), the root-to-shoot ratios of both cultivars significantly increased with increasing stress concentrations. Specifically, compared to the CK, the root-to-shoot ratio of HN-44 increased by 12.77%-38.30% under the T1-T3 treatments, while that of HN-65 increased by 20.20%-37.23%. This indicates that during the initial stage of stress, both cultivars exhibited a tendency to partition assimilates toward the roots. However, as the stress prolonged (6-12 d), the two cultivars exhibited contrasting allocation dynamics at 12 d. For HN-44, the root-to-shoot ratio under the T1 treatment decreased by 14.92% compared to the CK, whereas no significant differences from the CK were

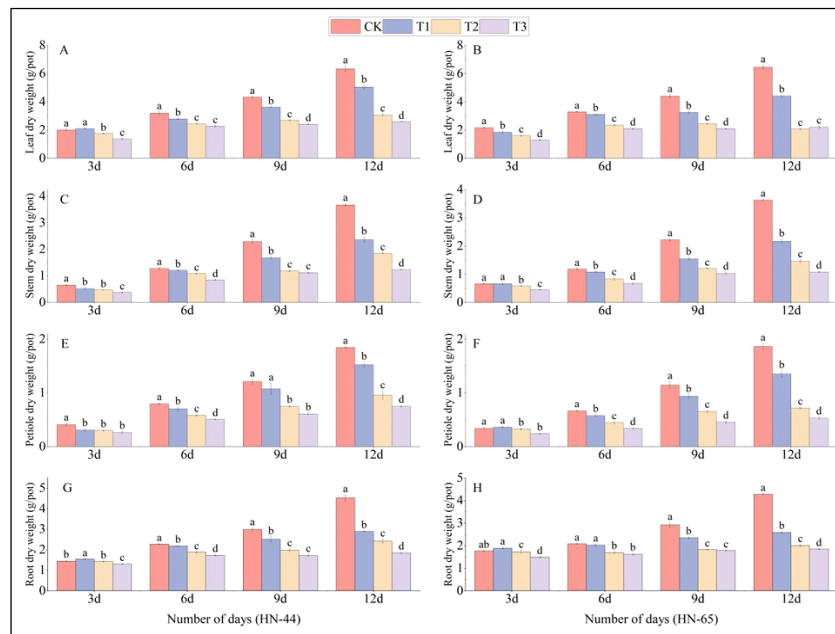


Fig 2: Effects of drought stress on the shoot and root dry weights of soybean seedlings.

observed under the T2 and T3 treatments. In contrast, HN-65 maintained a relatively high root-to-shoot ratio under the T2 and T3 treatments at 12 d, increasing by 25.23% and 28.70% relative to the CK, respectively. This suggests that under long-term stress, HN-44 was able to gradually adjust and maintain a relatively normal root-to-shoot balance, exhibiting superior overall growth coordination. Meanwhile, the persistently and significantly elevated root-to-shoot ratio in HN-65 was likely due to a more severe inhibition of its shoot (leaves, stems and petioles) biomass, resulting in a passive increase in the root-to-shoot ratio. This further highlights the high sensitivity of HN-65 to drought conditions.

Effects of drought stress on biomass allocation proportions in soybean

As illustrated in Fig 4, drought stress significantly altered the dry matter allocation proportions among various organs in both soybean cultivars, with HN-44 and HN-65 exhibiting differences in the magnitude and direction of allocation adjustments. Overall, during the early stage of stress, both cultivars generally exhibited an increasing trend in root mass fraction (RMF) accompanied by a decrease in leaf mass fraction (LMF). However, during the late stage of stress, this allocation pattern diverged significantly between the two cultivars.

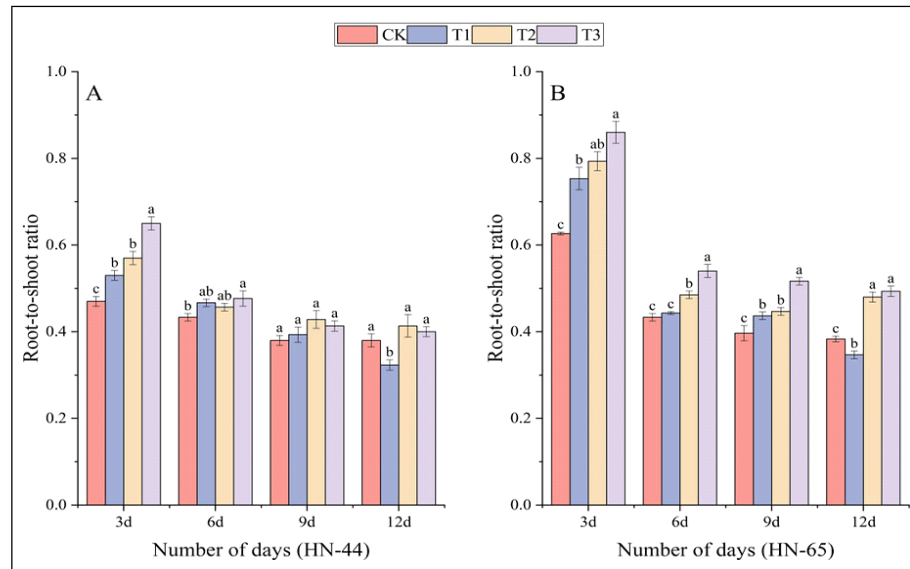


Fig 3: Effects of drought stress on the root-to-shoot ratio of soybean seedlings.

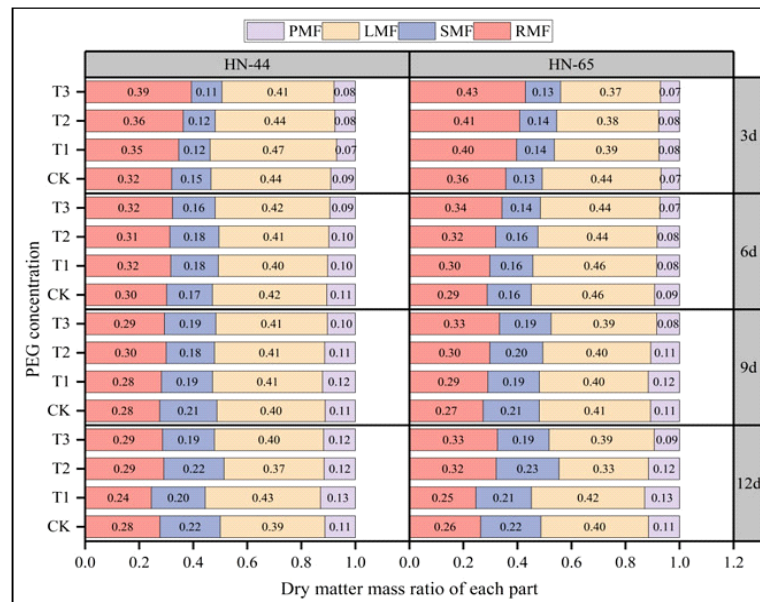


Fig 4: Effects of drought stress on biomass allocation proportions of soybean seedlings.

During the initial stress period (3 d), both cultivars displayed a stress response by preferentially partitioning assimilates to the belowground parts. With increasing PEG concentrations, the RMFs of HN-44 and HN-65 increased significantly, rising by 21.88% and 19.44% under the T3 treatment compared to the CK, respectively. In comparison, the LMF of HN-65 continuously decreased with increasing stress intensity (dropping from 0.44 in the CK to 0.37 under T3, a decrease of 15.91%). Conversely, the LMF of HN-44 exhibited a transient increase under the T1 treatment (0.47, an increase of 6.82% relative to the CK) before decreasing to 0.41 under T3 (a decrease of 6.82% relative to the CK). This indicates that the drought-tolerant cultivar could still maintain leaf dry matter accumulation to a certain extent during the early stage of stress. Additionally, the stem mass fraction (SMF) of HN-44 showed a downward trend with increasing stress at 3 d, whereas the SMF of HN-65 exhibited minimal overall changes. The petiole mass fractions (PMF) of both cultivars fluctuated only slightly at 3 d (ranging from approximately 0.07 to 0.09). During the middle stage of stress (6-9 d), the RMFs of both cultivars continued to rise with increasing stress intensity, but HN-44 exhibited relatively smaller changes, demonstrating a stronger allocation homeostasis. At 9 d of stress, the RMF of HN-65 under the T3 treatment was 0.33 (a 22.22% increase over the CK), whereas the RMF of HN-44 under T3 was 0.29 (only a 3.57% increase over the CK). Furthermore, the PMF of HN-65 under the T3 treatment at 9 d decreased to 0.08 (a 27.27% reduction compared to the CK), indicating a pronounced reduction in dry matter investment into petioles under prolonged stress.

As the stress prolonged to 12 d, the dry matter allocation of the two cultivars diverged significantly.

For HN-44, the RMF under the T1 treatment decreased to 0.24 (a 14.29% reduction compared to the CK), while its LMF increased to 0.43 (a 10.26% increase over the CK's 0.39) and its PMF rose to 0.13 (an 18.18% increase over the CK's 0.11). Under the T2 and T3 treatments, its RMF had retreated to levels essentially consistent with the CK and both LMF and PMF were maintained at normal or slightly higher levels than the CK. This suggests that during the late stage, the drought-tolerant cultivar can support photosynthesis and growth coordination by maintaining investment in shoot structures such as leaves and petioles. In contrast, the RMF of HN-65 under the T2 and T3 treatments remained relatively high, with a 26.92% increase under T3 relative to the CK. Meanwhile, its LMF under the T2 treatment significantly decreased to 0.33 (a 17.50% reduction from the CK's 0.40). This indicates that the dry matter investment in the shoots of the sensitive cultivar was more severely inhibited under long-term stress and the persistent elevation of its RMF was more likely a passive allocation shift caused by impaired shoot growth.

Effects of drought stress on the root-shoot growth relationship

To evaluate the impact of drought stress on plant biomass allocation strategies, the shoot and root biomass of the two cultivars under various PEG treatments were log-transformed and allometric growth equations were fitted (Fig 5). The results indicated that the log-transformed root and shoot biomass exhibited robust linear relationships across all treatments (all $R^2 > 0.80$). Drought stress not only altered the absolute biomass of the plants but also significantly shifted their root-shoot growth trajectories. Overall, as the drought severity intensified, the growth

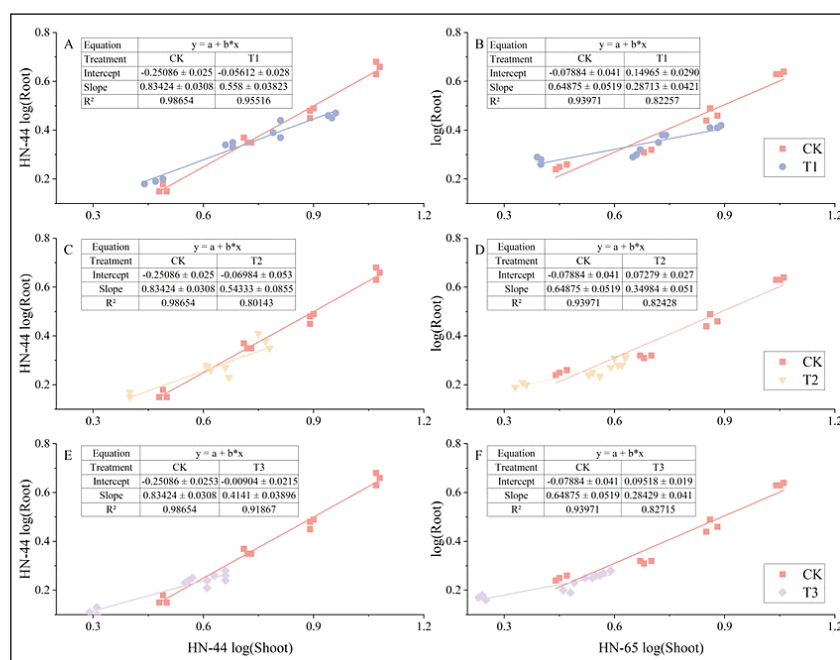


Fig 5: Allometric growth models of the root and shoot in soybean seedlings.

slopes of both cultivars exhibited a declining trend, indicating that water deficit disrupted the inherent biomass allocation patterns of the plants.

HN-44 demonstrated a more stable and moderate regulatory capacity. Under the CK condition, the growth slope of HN-44 was 0.834 ($R^2=0.987$). As drought stress intensified, its slope exhibited a gradual downward trend, with reductions ranging from 33.09% to 50.36% under the T1-T3 treatments. This suggests that under varying degrees of water deficit, HN-44 was capable of maintaining a relatively stable and predictable mechanism of synergistic root-shoot growth, adapting to the arid environment by adjusting its resource allocation.

In contrast, the growth relationship of HN-65 under drought exhibited profound sensitivity and instability. Under the CK condition, the slope for HN-65 was 0.649 ($R^2=0.940$). However, upon exposure to drought stress, its slope experienced a drastic decline, dropping by 46.22%-56.24% under the T1-T3 treatments. This result indicates that HN-65 is more susceptible to water deficit and the relative expansion capacity of its root system in tandem with shoot growth is rapidly suppressed.

Multifactorial analysis of variance on soybean morphology and biomass accumulation

To elucidate the effects of cultivar (C), treatment (T), time (D) and their interactions on soybean growth, a three-way analysis of variance (ANOVA) was performed on the morphological and biomass parameters (Table 1). The results indicated that the main effects of treatment (T) and time (D) were highly significant ($P<0.001$) for all measured parameters, accompanied by extremely high effect sizes (partial eta-squared, η_p^2 , ranging from 0.93 to 0.99 and 0.69 to 0.99, respectively). This demonstrates that water stress and growth duration are the primary determinants of plant phenotypic variations. Furthermore, with the exception of root dry weight, the main effect of cultivar (C) exerted a highly significant influence on all other morphological and biomass parameters ($P<0.001$).

Regarding interaction effects, the treatment $\times$ time (T $\times$ D) interaction was highly significant ($P<0.001$) across all parameters, indicating that the inhibitory effect of drought stress on plant growth was progressively and significantly exacerbated as the stress duration extended. Notably, the three-way interaction of cultivar, treatment and time (C $\times$ T $\times$ D) had a significant impact on leaf, stem and root dry weights, whereas it was not significant for plant height, leaf area and petiole dry weight. This finding suggests that under prolonged drought stress, the divergent drought tolerance strategies of the two cultivars are primarily manifested through alterations in internal biomass accumulation and allocation, rather than merely through modifications of external morphological dimensions.

Under drought stress, plants typically constrain their overall growth and limit leaf expansion to reduce transpirational area, which serves as a vital adaptive mechanism for maintaining internal water homeostasis

Table 1: Multifactorial analysis of variance on soybean morphology and biomass accumulation.

Parameters	Cultivar (C)		Treatment (T)		Day (D)		CT		C $\times$ D		T $\times$ D		C $\times$ T $\times$ D	
	F	η_p^2	F	η_p^2	F	η_p^2	F	η_p^2	F	η_p^2	F	η_p^2	F	η_p^2
Plant height	14.05***	0.18	261.51***	0.93	566.36***	0.96	3.35*	0.14	1.99	0.09	43.19***	0.86	1.15	0.14
Leaf area	74.52***	0.54	518.28***	0.96	48.05***	0.69	6.22**	0.23	0.72	0.03	46.46***	0.87	1.63	0.19
Leaf dry weight	59.66***	0.48	1436.43***	0.99	1526.49***	0.99	18.48***	0.46	20.78***	0.49	223.39***	0.97	5.9***	0.45
Root dry weight	3.49	0.05	636.03***	0.97	687.79***	0.97	1.69	0.07	34.35***	0.62	149.3***	0.96	2.14*	0.23
Stem dry weight	42.44***	0.40	1311.74***	0.98	2838.16***	0.99	1.47	0.07	22.52***	0.51	288.36***	0.98	3.48**	0.33
Petiole dry weight	63.09***	0.50	400.49***	0.95	844.14***	0.98	1.61	0.07	7.22***	0.25	75.16***	0.91	1.81	0.20

Note: C: cultivar; T: Treatment; D: Day. Values represent F-statistics and partial eta squared (η_p^2) from three-way ANOVA. Asterisks indicate significant differences: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

(Basu *et al.*, 2016). In our study, both soybean cultivars exhibited significant morphological suppression. However, the tolerant cultivar (HN-44) maintained active leaf expansion under prolonged stress, whereas the sensitive cultivar (HN-65) experienced severe growth stagnation. This difference suggests that drought-tolerant cultivars can delay leaf senescence and growth arrest through more effective osmotic adjustment or cellular homeostasis mechanisms during sustained water deficit (Fang and Xiong, 2015).

Furthermore, our results revealed an asynchronous response between morphological changes and biomass accumulation. While both cultivars adopted similar morphological strategies to restrict water loss, HN-44 maintained a significantly higher rate of dry matter synthesis. This indicates that despite morphological suppression, the tolerant cultivar may be associated with better maintenance of stomatal conductance and photosynthetic enzyme activity, thereby achieving greater water use efficiency and carbon assimilation under stress (Wang *et al.*, 2022; Yang *et al.*, 2021).

When confronted with environmental resource constraints, plants typically adjust the partitioning of dry matter among various organs (Latha *et al.*, 2024; Pavithra *et al.*, 2025). The "Optimal Partitioning Theory" postulates that plants tend to preferentially allocate more photoassimilates to the organs responsible for acquiring the most limiting resource, thereby maximizing overall growth performance (McCarthy and Enquist, 2007). In the early stages of stress (3 d), both cultivars increased their root mass fraction (RMF) and root-to-shoot (R/S) ratio. This early carbon shift toward the root system represents a rapid adaptive response to enhance water foraging capacity (Xu *et al.*, 2025).

However, sustaining a high proportion of root carbon allocation carries significant metabolic costs. As the stress prolonged to 12 d, the allocation strategies of the two cultivars diverged significantly. HN-44 adjusted its R/S ratio back toward control levels, promoting coordinated whole-plant growth rather than maintaining excessive root allocation. Conversely, HN-65 exhibited a continuously increasing R/S ratio. Crucially, our biomass analysis indicates that this high R/S ratio in HN-65 was not driven by active root growth, but was a passive consequence of severe shoot growth inhibition. Therefore, an excessively high R/S ratio under severe drought may not indicate superior drought tolerance, but rather reflect severe impairment of aboveground development (Palta and Turner, 2019).

When assessing plant responses to environmental stress, the root-to-shoot ratio at a single time point is frequently confounded by the absolute size of the plant. Consequently, observed variations in biomass allocation across different environments may merely reflect size-dependent variations rather than genuine shifts in allocation strategies (Weiner, 2004). Our results demonstrated that drought altered the allometric trajectories of both cultivars,

but their adaptive capacities differed. HN-44 exhibited a gradual decrease in its allometric slope, indicating a stable, regulated adjustment of root-shoot coordination to adapt to the arid environment. In contrast, HN-65 showed a sharp decline in its growth slope. This drastic reduction implies a severe disruption of its developmental coordination mechanism. This indicates that HN-65 is exceedingly vulnerable to water deficit; drought not only rapidly suppressed its overall growth but also drastically impaired the relative expansion capacity of its root system in tandem with shoot growth.

CONCLUSION

This study systematically elucidated the responses and biomass allocation mechanisms of soybean cultivars with contrasting tolerances to drought stress. Our findings demonstrate that although drought stress significantly constrains overall biomass accumulation in soybean plants, the elevated root-to-shoot ratio observed under water deficit serves as a crucial morphological adaptation to mitigate early-stage drought stress. The drought-tolerant cultivar, HN-44, exhibited a superior growth performance, which is inextricably linked to its capacity to sustain a higher proportion of belowground biomass allocation, effectively attenuate the decline in its allometric scaling slope and maintain a dynamic equilibrium in the relative growth rates between roots and shoots. Furthermore, the allometric analysis profoundly reveals that the drought tolerance of soybean hinges not merely on the absolute retention of root biomass or a simplistic elevation of the root-to-shoot ratio, but, more fundamentally, on preserving the stability of the coordinated shoot-root developmental trajectory.

ACKNOWLEDGEMENT

This work was supported by Scientific Research Startup Project for Doctoral Talent Introduction at Heilongjiang Agricultural Engineering Vocational and Technical University.

Disclaimers

The views and conclusions expressed in this article are solely those of the authors and do not necessarily represent the views of their affiliated institutions. The authors are responsible for the accuracy and completeness of the information provided, but do not accept any liability for any direct or indirect losses resulting from the use of this content.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

REFERENCES

- Basu, S., Ramegowda, V., Kumar, A. and Pereira, A. (2016). Plant adaptation to drought stress. *F1000Research*. 5: F1000 Faculty Rev-1554.

- Christian, J.I., Martin, E.R., Basara, J.B., Furtado, J.C., Otkin, J.A., Lowman, L.E., Hunt, E.D., Mishra, V. and Xiao, X. (2023). Global projections of flash drought show increased risk in a warming climate. *Communications Earth and Environment*. **4**: 165.
- Dilawari, R., Kaur, N., Priyadarshi, N., Prakash, I., Patra, A., Mehta, S., Singh, B., Jain, P. and Islam, M.A. (2022). Soybean: A Key Player for Global Food Security. In: *Soybean Improvement: Physiological, Molecular and Genetic Perspectives*. Springer. pp. 1-46.
- Esan, V.I., Obisesan, I.A. and Ogunbode, T.O. (2023). Root system architecture and physiological characteristics of soybean (*Glycine max* L.) seedlings in response to PEG6000 simulated drought stress. *International Journal of Agronomy*. <https://doi.org/10.1155/2023/9697246>.
- Fang, Y. and Xiong, L. (2015). General mechanisms of drought response and their application in drought resistance improvement in plants. *Cellular and molecular life sciences*. **72**: 673-689.
- Felisberto, G., Schwerz, F., Umburanas, R.C., Dourado-Neto, D. and Reichardt, K. (2023). Physiological and yield responses of soybean under water deficit. *Journal of Crop Science and Biotechnology*. **26**: 27-37.
- Guo, C., Bao, X., Sun, H., Zhu, L., Zhang, Y., Zhang, K., Bai, Z., Zhu, J., Liu, X. and Li, A. (2024). Optimizing root system architecture to improve cotton drought tolerance and minimize yield loss during mild drought stress. *Field Crops Research*. **308**: 109305.
- Huang, F., Yuan, H., Yang, J. and Li, X. (2026). Effects of drought stress during branching and pod formation stages on Morpho-physiology and yield in soybean. *Legume Research-An International Journal*. **49(3)**: 464-469. doi: 10.18805/LRF-908.
- Jaleh, D. (2017). Metabolic Adjustments, Assimilate Partitioning and Alterations in Source-sink Relations in Drought-stressed Plants. In: *Photoassimilate Distribution Plants and Crops Source-Sink Relationships*. [(eds.) Eli Zamski, Arthur A. Schaffer]. 1st Edition. Chapter 17. Routledge. pp. 407-420. <https://doi.org/10.1201/9780203743539>.
- Kim, J., Lee, C., Park, J.E., Mansoor, S., Chung, Y.S. and Kim, K. (2023). Drought stress restoration frequencies of phenotypic indicators in early vegetative stages of soybean (*Glycine max* L.). *Sustainability*. **15(6)**: 4852.
- Kumari, S., Dambale, A.S., Samantara, R., Jincy, M. and Bains, G. (2025). Introduction, History, Geographical Distribution, Importance and Uses of Soybean (*Glycine max* L.). In: *Soybean Production Technology: Physiology, Production and Processing*. Springer. pp 1-17.
- Kunert, K.J., Vorster, B.J., Fenta, B.A., Kibido, T., Dionisio, G. and Foyer, C.H. (2016). Drought stress responses in soybean roots and nodules. *Frontiers in Plant Science*. **7**: 1015.
- Latha, P., Anitha, T., Swethasree, M., Srividya, A. and Kumar Reddy, C.K. (2024). Effect of moisture stress on dry matter production, dry matter partitioning and yield in groundnut (*Arachis hypogea* L.) genotypes. *Legume Research-An International Journal*. **47(7)**: 1128-1135. doi: 10.18805/LR-5105.
- Lawlor, D. (1970). Absorption of polyethylene glycols by plants and their effects on plant growth. *New Phytologist*. **69**: 501-513.
- McCarthy, M. and Enquist, B. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*. **21(4)**: 713-720.
- Palta, J.A. and Turner, N.C. (2019). Crop root system traits cannot be seen as a silver bullet delivering drought resistance. *Plant and Soil*. **439**: 31-43.
- Pavithra, N., Jayalalitha, K., Sujatha, T., Harisatyanarayana, N., Jyothi Lakshmi, N. and Roja, V. (2025). Evaluation of blackgram (*Vigna mungo* L.) genotypes for dry matter partitioning, reproductive efficiency and yield under high temperature stress. *Legume Research*. **48(1)**: 75-85. doi: 10.18805/LR-5287.
- Poorter, H., Fiorani, F., Stitt, M., Schurr, U., Finck, A., Gibon, Y., Usadel, B., Munns, R., Atkin, O.K. and Tardieu, F. (2012). The art of growing plants for experimental purposes: A practical guide for the plant biologist. *Functional Plant Biology*. **39**: 821-838.
- Rajeswar, S. and Narasimhan, S. (2021). Peg-induced drought stress in plants: A review. *Research Journal of Pharmacy and Technology*. **14**: 6173-6178.
- Shadakshari, T., Yathish, K., Kalaimagal, T., Gireesh, C., Gangadhar, K. and Somappa, J. (2014). Morphological response of soybean under water stress during pod development stage. *Legume Research-An International Journal*. **37(1)**: 37-46. doi: 10.5958/j.0976-0571.37.1.006.
- Wang, B., Yang, X., Chen, L., Jiang, Y., Bu, H., Jiang, Y., Li, P., Cao, C. (2022). Physiological mechanism of drought-resistant rice coping with drought stress. *Journal of Plant Growth Regulation*. **41**: 2638-2651.
- Wang, L., Liu, L., Pei, Y., Dong, S., Sun, C., Zu, W. and Ruan, Y. (2012). Drought resistance identification of soybean germplasm resources at bud stage. *Journal of Northeast Agricultural University*. **43**: 36-43.
- Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*. **6(4)**: 207-215.
- Xu, C., McDowell, N.G., Fisher, R.A., Wei, L., Sevanto, S., Christoffersen, B.O., Weng, E. and Middleton, R.S. (2019). Increasing impacts of extreme droughts on vegetation productivity under climate change. *Nature Climate Change*. **9**: 948-953.
- Xu, W., Zhang, W., Yu, Y., Sun, W., Yu, L., Shang, D., Xue, C. and Zhang, Q. (2025). Response of crop photosynthetic product allocation under different water supply conditions: A global synthetic analysis. *Field Crops Research*. **333**: 110-104.
- Yang, C., Zhang, D., Li, X., Shi, Y., Shao, Y., Fang, B., Yue, J., Wang, H., Qin, F. and Cheng, H. (2021). Drought effects on photosynthetic performance of two wheat cultivars contrasting in drought. *New Zealand Journal of Crop and Horticultural Science*. **49**: 17-29.
- Yavas, I., Jamal, M.A., Din, K.U., Ali, S., Hussain, S. and Farooq, M. (2024). Drought-induced changes in leaf morphology and anatomy: Overview, implications and perspectives. *Polish Journal of Environmental Studies*. **33**: 1517-1530.