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Morpho-physiological and water use performance of soybean cultivars under drought stress at early growth stages

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Abstract

Drought is an important environmental stress for soybean (*Glycine max* (L) Merr.), which frequently occurs under second-crop conditions in the Mediterranean region of Türkiye and negatively affects early plant growth. In this study, we investigated the effects of drought stress (soil water content maintained at a constant 50% field capacity) on the early growth stage (V_3 stage) of different soybean cultivars (Ataem-7, BATEM Erensoy, Göksoy, and Lider). Twenty-seven-day-old soybean plants were exposed to drought stress for 20 days. Morphological (plant height, root length, seedling fresh and dry weight, root fresh and dry weight, and leaf area), physiological (leaf temperature, chlorophyll rate (CR), leaf relative water content (RWC), and electrolyte leakage (EL)), and water use (total water consumption (TWC), and water use efficiency (WUE)) traits were assessed. The results revealed a significant decrease in plant height, root length, leaf area, root and shoot fresh and dry weights, and RWC, and an increase in CR under drought stress. Although Lider and BATEM Erensoy exhibited better growth than the other cultivars under control conditions, their root and shoot growth decreased significantly under water stress. Notably, Ataem-7 presented a lower TWC and WUE difference between the drought treatment and the control, and this cultivar efficiently used water for dry matter production in the shoot and root parts. As a result, there were significant genotypic differences in drought susceptibility among the soybean cultivars, and Ataem-7 showed greater tolerance to drought than the other soybean cultivars did during the early growth stage.

Keywords: *Glycine max* (L.) Merr., Drought, Water use efficiency, Electrolyte leakage

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INTRODUCTION

Soybean (*Glycine max* (L.) Merr.) is the most important legume crop, with high contents of protein (36-45%) and oil (18-24%) in the seeds (Fehr, 1980; Pratab et al., 2012). It accounts for nearly 1/3 of global edible oil and 2/3 of protein sources (Sincik et al., 2008; Ergin et al., 2023). For this reason, it is the most popular oilseed crop in the world and is cultivated on a large area of 134 million hectares (FAO, 2024). The soybean is cultivated on an area of 38,000 hectares and is widely grown in the Mediterranean region of Turkey as the main and second crop after wheat or barley. Approximately 75% of soybeans are produced as a second crop (TUIK, 2024), which means that they can usually be planted in June when the temperature is above 30 °C and the risk of early drought due to low rainfall is high.

Drought stress is one of the most severe abiotic stresses affecting plant growth, especially in arid and semiarid regions of the world, as it suppresses the growth and development of plants during their life cycle. It inhibits various physiological events, such as the rapid degradation of proteins, membrane lipids, and photosynthetic pigments, and increases cell membrane damage due to increased ROS levels (Ahmedizadeh et al., 2011; Basal et al., 2020). These damages are not the same at every stage of plant development. Depending on the plant species, certain stages, such as germination, seedling, or flowering, could be the most critical stages for water stress

(Sinclair et al., 2010). Drought stress can affect soybean from germination to late blooming (Maleki et al., 2013), potentially reducing growth and seed yield by up to 40% (He et al., 2017; Ingwers et al., 2022; Yang et al., 2023), particularly during the flowering stage. The reduction in seed yield due to drought at the reproductive stage was 46-71% (Samarah et al., 2006). However, soybean cultivars may react differently to drought stress, with drought-tolerant genotypes retaining elevated traits such as leaf area and chlorophyll content even when exposed to drought stress in the vegetative stage (Yan et al., 2020). Some genotypes can recover from drought-induced injuries upon rewatering, resulting in compensatory effects on growth (Dong et al., 2019). Drought-tolerant genotypes in the early stages of development experience minimal damage and exhibit only slight decreases in yield (Yan et al., 2020; Yang et al., 2023). The screening of genotypes in early growing stages by monitoring certain physiological parameters linked with drought resistance is one strategy to improve selection efficiency (Khan et al., 2016; Guzzo et al., 2021; Simondi et al., 2022). Additionally, understanding the mechanisms of drought tolerance can help in developing cultivars that use water more efficiently and maintain high yields (Yang et al., 2023). Soybean plants develop a variety of mechanisms for drought adaptation. One mechanism is to improve the tolerance of soybean genotypes with relatively high water use efficiency. Another is the decline in whole plant water use during a soil water deficit event. Low leaf epidermal conductance is the third physiological trait that may increase drought tolerance and prolong crop survival during severe water stress (Hufstetler et al., 2007; Sadok and Sinclair, 2011). Therefore, this study aimed to identify the drought response of some soybean cultivars during the first three foliate stages via morphological, physiological, and water use features.

MATERIALS AND METHODS

This study was conducted at the Seed Science and Technology Laboratory of Eskişehir Osmangazi University, Türkiye, in 2023. Four soybean cultivars, Lider registered by Pro Gen Seed Inc. in 2014, and Ataem-7, BATEM Erensoy and Göksoy by Batı Akdeniz Agricultural Research Institute (Antalya) in 2006, 2010, and 2019, respectively, were used.

Plant growth conditions

The seeds of soybean cultivars were pre-germinated in Petri dishes at 20 °C for 48 h on filter paper moistened with distilled water. The seeds with radicle protrusion were transplanted into plastic pots (0.5 L) filled with a mixture of sieved field soil, perlite, and vermiculite (6:1:1 v:v:v). Just after transplanting, the plants were fertilized with the basal macronutrients N, P, and K (8-8-8). Eight plants from each cultivar were grown up to the V_1 stage (the first trifoliate), as reported by Fehr et al. (1971), in a growth chamber at 22 °C/18 °C day/night and 70-75% relative humidity.

Drought treatment

The field-water holding capacity (FC) of the soil mixture was determined before the experiment via the methodology modified by Liyanage et al. (2022). The soil was kept moist at 80% FC until the first leaf fully expanded (V_1 stage, 27 days after the emergence of the plants). The plants were separated into two plots, the control and drought stress plots, which were subjected to 80% and 50% FC for 20 days, respectively. By weighing each pot every other day, the water content of the pots was adjusted to the respective FC.

Assessment of morphological characteristics

The plants were harvested by cutting them from the soil surface and separating the aboveground parts from the underground parts. The leaves were removed as soon as the fresh plant biomass (shoot fresh weight) was weighed. All the leaves were scanned to compute the leaf area via ImageJ software (Cosmulescu et al., 2020). After the roots were washed and cleaned gently, the tap root was measured. After being dried for 24 hours at 80 °C in an oven, the samples of the roots and shoot sections were weighed.

Evaluation of physiological characteristics

Leaf temperature was measured via a Trotec BP21 infrared thermometer (Germany) before harvest. The chlorophyll content was estimated as the SPAD value, via a portable chlorophyll meter Konica Minolta SPAD-502 (Japan). Three consecutive readings were collected from distinct positions of fully expanded leaves (specifically, the middle leaflets of the 3^{rd} and 4^{th} leaves). These readings were combined to provide a single value for each duplicate. The third and fourth leaves from the apex were subsequently used for determining the leaf relative water content (RWC) and electrolyte leakage, respectively.

Leaf RWC was determined via the equation (1):

$$RWC\ (\%) = [(FW-DW)/(TW-DW)]\times 100 \quad (1)$$

where FW = is the fresh weight of the leaf, DW = is the dry weight of the leaf after drying to a constant weight at 80 °C for 24 h, and TW = is the turgid weight after the leaf samples were immersed in distilled water in a closed Falcon tube for 24 h in the dark at 20 °C (Batool et al., 2020).

Electrolyte leakage (membrane permeability) was determined via the method developed by Hniličková et al. (2019), with a few minor modifications. For each replicate, the third leaf located at the top of each plant was selected and washed with distilled water to remove electrolytes from the leaf surface. Six disks with a diameter of 5 mm were taken from each leaf after a gentle surface-drying process using paper towels. The samples were first weighed and then transferred into 50-mL glass tubes with 20 mL of distilled water before being placed in a dark incubator at 20 °C for 24 h. After incubation, the electrical conductivity (EC_1) of the bathing solution was measured at 25 °C via a WTW 3.15i EC meter (Germany). The samples were subsequently subjected to incubation inside a thermostatic water bath set at 90 °C for 40 min to eradicate all the cells. The electrical conductivity (EC_2) was measured at 25 °C after the tubes were cooled to room temperature. The electrolyte leakage (EL) was expressed as a percentage of EC_1/EC_2 (Kaya, 2023).

Evaluation of water use efficiency

The pots were weighed every other day and watered according to the determined drought levels. The total amount of water consumed during the study determined the overall water consumption value of the plants. The water use efficiency (WUE) was calculated using the formula (2) (He et al., 2017).

$$\text{WUE} = (\text{shoot dry matter} + \text{root dry matter})/\text{total water consumption} \quad (2)$$

Water consumption per shoot and root dry weight was obtained by dividing shoot dry weight by total water consumption.

Statistical analysis

The data were evaluated by a completely randomized design (CRD) with four replications using the MSTAT-C (Michigan State University, v. 2.10) program. The means were grouped by Duncan's Multiple Range Test at the $p < 0.05$ level. The R program was used to determine the Pearson's correlation coefficients between the characteristics and significance levels ($p < 0.01$).

RESULTS AND DISCUSSION

This study was conducted to determine the effects of drought stress on soybean cultivars at the early growth stage. A significant difference was determined for the investigated characteristics ($p < 0.05$) (Table 1).

Table 1. Main effects of drought stress on morphological characteristics of soybean cultivars

	Plant height (cm)	Leaf area (cm^2)	Shoot fresh weight (g $plant^{-1}$)	Shoot dry weight (mg $plant^{-1}$)
Drought stress (A)				
Drought	9.7^{b}	85.0^{b}	2.21^{b}	462^{b}ǂ
Control	13.3^{a}	161.9^{a}	4.24^{a}	791^{a}
Cultivar(B)				
Ataem-7	12.0^{a}	136.3^{a}	3.47^{b}	683^{b}
BATEM Erensoy	10.8^{b}	113.6^{b}	2.74^{c}	573^{c}
Göksoy	10.7^{b}	98.9^{c}	2.76^{c}	504^{d}
Lider	12.6^{a}	145.1^{a}	3.94^{a}	746^{a}
Analysis of variance				
A	**	**	**	**
B	**	**	**	**
A×B	**	**	**	**

ǂ: Means followed by the same letter(s) are not significant, **: significance level at $p < 0.01$.

Drought caused a significant decrease in the plant height of the soybean cultivars (Figure 1). Lider was the cultivar most adversely affected by drought, with a reduction of 40.9% (Figure 2A), whereas the reduction rates in plant height of the other cultivars were ranged from 20.0% to 21.7%. The Lider (12.6 cm) and Ataem-7 (12.0 cm) seedlings were longer than the other cultivars were. Drought not only shortened the plant height but also reduced the leaf area of the soybean cultivars.

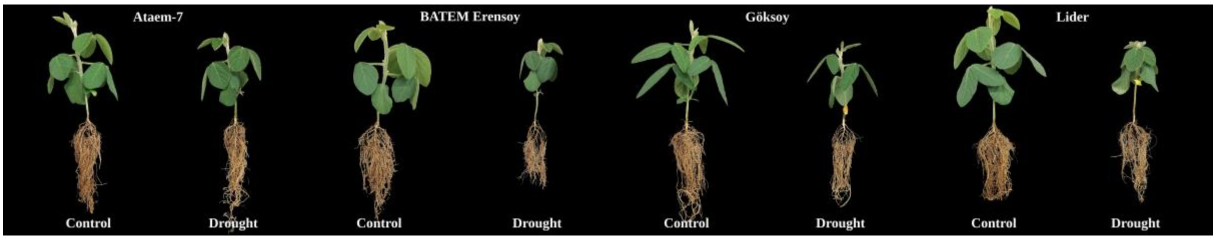

Figure 1. Seedlings of soybean cultivars under drought stress

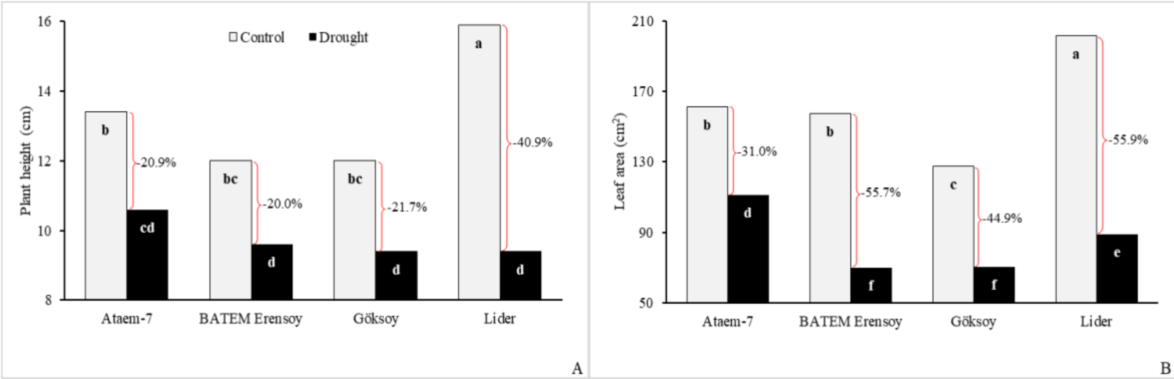

Figure 2. Changes in the plant height (A) and leaf area (B) of soybean cultivars under drought stress. The letter(s) on each column indicate significance at $p < 0.05$.

Leaf area is one of the most sensitive parameters to drought, and plants slow their leaf growth to protect themselves and continue their lives. The leaf area of the soybean cultivars significantly decreased with drought. The maximum reduction rates were noted in Lider (55.9%) and BATEM Erensoy (55.7%). Compare with the other cultivars, Ataem-7 was less affected by drought, decreasing the leaf area by 31.0% (Figure 2B). In a previous study, Poudel et al. (2023) reported a significant reduction in the leaf area of 10 soybean cultivars under drought stress. Similarly, Aziez (2023) reported that the maximum leaf size was determined at 100% field capacity while the lowest leaf size was at 25% field capacity in soybean. Water deficit inhibited the growth of the soybean cultivars. Miranda et al. (2023) observed a significant reduction in the fresh and dry weights of soybean seedlings as drought severity increased from 45% to 30% field capacity. In addition, the responses of cultivars varied. Similarly, Yan et al. (2020) found that root length varied with genotype, water application, and their interaction. Lumactud et al. (2022) observed that, compared with root, soybean shoots were more susceptible to drought, which led to the rapid suppression of shoot development. They demonstrated lower biomass in roots and shoots under drought stress than did the well-watered control. These results agree with those of the present study.

Table 2. Changes in the root characteristics of soybean cultivars under drought stress

	Root length (cm)	Root fresh weight (g plant^{-1})	Root dry weight (mg plant^{-1})
Drought Stress (A)			
Drought	18.8^{b}	2.33^{b}	352$^{b⸸}$
Control	25.1^{a}	4.83^{a}	591^{a}
Cultivar(B)			
Ataem-7	21.3^{bc}	4.47^{a}	564^{a}
BATEM Erensoy	20.6^{c}	2.77^{d}	410^{c}
Göksoy	21.6^{b}	3.37^{c}	426^{c}
Lider	24.3^{a}	3.72^{b}	487^{b}
Analysis of variance			
A	**	**	**
B	**	**	**
A×B	**	**	**

⸸: Means followed by the same letter(s) are not significant, **: significance level at $p < 0.01$.

The shoot fresh and dry weights also decreased by approximately 50% under drought stress and, the greatest reduction in seedling fresh weight was detected in Lider (Table 1). The shoot fresh and dry weights of Lider and Göksoy were lower than those of the other cultivars (Figure 3A and 3B). Lider (12.6 cm) and Ataem-7 (12.0 cm) plants had longer shoots than did the other cultivars. Drought caused a reduction in soybean growth. Our results align with the findings of Fatema et al. (2023), who determined shorter plants in soybean under water stress, and the findings of Desclaux et al. (2000), who reported the inhibitory effects of drought on the vegetative growth of soybean plants during the early growth stage.

Drought significantly impeded root development, but the cultivars responded differently (Table 2). As expected, the root length and fresh and dry weights of the soybean cultivars were substantially lower under drought stress, and the longest root length (24.3 cm) was measured in Lider. Under drought stress, the root length decreased by 37.6% in BATEM Erensoy, 35.6% in Lider, and 21.5% in Göksoy. The heaviest fresh (4.47 g plant^{-1}) and dry weights (564 mg plant^{-1}) of the roots were recorded in Ataem-7. It can be inferred that the root characteristics of Ataem-7 were the most stable, as minimal changes in root growth were observed between drought-exposed and control plants (Figure 3). The decrease in fresh root weight of the soybean cultivars due to drought stress ranged from 36.1% to 60.5% (Figure 3C). Significant reductions in root dry weight were also observed, with the greatest reductions in Lider (48.7%) and Göksoy (47.2%) (Figure 3D).

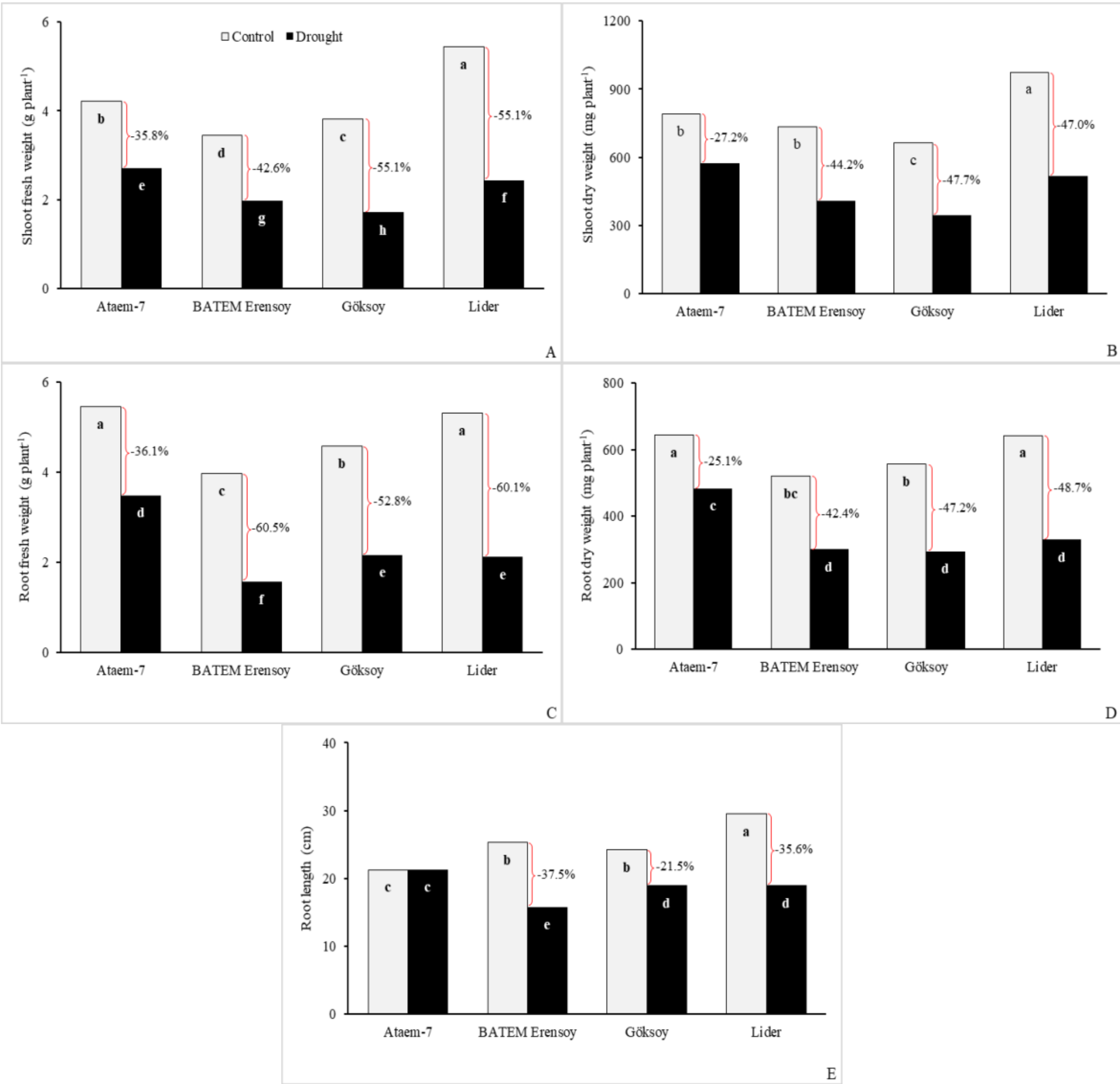

Figure 3. Changes in shoot fresh weight (A), shoot dry weight (B), root fresh weight (C), root dry weight (D), and root length (E) of soybean cultivars under drought stress. The letter(s) in each column indicate significance at $p < 0.05$.

Although the leaf temperatures did not vary with drought, significant differences were noted among the soybean cultivars. Of soybean cultivars, a relatively higher mean leaf temperature was recorded in Ataem-7 , whereas the lower was recorded in Göksoy (Table 3). The chlorophyll content was higher in plants subjected to drought than in control plants. Lider had the lowest chlorophyll rate among the soybean cultivars (37.4 SPAD). Increased chlorophyll content due to drought stress was more pronounced in Lider and Göksoy (Figure 4A). The RWC of the soybean cultivars decreased in a similar manner due to drought, and no significant differences among the soybean cultivars was detected. On the other hand, drought caused a reduction in the RWC of BATEM Erensoy by 18.6%, followed by Göksoy (17.9%), Lider (15.6%), and Ataem-7 (10.4%) (Figure 4B). Compared with control plants, drought-stressed plants leaked significantly more electrolytes. Among the cultivars, the highest leakage was recorded in Lider and Ataem-7 (Table 3). Our results are in agreement with the findings of Tiwari et al. (2023), who reported that electrolyte leakage increased under drought stress in chickpea. The relative water content was reduced in soybean plants exposed to drought, but this reduction varied among the soybean cultivars. Under drought stress, the lowest reduction in leaf water content was detected in Ataem-7, and the highest was recorded in BATEM Erensoy and Göksoy. Zegaoui et al. (2017) stated that plants can regulate water use when exposed to water stress; therefore, the relative water content of leaves could be used to determine their resistance to drought stress. Mishra and Patidar (2023) also found that drought-tolerant genotypes of several crops presented relatively high leaf-relative water content under water stress and revealed significant differences in RWC among soybean cultivars. This difference might be explained by genotypic variations that vary in their capacity to regulate stomata-mediated water loss during transpiration or their ability to absorb water from the soil. Moreover, Delevar et al. (2023) reported that drought stress damaged the membrane system and chlorophyll content of soybean leaves.

Table 3. Main effects of drought stress on physiological characteristics of soybean cultivars

	Leaf temperature (°C)	Chlorophyll rate (SPAD)	Relative water content (%)	Electrolyte leakage (%)
Drought Stress (A)				
Drought	26.7	41.8[a]	75.7[b]	18.4[bɫ]
Control	26.6	35.3[b]	89.8[a]	20.3[a]
Cultivar(B)				
Ataem-7	26.8[a]	38.4[ab]	83.0	19.9[ab]
BATEM Erensoy	26.7[ab]	39.8[a]	81.4	18.6[b]
Göksoy	26.3[c]	38.7[ab]	83.4	18.7[b]
Lider	26.6[b]	37.4[b]	83.3	20.2[a]
Analysis of variance				
A	*ns*	**	**	**
B	**	*	*ns*	*
A×B	*ns*	*	*	*ns*

ɫ: Means followed by the same letter(s) are not significant, *, **: significance level at $p < 0.05$ and $p < 0.01$, respectively; ns: not significant.

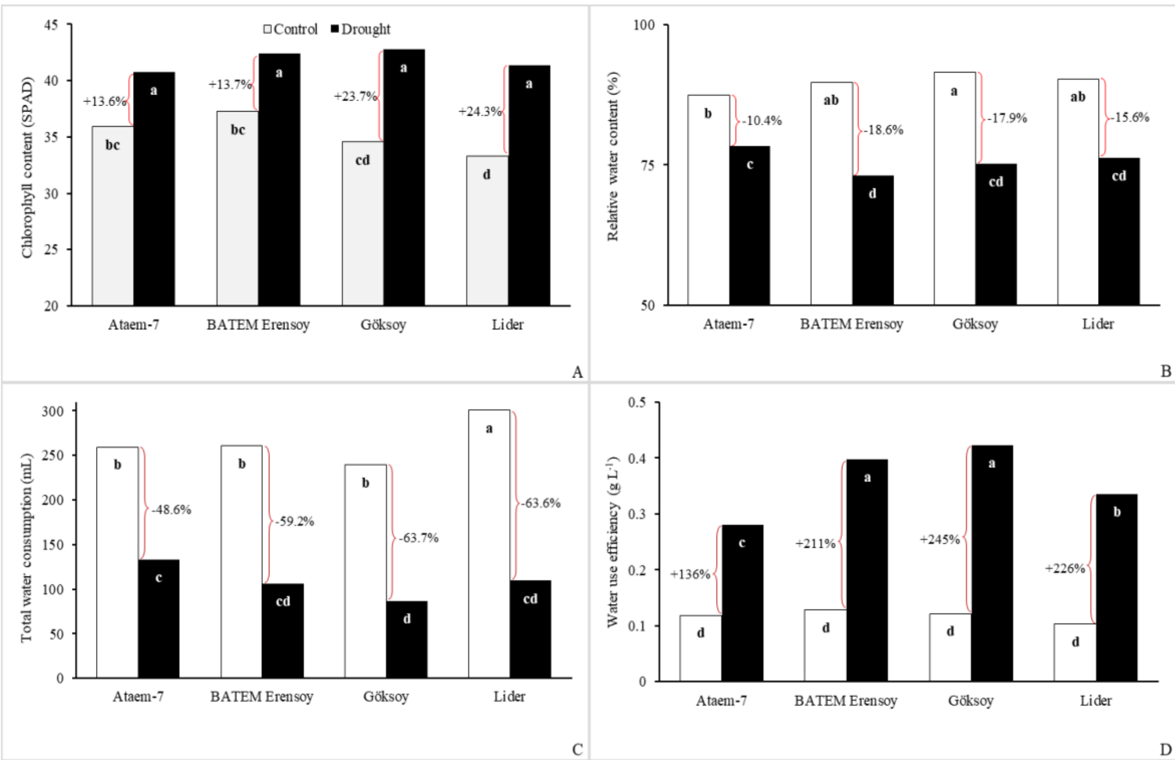

Figure 4. Changes in chlorophyll content (A), relative water content (B), total water consumption (C), and water use efficiency (D). The letter(s) in each column indicate significance at $p < 0.05$

Plant water consumption changes when water availability is limited. Among the soybean cultivars, Ataem-7 had the highest water use efficiency, whereas Göksoy (63.7%) and Lider (63.6%) had the highest water consumption (Figure 4C). Water use efficiency (WUE) reflects the water production of a plant under various irrigation water availability and soil moisture conditions. Drought-tolerant plants can maintain their physiological progress while also adjusting their water consumption. In general, the WUE of plants decreases under water deficit conditions, and vice versa, plants fail to generate optimal yields, and a greater transpiration rate results in a lower WUE under drought stress (Farajollahi et al., 2023). In this study, the WUEs of soybean cultivars were similar to each other under unstressed conditions, but they responded differently to drought. Göksoy achieved the highest WUE, followed by Batem Erensoy. Compared with the other cultivars, Ataem-7 presented the minimum increase in WUE due to drought (Figure 4D). This result is in line with the findings of Guo et al. (2023), who reported that, compared with the control, drought stress considerably increased the photosynthetic water-use efficiency in maize cultivars.

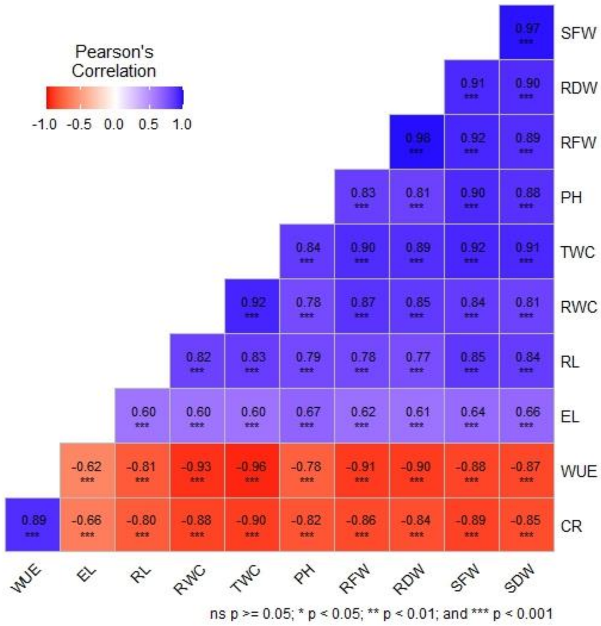

Figure 5. Pearson's correlation coefficients between the investigated characteristics. PH: Plant height, EL: Electrolyte leakage, RL: Root length, RWC: Relative water content, CR: Chlorophyll content, TWC: Total water consumption, WUE: Water use efficiency, RFW: Root fresh weight, RDW: Root dry weight, SFW: Shoot fresh weight, SDW: Shoot dry weight

The correlation coefficients between the examined characteristics and significance levels are given in Figure 5. The total water consumption (TWC) was highly correlated with shoot fresh weight (SFW) (r = 0.92***). Additionally, the relationship between TWC and RFW was significantly positive (r = 0.90***). WUE was correlated with CR (r = 0.89***), suggesting that increased WUE may stimulate CR. As expected, a negative and significant correlation was detected between TWC and WUE (r = -0.96***). In addition, TWC was significantly related to RFW (r = 0.90**) and SFW (r = 0.92***). Recent studies demonstrated that the wue had significant relationships with root fresh and dry weight under long-term drought stress and that root dry weight should be a useful selection criterion for high WUE (Puangbut et al., 2009; Wijewardana et al., 2019; Gebre and Earl, 2021).

CONCLUSION

This study demonstrated that drought stress resulted in a decreased leaf area, relative water content, seedling fresh weight, seedling dry weight, root length, root fresh weight, and root dry weight, while soybean cultivars showed different responses to drought. Higher total water consumption and lower water use efficiency were obtained from the plants subjected to drought in terms of the characteristics mentioned above. Among the soybean cultivars, Ataem-7 appeared more tolerant to drought stress because it had the lowest percent reduction in both morphological and physiological traits. Drought tolerance stems from improved root growth and total water use under drought, and these traits should be considered for promising breeding traits in soybean.

Compliance with Ethical Standards

Peer-review

Externally peer-reviewed.

Declaration of Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Author contribution

NE, MDK and EGK designed the study. NE and PH executed the experiments and analyzed the data. All the authors interpreted the data, critically revised the manuscript for important intellectual content and approved the final version.

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