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Enhancing Drought Tolerance in Two Soybean Genotypes with Varied Susceptibilities Through Foliar Application of Acetic Acid

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Abstract
Soybean is a very important food legume because of its high protein and oil concentrations. However, soybean is vulnerable to drought stress, which has become more severe and occasional in many regions worldwide. To alleviate drought's influence, the application of certain agents is increasingly gaining attention as it is economically affordable and practically applicable. Acetic acid (AA) is, by far, one of the cheapest agents that are reported to have potential benefits against drought; however, no accurate data on its influence on soybean genotypes differing in their drought tolerance are published. An experiment was conducted in a controlled environment to evaluate the effects of AA on the morpho-physiology of two soybean (*Glycine max* (L.) Merr.) genotypes: drought-tolerant 'Speeda' and drought-susceptible 'Coraline.' Chlorophyll-a and total carotenoids, stomatal conductance, and specific leaf area of both soybean genotypes decreased under water deprivation conditions. However, AA application enhanced these traits significantly. Drought reduced the optimal and the actual photochemical efficiency of PSII of 'Coraline,' but not 'Speeda.' The application of AA could not enhance the relative water content of both genotypes. Root and shoot morphology were negatively influenced by drought in both genotypes; however, AA helped in restoring these traits in 'Coraline,' but not 'Speeda,' indicating that AA application might be more beneficial in the case of drought-susceptible soybean genotypes.

Keywords Abiotic stress · Exogenous spray · Morpho-physiology · Water deprivation

Introduction

For thousands of years, soybean (*Glycine max* (L.) Merr.) has historically been used as a forage and a major protein and oil crop. Soybean is one of the most important food legumes due to its high protein (about 40%) and oil (about 20%) concentrations, as well as carbohydrates and minerals (Maleki et al. 2013). In the last four decades, soybean production has remarkably grown (Müller et al. 2021), however, to meet the expanding human population's need for plant protein, soybean production will have to increase by 70% over the next few years (Godfray et al. 2010; Tilman et al. 2011).

Droughts are anticipated to become even more often and severe in many regions of the world, putting significant strain on global agricultural supply (Zia et al. 2021; Gáspár et al. 2022). According to Wei et al. (2018), soybean yields can drop by more than half under dry or drought conditions, resulting in significant losses incurred for agricultural producers. Drought stress is a critical nonbiological force that can influence the morphological, physiological, and molecular processes such as photosynthesis immediately and extensively (Nabi et al. 2021), in addition to other light-related physiological parameters such as chlorophyll content and fluorescence (Basal et al. 2020). It also reduces leaf area, biomass output, and stem extension, affects cellular turgor pressure, inhibits water uptake and content, and impairs gas exchange efficiency and nutrient uptake, according to numerous studies (Khatun et al. 2021; Hussain et al. 2018; Dos Santos et al. 2022). Drought stress can also promote the formation of reactive oxygen species (ROS) and membrane lipid peroxidation, resulting in poor plant growth and, in extreme situations, death (Nadeem et al. 2019). Considering the impact of drought stress on plants becomes crucial as a

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result of these concerns, as this knowledge may be utilized to enhance irrigation scheduling techniques, lowering drought-related variations in food output. When germinating seeds are subjected to severe stress, restrained germination is likely (Swigonska and Weidner 2013).

Treating plants with cost-effective sensing molecule(s) (SMs) has garnered considerable attention for its potential to alleviate drought in a variety of agricultural crops, including soybean. Additionally, it was found that ROS play a major part in controlling stomatal closure to maximize irrigation efficiency (Huang et al. 2009). Chen et al. (2016) found that foliar application of hydrogen sulfide (H_2S) enhanced the water potential and osmolarity of *Spinacia oleracea* leaves under drought stress by lowering malondialdehyde (MDA) levels. Furthermore, at low concentrations, H_2S is known for its critical part in the regulation of physiological mechanisms in plants, including germination of seeds (Li et al. 2020), root development (Hu et al. 2020), stomatal conductance (Lisjak et al. 2011), photosynthesis (Chen et al. 2011), and toleration of abiotic and biotic stresses (Shi et al. 2015). Ethanol also has appeared as an outstanding example of organic SMs that have already demonstrated promising results in alleviating the harmful effects of various abiotic stresses in rice (Kato-Noguchi et al. 2001), soybean (Das et al. 2022) and Arabidopsis (Nguyen et al. 2017).

Acetic acid (CH_3COOH), commonly known as ethanolic acid, is the most abundant carboxylic acid found in lignocellulosic hydrolysates. A dilute (roughly 5% by concentration) acetic acid solution is obtained through fermentation and oxidation of naturally occurring carbohydrates (Brown and Poon 2016). Exogenous acetic acid (AA) uses for mitigating abiotic stressors such as drought, salt, and copper stress are substantial (Matsui et al. 2016). Transcriptome profiling in cassava (*Manihot esculenta*) revealed that AA supplementation improved tolerance of drought by upregulating genes involved in the abscisic acid (ABA) signaling pathway (Utsumi et al. 2019). Sun et al. (2022) proved in apple plants, that the external application of AA influenced the ABA- and jasmonic acid-induced mitogen-activated protein kinase (MAPK) signaling pathways. When compared to only water-sprayed plants, AA-sprayed plants had higher root biomass, which may put up to improved water and nutritional status maintenance, delayed photosynthetic pigment decomposition, and improved photosynthetic rate (Mostofa et al. 2021). Drought-induced effects were mitigated by foliar application of AA, as evidenced by improvements in soybean growth and leaf phenotypes, shoot height, shoot and root DW, total leaf area per trifoliate, and leaf succulence (Rahman et al. 2021); however, the potential different responses of soybean genotypes varying in drought tolerance are lacking. Moreover, the fluorescence traits in response to the sole and the mutual effect of drought and AA application are not fully studied either. In a big field experiment, a total of 25 soybean genotypes were subjected to drought stress during 2017, 2018 and 2019 cropping years (Basal 2021). Based on their performance, 2 genotypes different in their susceptibility to water deprivation; Coraline (drought-susceptible) and Speeda (drought-tolerant) were chosen for this study. Our research focused on evaluating the possible impact of acetic acid in reducing the drought effect on these genotypes by evaluating certain morpho-physiological traits.

Materials and Methods

Experimental Conditions and Treatments

The experiments were conducted at the University of Debrecen, Institute of Crop Sciences at the climatic room of the department of applied plant biology under controlled conditions in 2022. Relative humidity was maintained between 65 and 75%, the light/dark cycle was 16–8 h with a respective 24–20 °C temperature periodicity, and light intensity was kept at a constant 300 µmol $m^{-2}s^{-1}$ during daytime.

The seeds of the two soybean genotypes, 'Speeda' and 'Coraline,' were surface sterilized for 20 min with 6% (*v*/*v*) H_2O_2, rinsed well with deionized water, and geotropically germinated within moist filter sheets at 22 °C. Seedlings with good vigor were potted in 1.7 L pots after germination. Three seedlings were placed in each pot. Each pot received 170 ml of a dicot nutritional solution containing 2.0 mM $Ca(NO_3)_2{\cdot}4H_2O$; 0.7 mM K_2SO_4; 0.5 mM $MgSO_4{\cdot}7H_2O$; 0.1 mM KH_2PO_4; 0.1 mM KCl; 0.5 µM $MnSO_4{\cdot}4H_2O$; 0.5 µM $ZnSO_4{\cdot}7H_2O$; 0.2 µM $CuSO_4{\cdot}5H_2O$ and 10 µM H_3BO_3, iron was provided in the form of 10^{-4}M Fe-EDTA (Cakmak and Marschner 1990). Every 3 days, the nutrient solution in each pot was replaced with a fresh one. Drought was induced using PEG 6000 (VWR International bvba Geldenaaksebaan, Leuven, Belgium) when the plants reached the V3 stage (BBCH 103) (Meier 2018) and kept for 8 days. The PEG concentrations were 0% (*D*0 = control) and 10% (*D*1 = drought stress treatment). Along with 10% PEG treatment, 2 ml of 20 mM Acetic Acid (AA) was sprayed on drought-stressed plants each time the nutrient solution was changed, starting from the day PEG was applied until the end of the experiment (8 days after drought stress application) (i.e., at days 1,4 and 7 of PEG imposition). Each treatment had 3 replications. Thus, there were 3 treatments: control treatment (D0), growing in ideal conditions with no drought stress; drought-stressed treatment (D1) and drought-stressed treatment with acetic acid spray applied (D2). The total number of pots was 18 (2 genotypes × 3 treatments × 3 replications).

Determination of Chlorophyll-a, Chlorophyll-b, and Total Carotenoids

The extraction of chlorophyll-a, chlorophyll-b and total carotenoids was done using the procedure outlined by (Moran and Porath 1980). Fifty mg of each fresh leaf was diluted in 5 ml *N*,*N*-Dimethylformamide (*N*,*N*-DMF). This mixture was then kept in 4 °C for 72 h before the pigment extract concentration was evaluated using UV–Vis spectrophotometry (Metertech SP-830 PLUS, Taiwan) at three wavelengths: 480, 647, and 664 nm. Calculations of chlorophyll-a and chlorophyll-b, as well as total carotenoids, were made using the following equations (Wellburn 1994).

Determination of Chlorophyll Fluorescence Parameters

To quantify chlorophyll fluorescence parameters on dark-adapted leaves, light exclusion clips were placed to the central part of each leaf (avoiding main veins) for 20 min. The characteristics of chlorophyll fluorescence were determined in compliance with Schreiber et al. (1986) using a portable chlorophyll fluorometer-PAM-2100 (WALZ, Germany). The youngest, fully developed leaves were dark-adapted for 20 min. After dark adaptation, the initial fluorescence (F_o) was excited by weak light (0.1 µmol m^{-2} s^{-1}). The maximal fluorescence (F_m) was induced by white saturating flash (8000 µmol m^{-2} s^{-1}) (fast phase of chlorophyll fluorescence). The difference between maximum and minimum fluorescence is referred to as variable fluorescence (F_v). The F_v/F_m ratio is an indicator of the maximum quantum yield of photosystem II (a quantitative measure of the maximal photochemical efficiency of photosystem II, called optimal photochemical activity (Kitajima and Butler 1975)).

Additionally, the F_v/F_o value was calculated as an indicator of the size and the number of active photosynthetic reaction centers (Dan et al. 2000). The actual photochemical efficiency of PSII ($\Delta F/F_m' =$ Yield) was determined under growing light intensity.

Determination of Relative Water Content

Five fully matured leaves were collected, and their fresh weight (FW) was determined immediately. The dry weight (DW) of the sample leaves was determined by drying them to a constant mass (after 72 h) at 70 °C. The relative water content (RWC) was determined as follows (Cheng et al. 2012):

$$\text{RWC}\ (\%) = \{(Fw - Dw)/Fw\} * 100\%$$

Determination of Specific Leaf Area

The specific leaf area (SLA) was calculated by drying five leaf disks from the same fully matured leaves with known area at 70 °C for 48 h, then determining the dry weight and calculating the SLA as stated by Wilson et al. (1999).

Determination of Stomatal Conductance

The AP4 porometer was used to determine the stomatal conductance (g_s) (Delta-T devices, UK). It was calculated by taking the average of four values from the youngest fully developed leaves of each repetition.

Determination of Shoot and Root Morphological Traits

On harvest day, one plant was selected from each pot. The roots and shoots were separated. After measuring the length with a standard ruler, they were separately weighed to determine the fresh weight. Following that, they were oven-dried for 72 h at 70 °C and the dry weight was determined.

Determination of Root Volume

Roots of each sample were placed in a graded (ml) tube containing a known volume of water and the rise in water volume upon root insertion, which represents the root volume (cm^3) was determined.

Statistical Analyses

The analysis of variance (2-way ANOVA) test was conducted to compare the means of the different treatments (alpha = 0.05). When the difference was significant, the Turkey HSD post hoc test was conducted to indicate the statistically different means ($p \leq 0.05$) using GenStat software (Genstat V 26, VSNi, UK).

Results

Morphological Parameters of the Roots

In 'Speeda,' the root dry weight was not affected by the imposition of drought stress. However, the plant roots of the drought-stressed treatment that received AA foliar spray had significantly lower dry weight (Fig. 1A). In 'Coraline,' on the other hand, the AA foliar application resulted in significantly higher root dry weight as compared to the other treatments.

The root dry weight of AA-sprayed plants (D2) was significantly higher in 'Coraline' as compared to 'Speeda,'

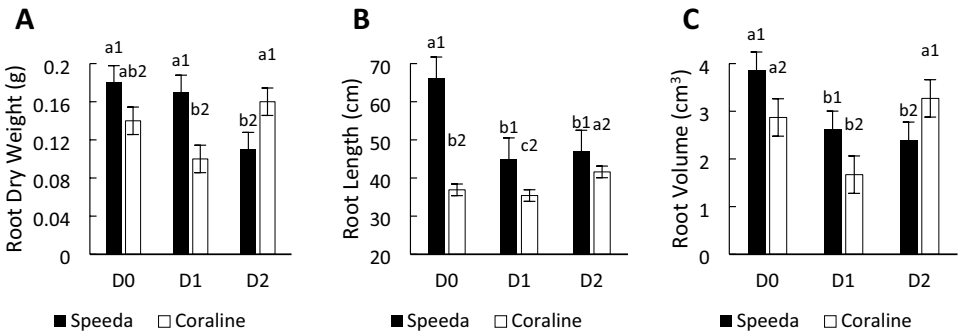

Fig. 1 Root dry weight (**A**), root length (**B**), and root volume (**C**) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

whereas it was significantly lower in both (D0) and (D1) treatments (Fig. 1A).

Both the root length and the root volume of 'Speeda' plants decreased significantly as a consequence of drought stress application. Moreover, the AA application did not have a measurable effect on any of these traits. In Corlaine, however, the foliar spray of AA significantly increased both the root length and the root volume of the drought-stressed plants (D2) as compared to the non-treated, drought-stressed counterparts (D1) (Fig. 1B, C).

'Speeda' had longer roots, regardless of treatment, and higher root volume in both (D0) and (D1) treatments, whereas the AA-treated (D2) treatment of 'Coraline' had significantly higher root volume as compared to (D2) treatment of 'Speeda' (Fig. 1B, C).

Morphological Parameters of the Shoots

Drought stress imposition significantly decreased the shoot dry weight of both genotypes. The foliar spray of AA significantly increased the shoot dry weight of 'Coraline' plants, but not of 'Speeda.' The drought-stressed (D1) 'Speeda' plants had significantly higher shoot dry weight as compared to 'Coraline' counterparts (Fig. 2A).

In 'Speeda', drought stress reduced the shoot length; however, the reduction was insignificant, and the AA foliar spray did not enhance this trait. On the contrary, drought significantly decreased the shoot length of 'Coraline' plants, and the AA application could significantly enhance this trait and keep the shoot length on a level very close to that of the control plants. 'Speeda' had higher shoot dry weight in both (D0) and (D1) treatments as compared to 'Coraline,' and also higher shoot length in all treatments (Fig. 2B).

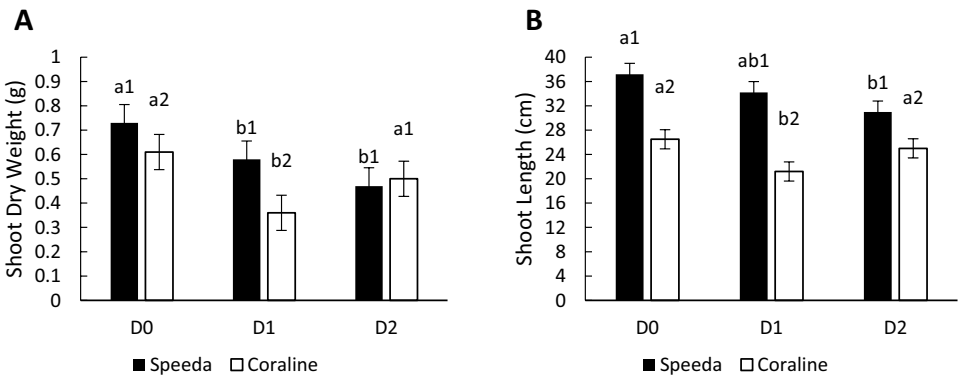

Fig. 2 Shoot dry weight (**A**) and shoot length (**B**) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

Specific Leaf Area

Drought stress imposition resulted in decreased specific leaf area (SLA) in both genotypes; however, the decrease was insignificant. The SLA significantly increased in both genotypes in drought-stressed plants sprayed with AA (D2) as compared to (D1) counterparts (Fig. 3).

Regardless of treatment, the differences between the 2 genotypes were slight and insignificant.

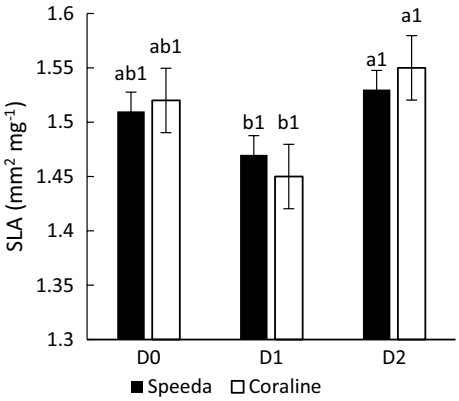

Fig. 3 Specific leaf area of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

Chlorophyll Fluorescence Parameters

The optimal photochemical efficiency of PSII (Fv/Fm) (Fig. 4A), the size, and number of active photosynthetic reaction centers (Fv/Fo) (Fig. 4B) and the actual photochemical efficiency of PSII (Yield) (Fig. 5) decreased in both genotypes when drought stress was imposed, with more announced effect in the case of 'Coraline.' These traits were positively influenced by the AA foliar application as their values were restored to levels very close to the control counterparts.

Drought stress resulted in decreased Fv/Fm value in both genotypes similarly; however, 'Coraline' plants had significantly higher Fv/Fm values under both control (D0) and AA-treated (D2) treatments (Fig. 4A). Moreover, the actual photochemical efficiency was higher in 'Coraline,' regardless of treatment (Fig. 5).

Chlorophyll-a and Chlorophyll-b Contents

Chlorophyll-a level in control treatment (D0) was insignificantly higher as compared to the drought-stressed treatment (D1) in both genotypes. However, the application of AA (D2 treatment) has led to statistically significant increase in chlorophyll-a content as compared to (D1) treatment (Fig. 6A). The differences between the 2 genotypes were insignificant, regardless of treatment.

In both genotypes, drought stress did not result in measurable changes in chlorophyll-b content, however, a significant increase in this trait was recorded in (D2) treatment in both genotypes. The concentration of chlorophyll-b was higher in 'Coraline' in (D0), but lower in (D1) and (D2) treatments as compared to 'Speeda'; however, these differences were insignificant (Fig. 6B).

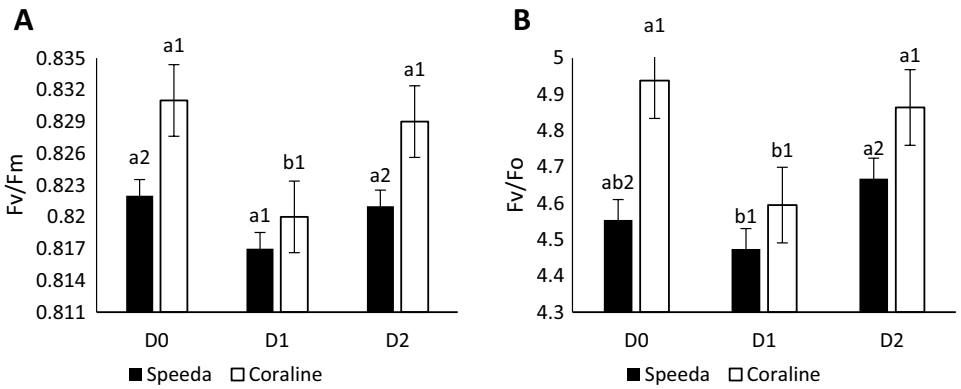

Fig. 4 Optimal photochemical efficiency of PSII (F_v/F_m) (A) and the size and the number of active photosynthetic reaction centers (Fv/Fo) (B) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

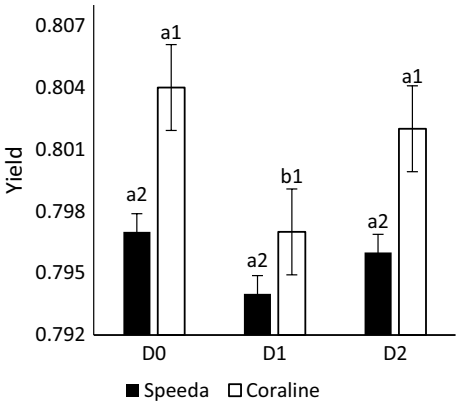

Fig. 5 Actual photochemical efficiency of PSII (yield) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

Total Carotenoids Content

Drought stress resulted in significant reduction in the total carotenoids in both genotypes. However, the drought-stressed plants that were sprayed with AA (D2) had significantly higher total carotenoids content as compared to the drought-stressed treatment (D1). Moreover, (D2) treatment resulted in total carotenoids content that was higher than the control plants in 'Coraline' genotype (Fig. 7).

Stomatal Conductance

Significant reduction in the stomatal conductance was recorded in both genotypes as a consequence of subjecting the plants to drought stress. However, the foliar application of AA enhanced this trait in both genotypes, with more announced effect in 'Speeda' genotype, where the increase was significant as compared to the drought-stressed counterpart (Fig. 8). Drought stress (D1) reduced the stomatal conductance of both genotypes to similar levels; however, the response of 'Speeda' to foliar AA application (D2) was significantly higher than that of 'Coraline' (Fig. 8).

Relative Water Content

The relative water content significantly decreased in both genotypes as a result of drought stress imposition, and the AA foliar spray could not alleviate the effect of drought. Both genotypes reacted similarly, and there were no measurable differences between them (Fig. 9).

Discussion

The optimal photochemical efficiency of PSII is an indicative trait that is widely used to assess the physiological response of drought-stressed plants (Song et al. 2022). In our experiment, the optimal photochemical efficiency of PSII (F_v/F_m), the actual photochemical efficiency of PSII (Yield) and the size and number of active photosynthetic reaction centers (F_v/F_o) decreased in both genotypes under drought stress conditions, with more announced effect on the drought-susceptible genotype (Figs. 4A, B and 5). Zlatev and Lidon (2012) reported a decrease in F_v/F_m and concluded that it can be a measure of photosynthetic down-regulation. Zhang et al. (2016) also reported that the optimal photochemical efficiency of PSII (F_v/F_m) decreased in response to drought stress. We found out that the application of AA restored F_v/F_m, yield and F_v/F_o traits to levels very close to the control counterparts. In their experiment, Khan

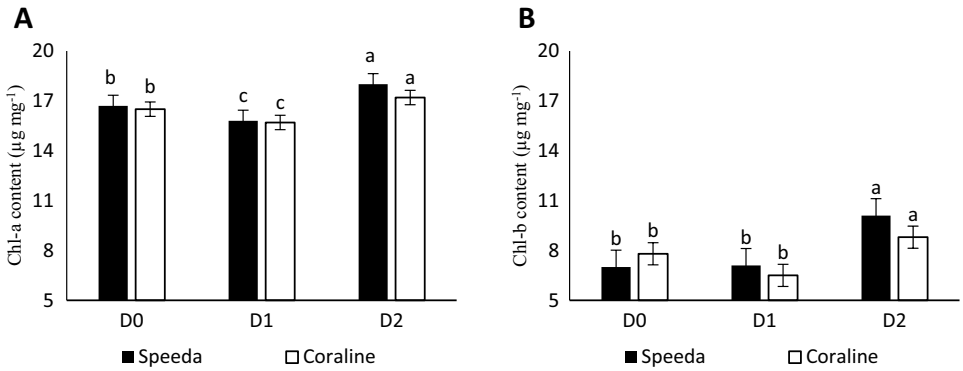

Fig. 6 Chlorophyll-a content (**A**) and chlorophyll-b content (**B**) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

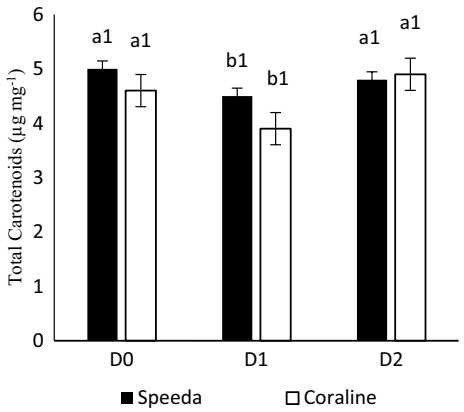

Fig. 7 Total carotenoids content of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

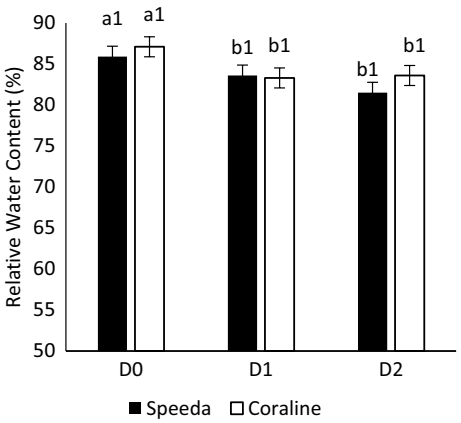

Fig. 9 Relative water content of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

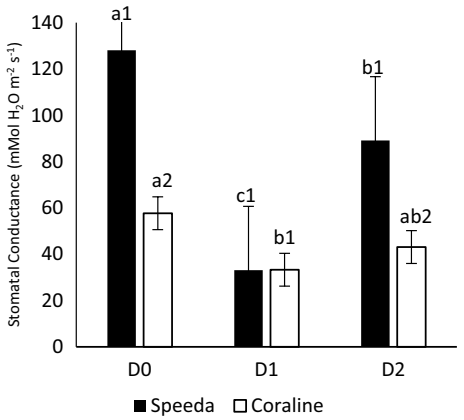

Fig. 8 Stomatal conductance of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n=3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes

et al. (2023) reported that salicylic acid (SA) significantly increased both F_v/F_m and yield traits of lemongrass. This increase can be explained by the stimulatory effect of growth biostimulators such as SA on RuBisCO and brassinosteroid analogues DI-31 (Pérez-Borroto et al. 2021) on chlorophyllase enzyme activity. Earlier, Lima and Lobato (2017) indicated that growth biostimulators enhanced light absorption and electron flow, leading to higher quantum efficiency of PSII.

Stomatal conductance is used to quantify the amount of CO_2 and water vapor exchanged between the ambient and interior leaf (Atteya 2003). To survive a prolonged duration of drought, it is critical for soybean leaves to modify their stomatal conductance in order to avoid excessive water loss (Ku et al. 2013). In the current experiment, drought decreased the stomatal conductance in both genotypes significantly, and the foliar application of AA enhanced this trait in both genotypes, with more announced effect in the drought-tolerant genotype (Fig. 8). According to Chowdhury (2016), drought stress led to a 42% reduction in stomatal conductance in leaves that are drought stressed leaves in comparison to unstressed. Zhang et al. (2016) discovered a 98.8 percent reduction in stomatal conductance under drought; they stated that decrease in stomatal conductance was caused by a decreased ratio of open stomata to stomatal aperture size in crops exposed to drought. According to Razmi et al. (2017), water stress decreased the stomatal conductance of three soybean leaflets as compared to their non-drought-stressed counterparts, and a foliar application of 0.4 mM salicylic acid (SA) significantly reversed drought-induced stomatal closure and improved it. In comparison to the detrimental effect of water scarcity, SA treatments increased stomatal conductivity. Sadeghipour (2012) found that SA treatment resulted in less stomatal conductance loss than control plants for both common bean genotypes under both control and water-stressed situations. The prevention of stomatal conductance reduction with the administration of SA is critical for maintaining photosynthetic activity and minimizing damage (Idrees et al. 2010).

The leaf water capacity and relative water content are valuable indicators of a plant's physiological water status (Gonzales and Gonzales-Vilar 2001). We observed significant reductions in the relative water content in both genotypes as a result of drought stress imposition, and these reductions were not influenced by AA application (Fig. 9). It was previously reported that under water deficit conditions, drought-stressed plants with AA treatment had decreased transpiration rate, stomatal conductance, and leaf temperature, which was associated with higher RWC (He et al. 2019). However, in that particular experiment, drought stress was imposed during reproductive stages, and that might explain the contradictory conclusion, taking into consideration the previously mentioned conclusion by Maleki et al. (2013) that the stage at which soybean plants suffer from drought can play a key role in the response and the consequences.

In the current experiment, drought stress reduced the specific leaf area (SLA) in both genotypes. The SLA significantly increased in both genotypes in drought-stressed plants sprayed with AA (D2) as compared to (D1) counterparts, where drought stress was imposed without the pretreatment with AA (Fig. 3). The enhanced leaf area in (D2) treatment might be justified by promoting cell division and cell expansion as suggested by Khandaker et al. (2017) when using gibberellic acid (GA) as an exogenous foliar spray. Basal and Szabó (2020) concluded that drought stress at reproductive stages significantly decreased the leaf area of 2 soybean genotypes.

Chlorophylls are the primary pigmentations involved in absorption of light, transfer, transfiguration, and chlorophyll concentration is a key indicator of photosynthetic activity (Liu et al. 2007). We found out that chlorophyll-b content was not affected measurably by drought stress in either genotype; however, it was significantly increased in the AA-treated (D2) treatment in both genotypes, indicating that AA may play a role in the production and/or slowing the degradation of photosynthetic pigments, resulting in increased photosynthesis capacity during drought, as reported by Rahman et al. (2021). Drought stress reduced light absorption, according to Dong et al. (2015), resulting in changes in leaf area index and also leaf chlorophyll content. According to Zhang et al. (2016), chlorophyll-a was notably decreased in drought-stressed plants compared to control plants. Drought stress resulted in a considerable decrease in chlorophyll-a + chlorophyll-b (from 19.5 to 13.0 mg g^{-1} DW), signifying a lowered ability for light absorption and conversion (Tang et al. 2017). Drought stressed plants had a substantial reduction in photosynthetic pigment concentration, but drought-stressed plants treated with AA preserved the same level of photosynthetic proportionality and photosynthetic pigments throughout the drought period (Rahman et al. 2021). The potential benefits of AA treatment on reduced photosynthetic pigment deterioration and increased photosynthesis proportionality have been recently demonstrated in mung bean grown under seawater-induced salt stress (Rahman et al. 2019), lentil grown under copper stress (Hossain et al. 2020) and cassava grown under drought stress (Rahman et al. 2019; Utsumi et al. 2019). Also, the results are in compliance with Sun et al. (2022), whose results indicated that apple plants treated with AA were more drought-tolerant than those treated with water.

Carotenoids have a role in scavenging reactive oxygen species (ROS), stabilizing photosynthetic complexes, assisting with energy dissipation, and assisting plants in mitigating the negative impacts of drought stress (Moharekar et al. 2003). In the current experiment, the total carotenoids in both genotypes decreased significantly as a consequence of drought stress imposition (Fig. 7). Razmi et al. (2017) concluded that in comparison to control, treating soybean genotypes with salicylic acid increased the overall amounts of photosynthetic pigments (carotenoids) in leaves. By distributing surplus energy from light surrounding Photosystem II (PS II) mainly via the xanthophylls cycle, carotenoids can protect chlorophylls from damage (Carol and Kuntz 2001). As a result, it provides critical protection for the photosynthetic system, and its content can represent a plant's capacity for adaptation to its environment (Tang et al. 2017). Zhang et al. (2016) previously found that drought stress reduced carotenoids composition significantly when compared to control, a finding that was eventually revealed by Tang et al. (2017), who found that revealing plants to drought stress resulted in a notable decrease in carotenoid content. In the current experiment, (D2) treatment had significantly higher total carotenoids content as compared to (D1) treatment. Moreover, (D2) treatment resulted in total carotenoids content higher than that of the control plants in 'Coraline' genotype (Fig. 7). It was previously reported that low concentrations of exogenously applied growth regulators (e.g., H_2O_2) can induce the synthesis of certain enzymes and/or proteins related to photosynthesis process (Jiang et al. 2012), resulting in enhanced pigment content (Liu et al. 2010). Similar conclusions were also reported on soybean in the case of exogenous melatonin (Cao et al. 2019) and ethanol (Das et al. 2022). The mechanism by which these agents enhance photosynthetic pigment content (including carotenoids) is reducing the degradation rate of these pigments under drought stress conditions (Rahman et al. 2022).

The level of response of stressed plants to growth regulators applied is also genotype-dependent. For example, Mohamed and Latif (2017) concluded that methyl jasmonate enhanced drought stress tolerance of "Giza 22" soybean genotype more than that of "Giza 35" genotype. Although we did not measure the endogenous hormonal and enzymatic activities, yet our results show genotype-dependent morpho-physiological differences in response to drought stress imposition and AA application, suggesting that a molecular

analysis will help further in understanding the response of different soybean genotypes to drought and AA application and, thus, selecting the genotypes that better respond to AA application under drought stress conditions.

In our experiment, the root dry weight of the drought-tolerant genotype was not affected by the imposition of drought stress. However, the plant roots of the drought-stressed treatment that received AA foliar spray had significantly lower dry weight (Fig. 1A). On the other hand, the AA foliar application resulted in significantly higher root dry weight as compared to the other treatments in the case of the drought-susceptible genotype. These different reactions can be a result of the differences between the 2 genotypes in terms of their response drought stress and AA application and might be a key factor when selecting genotypes to be cultivated under unfavorable conditions.

Drought stress significantly decreased both the root length and the root volume of 'Speeda' plants, and the AA application did not influence any of these traits remarkably. In 'Corlaine,' however, AA application significantly increased both the root length and the root volume of (D2) treatment as compared to (D1) treatment (Fig. 1A, B). In their experiment, Bashir et al. (2019) concluded that the root length of 8 soybean genotypes decreased significantly as a result of the drought stress imposed by a 10% PEG solution. A similar conclusion was also reported later by Sohag et al. (2020). In addition, it was previously reported that the exogenous application of H_2O_2 on rice plants (Sohag et al. 2020) and ethanol on soybean (Rahman et al. 2021) could partially alleviate the negative effects of drought stress on the root morphology, which is in line with our findings on 'Coraline' plants.

Drought stress has been linked to a decrease in soybean biomass (Khan and Komatsu 2016). We found out that shoot dry weight decreased significantly in both genotypes under drought stress conditions, and the shoot dry weight of drought-stressed 'Coraline' plants, but not of 'Speeda,' was significantly higher in AA-treated treatment (D2) than in (D1) treatment. The drought-stressed (D1) 'Speeda' plants had significantly higher shoot dry weight as compared to 'Coraline' counterparts (Fig. 2A). We also found out that in 'Speeda,' drought stress reduced the shoot length of both genotypes, with more announced effect on 'Coraline' genotype, and the AA foliar spray did not enhance this trait in 'Speeda,' but could significantly enhance it in 'Coraline' and keep the shoot length on a level very close to that of the control plants (Fig. 2B). When drought stress was imposed at R4 stage rather than V4 stage, biomass was drastically reduced (Maleki et al. 2013), indicating that the stage of soybean life cycle at which drought occurs has an effect as well. Previously, Mak et al. (2014) reported that drought stress significantly decreased the shoot length of soybean plants. Garcia et al. (2010) reported the different examined soybean genotypes to be significantly different in plant height compared to one another. Our results support this conclusion as 'Speeda' had higher shoot length in all treatments. According to Hossain et al. (2014), drought stress reduced plant height in drought-sensitive and also in drought-tolerant soybean genotypes; nevertheless, the drought-vulnerable genotype had a length rated at 44.3% of the height of control plants, while the two drought-tolerant genotypes had height values of 56.7% and 59.1%, respectively. The authors ascribed this decline to a drought resistance mechanism. Ahmad et al. (2021) reported that drought reduced both shoot length and weight; however, the application of 100 mM salicylic acid increased these parameters significantly. The Authors allocated the decrease in these parameters to increased reactive oxygen species (ROS) accumulation and to changes in the proteins in the cellular walls (Boyer and Westgate 2004).

Conclusions

Drought stress decreased both chlorophyll-a and total carotenoids, the stomatal conductance, and the specific leaf area of both soybean genotypes. However, the foliar application of 20 mM acetic acid enhanced these traits significantly. Drought stress had a negative effect on the optimal and the actual photochemical efficiency of PSII of 'Coraline,' but not 'Speeda,' and the AA could alleviate that effect. The application of AA could not enhance the relative water content of the drought-stressed plants of both genotypes. The morphology of both the roots and shoots was negatively influenced by the drought application in both genotypes; however, the AA application helped in restoring these traits in 'Coraline,' but not 'Speeda,' indicating that AA application might be more beneficial in the case of drought-susceptible soybean genotypes.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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