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Effects of abscisic acid and sodium nitroprusside priming on yield and quality of peanut (*Arachis hypogaea* L.) under drought stress

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Abstract: This study tested the impact of priming peanut seeds from the VD01-2 cultivar with either 6 mg/L of abscisic acid or 20 mg/L of sodium nitroprusside to prevent damage from drought stress. Throughout the development of peanuts under drought-stress conditions, various morphological, physiological, and biochemical changes were analyzed. According to the study, it was determined that priming with SNP had a more significant effect than priming with ABA. The use of sodium nitroprusside priming resulted in an improvement in both the yield and quality of peanuts when grown under drought conditions. Furthermore, the findings indicate that the use of sodium nitroprusside priming showed an increase in chlorophyll content, gas exchange capacity, and antioxidant activities while reducing lipid peroxidation.

Keywords: abscisic acid; drought stress; peanut; sodium nitroprusside; yield

Peanuts are a nutritious crop with high levels of vitamins and minerals. Their seeds contain 45% oil, 25% protein, 20% carbohydrates, and 5% fiber (Mingrou et al. 2022). Peanut processing by-products can be used as livestock feed and biodegradable manure (Toomer 2020). However, drought stress is a significant challenge in peanut production, necessitating the development of strategies to enhance drought tolerance in crops. Although there are various methods available to enhance drought tolerance in plants, seed priming remains a preferred approach for several reasons. Seed priming is a cost-effective and practical method that can be easily implemented on a large scale (Puppala et al. 2023). Moreover, seed priming offers the advantage of early intervention and long-lasting effects. By treating the seeds, the priming process initiates stress adaptation mechanisms at an early stage, even before germination. This early exposure to stress signals prompts the seeds to activate protective responses and metabolic changes that enhance their ability to withstand drought conditions. As a result, when the primed seeds germinate and grow, they are already equipped with a heightened tolerance to drought stress (Pagano et al. 2023).

Abscisic acid (ABA) is a phytohormone that acts as a critical signalling molecule in drought stress signalling pathways. When plants experience drought conditions, ABA production increases, leading

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to various physiological and biochemical responses that help plants cope with water scarcity. ABA regulates stomatal closure, reducing transpiration rates and conserving water within the plant. ABA is a plant hormone that plays a crucial role in regulating seed dormancy and germination. ABA accumulates in mature seeds and prevents germination under unfavorable conditions, such as drought or high salinity. It also induces the synthesis of protective proteins and antioxidants, enhancing the plant's ability to withstand oxidative stress caused by drought (Muhammad et al. 2022). Besides, sodium nitroprusside (SNP), a nitric oxide (NO) donor, is a reactive nitrogen species that plays important roles in various physiological processes in plants. It is a highly reactive free radical gas with a short half-life, and its production and signaling functions have been extensively studied in plants. (Xia et al. 2022). In some cases, low levels of NO have been found to promote seed germination by stimulating enzymatic activity and enhancing the breakdown of storage reserves. NO enhances the activity of antioxidant enzymes, such as superoxide dismutase and catalase, mitigating the harmful effects of reactive oxygen species generated during drought stress. Furthermore, NO can regulate gene expression and signal transduction pathways, contributing to the activation of stress-responsive genes involved in drought tolerance (Stefanov et al. 2023). The previous study provided a foundation by demonstrating the positive effects of ABA and SNP priming on enhancing peanut seedlings' growth and stress tolerance under drought conditions at the seedling (Tran et al. 2023). However, whether these priming treatments can also improve yield and seed quality in mature peanut plants remains to be determined.

Therefore, beyond their role in promoting early growth, ABA and SNP priming may further enhance yield and seed quality under drought stress conditions. To investigate this hypothesis, the present study aims to evaluate the effects of ABA and SNP priming on the yield and quality of mature peanut plants subjected to drought sess. This research will extend the existing knowledge by assessing physiological and biochemical parameters associated with drought tolerance, including photosynthetic efficiency and antioxidant capacity. The outcomes of this research will contribute to developing effective strategies for enhancing peanut crop performance under drought stress conditions. Understanding the potential benefits of ABA and SNP priming in terms of increasing yield and seed quality will not only aid in the sustainable production of peanuts but also provide valuable insights into the physiological mechanisms underlying drought tolerance in crops.

MATERIAL AND METHODS

Plant materials and treatments. The VD01-2 peanut seeds were procured from the Research Institute of Oil and Oil Plant situated in Ho Chi Minh City, Vietnam. The seeds were subjected to different treatments, including immersion in water, 6 mg/L ABA, or 20 mg/L SNP for 18 hours at a temperature of 30 ± 2°C (Tran et al. 2022). After priming, the seeds were washed five times with distilled water and subsequently dehydrated by drying them to their original weight, which was approximately 0.5 g/seed at 30°C for four hours. The seeds were then planted in 30 cm height and 40 cm width pots containing soil with 60% moisture levels throughout the experiment, simulating moderate drought stress. The experimental garden was located in the plant physiology laboratory at the University of Science, Vietnam National University, Ho Chi Minh City, Vietnam, which experiences a tropical monsoon climate with an air humidity range of 75–80% and an air temperature of 28–29 °C. The soil in the experimental garden had an organic matter content of 24.91 g/kg, a total nitrogen content of 0.165%, a phosphorus content of 0.062%, and a potassium content of 0.93%. Additionally, the available Zn, B, Cu, and Mo contents were 33, 98, 26, and 0.9 mg/kg, respectively. The moisture levels in the pots were maintained using a moisture sensor and drip irrigation system. After 40 days, the third leaf of the plants treated with different methods was used to determine physiological and biochemical parameters. The yield and quality of the seeds were analyzed during harvest.

Detection of reactive oxygen species (ROS). According to the staining method of Xu et al. (2012), for localizing the H_2O_2 and O_2^- that were produced by the leaves, the treated leaves were immersed in 3.3'-diaminobenzidine (DAB) and nitroblue tetrazolium (NBT), respectively. Then, the leaves were stripped of chlorophyll by boiling alcohol and viewed under a stereo microscope (SZX10, Olympus, Japan).

Determination of the relative water content, electrolyte leakage, and epicuticular wax. The relative water content (RWC) of leaves was calculated following the method of Sade et al. (2015). The leaves electrolyte leakage (EL) and epicuticular wax content (EWC) were analyzed according to Abdelaal et al. (2020) and Mamrutha et al. (2010), respectively. The leaf electrolyte leakage was measured using an EC meter (HI2550, Hanna, Italy). The content of leaf epicuticular wax was determined by measuring the absorption of the wax-$K_2Cr_2O_7$ solution in hot acid and calculating it from the standardized PEG-3000 curve.

Determination of the photosynthetic pigment content, respiration and photosynthesis rate. The chlorophyll and carotenoid content were measured after being extracted by an ethanol solution, according to Lichtenthaler (1987). Gas exchange capacity was determined using a CO_2 sensor (EA80, Extech, USA) in a closed chamber under the temperature of 28°C. The measurements were taken in the absence of light to determine the respiration rate and in the presence of 10 000 lux light intensity to determine photosynthesis, as described by Thang et al. (2022).

Determination of the cation exchange capacity. The root cation exchange capacity (CEC) was analyzed according to Drake et al. (1951) with a moderate modification. The root was soaked in 0.01 N HCl (40 minutes) to exchange ions. Then, the root was repeatedly washed in distilled water to remove the excess H^+ ions. The absence of free H^+ ions was confirmed using the phenolphthalein test of the last washed-out water sample. The root was dipped in 1 N KCl (pH 7.0) for 40 minutes; afterwards, the root was dried, and this solution was titrated against 0.01 N KOH in the presence of the electrode of a pH meter in the beaker till pH was brought back to 7.0.

Determination of the soluble sugar, starch, protein, proline, and lipid. Following the Masuko et al. (2005) procedure, the total soluble sugar concentration was ascertained. The Miller (1959) technique was applied to figure out the amount of starch present. The protein content was determined in accordance with Bradford's description (1976). Paquin and Lechasseur's (1979) description was used to quantify proline content. The lipid content was extracted using organic solvents described by Shiva et al. (2008).

Determination of malondialdehyde, ascorbic acid, and α-tocopherol. The content of malondialdehyde (MDA) was determined by using the thiobarbituric acid method to assess the lipid peroxidation of the oxidative membrane damage (Davenport et al. 2003). According to the Saeed et al. (2018) method, the acid ascorbic and α-tocopherol contents were determined based on the reduction of iron with potassium dichromate in an acidic medium at 564 nm.

Determination of superoxide dismutase, catalase, ascorbate peroxidase and guaiacol peroxidase activity. The superoxide dismutase (SOD) activity was assessed by measuring the inhibition of the photochemical reduction of nitro blue tetrazolium at 560 nm. The activity of ascorbate peroxidase (APX) was determined by monitoring the oxidation of ascorbic acid and measuring the absorption at 298 nm. Guaiacol peroxidase (GPX) activity was measured at 463 nm. Catalase (CAT) activity was examined by measuring the decrease in absorption at 240 nm caused by H_2O_2, following the method of Elavarthi and Martin (2020).

Statistical analysis. The design of completely randomized blocks was used to organize all of the treatments. The mean and standard deviation from five replications were used to evaluate the results. Statistical software was used to perform a one-way analysis of variance (ANOVA) (version 26.0). The means were contrasted using Duncan's multiple range test with a 5% threshold of significance.

RESULTS

Effects of SNP and ABA priming on the peanut development under drought stress. Drought stress on the peanut obviously reduced plant growth, the number of pods, the number of seeds, and seed weight (Figure 1). The priming application of SNP to the drought-stressed plants significantly ameliorated the drought stress and increased the above indicators. According to Table 1, the number of pods exhibited a marked increase from an initial value of 2.5 to 12. Furthermore, the seed count demonstrated a significant increase from 5.1 to 24, and the seed weight also showed a notable increase from an initial value of 0.51 to 0.62. In terms of seed quality, drought stress increased the content of lipid, soluble sugar, and protein while decreasing the content of starch. SNP priming helps maintain high lipid content (approximately 530.8 mg/g) and increases soluble sugars (47.04 to 50.20 mg/g) and proteins (293.2 to 313.8 mg/g) compared to drought.

Changes in the relative water content, electrolyte leakage, MDA, epicuticular wax, and cation exchange capacity. The drought stress significantly increased the EL, membrane lipid peroxidation (measured as MDA content), and EWC, but sharply decreased relative water content in leaves and cation exchange capacity in roots (Table 2). The prim-

Figure 1. The growth of peanut under drought stress in different treatments: (A) – control; (B) – drought stress; (C) – ABA priming; (D) – SNP priming at harvest time; scale bar – 5 cm

ing with SNP significantly not only improved RWC (29.10 to 83.76 %) and CEC (2.51 to 4.73 meq/g) but also reduced the EL (33.80 to 18.28 %), EWC (60.80 to 44.60 μg/cm^2), and MDA (6.63 to 3.10 μmol/g) in leaves under drought stress.

Changes in the photosynthetic pigment content, respiration, and photosynthesis rate. Drought caused decreases in chlorophyll of leaves compared with control plants. On the contrary, the content of carotenoids in leaves sharply increased by twice times as compared with the control. SNP priming alleviated the harmful effect of drought via increases in the chlorophyll content was as high as that of the control (Figure 2). The gas exchange capacity of leaves was under drought stress and ABA priming was lower than that of the control. Under drought stress, applying SNP increased respiration and photosynthesis rates in leaves by about 20 and 40 μmol O_2/g/h, respectively (Figure 3).

Changes in the ROS and antioxidant capacity. Peanut leaves that were exposed to drought showed a higher accumulation of ROS than the control leaves. Under drought stress, the production of H_2O_2 (brown polymerization) is concentrated in the leaf veins instead of concentrated in mesophyll tissue in the case of superoxide (purple formazan deposits). The application of both ABA and SNP priming significantly reduced the accumulation of H_2O_2 and superoxide in mesophyll tissue compared with non-priming leaves (Figure 4). Under drought stress, the content of ascorbic acid and α-tocopherol strongly increased compared to the control. The SNP application increased ascorbic acid and α-tocopherol content in the leaves by 1.4- and 1.9-fold in comparison with drought stress, respectively. Regard of the antioxidant enzyme activity, there were no effects significantly in the activity of SOD, CAT, and GPX compared with the control. However, the APX activity in plants treated with SNP was higher than that of drought (Table 3).

Table 1. Effects of sodium nitroprusside (SNP) and abscisic acid (ABA) priming on pod number, seed number, seed weight, and contents lipid, starch, sugar and protein in seed of peanut at harvest time under drought stress

Treatment	Control	Drought	ABA + drought	SNP + drought
Pod number	16.60 ± 1.14^{a}	2.40 ± 0.55^{d}	5.00 ± 0.71^{c}	12.00 ± 0.71^{b}
Seed number	31.10 ± 3.54^{a}	5.10 ± 0.89^{d}	10.00 ± 1.41^{c}	24.00 ± 1.41^{b}
Seed weight (g)	0.62 ± 0.01^{a}	0.51 ± 0.03^{c}	0.60 ± 0.01^{b}	0.62 ± 0.01^{ab}
Lipid (mg/g DW)	490.8 ± 10.1^{c}	541.2 ± 16.8^{a}	511.6 ± 17.9^{bc}	530.8 ± 20.0^{ab}
Starch (mg/g DW)	64.15 ± 4.44^{a}	40.68 ± 2.72^{b}	34.40 ± 2.07^{c}	30.60 ± 1.67^{c}
Sugar (mg/g DW)	42.32 ± 0.88^{c}	47.04 ± 1.95^{b}	42.60 ± 1.82^{c}	50.20 ± 1.92^{a}
Protein (mg/g DW)	265.3 ± 7.5^{c}	293.2 ± 9.9^{b}	287.6 ± 8.3^{b}	313.8 ± 12.8^{a}

DW – dry weight

$^{a-c}$Values in the same row followed by different letters indicate statistical difference at $P < 0.05$

Table 2. Effects of sodium nitroprusside (SNP) and abscisic acid (ABA) priming on relative water content (RWC), electrolyte leakage (EL), malondialdehyde (MDA), epicuticular wax content (EWC), and cation exchange capacity (CEC) of peanut leaf under drought stress after 40 days

Treatment	Control	Drought	ABA + drought	SNP + drought
RWC (%)	85.68 ± 2.08^{a}	29.10 ± 2.99^{c}	49.70 ± 3.50^{b}	83.76 ± 3.05^{a}
EL (%)	13.64 ± 0.42^{d}	33.80 ± 1.56^{a}	25.22 ± 1.81^{b}	18.28 ± 1.80^{c}
MDA (μmol/g FW)	3.55 ± 0.11^{b}	6.63 ± 0.09^{a}	6.82 ± 0.22^{a}	3.10 ± 0.23^{c}
EWC (μg/cm^2)	15.60 ± 3.36^{c}	60.80 ± 4.32^{a}	42.20 ± 3.35^{b}	44.60 ± 3.65^{b}
CEC (meq/g FW)	4.89 ± 0.30^{a}	2.51 ± 0.27^{c}	3.10 ± 0.19^{b}	4.73 ± 0.24^{a}

FW – fresh weight

$^{a-d}$Values in the same row followed by different letters indicate statistical difference at $P < 0.05$

Changes in the soluble sugar, starch, protein, and proline in leaves. Compared with the control, drought stress dramatically decreased starch content while increasing soluble sugar, protein, and proline content. Seed priming with either ABA or SNP reduced the soluble sugar content by approximately 12.5% relative to drought stress. On the contrary, seed priming improved the content of starch and proline under

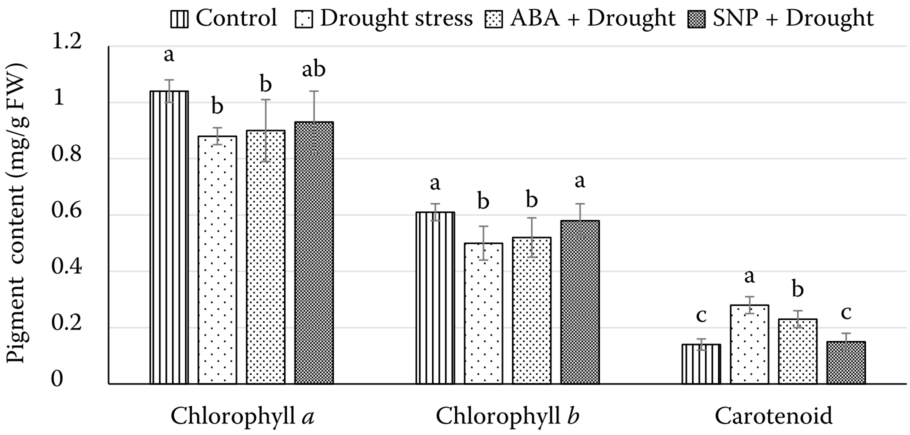

Figure 2. Effects of abscisic acid (ABA) and sodium nitroprusside (SNP) priming on the chlorophyll *a*, chlorophyll *b* and carotenoid content in leaves under drought stress after 40 days

Values within the column, followed by the different letters, indicate statistical difference at $P < 0.05$

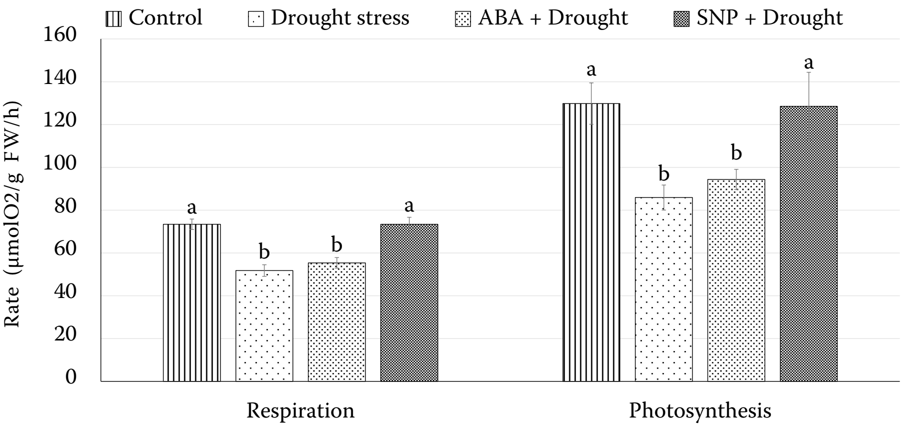

Figure 3. Effects of abscisic acid (ABA) and sodium nitroprusside (SNP) priming on the respiration rate and photosynthesis of leaves under drought stress after 40 days

Values within the column, followed by the different letters, indicate statistical difference at $P < 0.05$

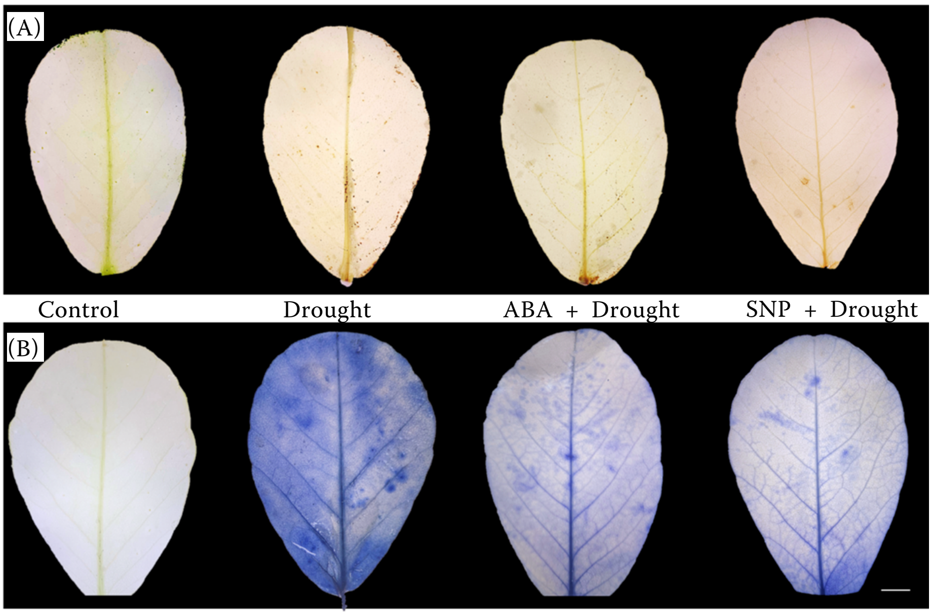

Figure 4. Drought-induced hydrogen peroxide (A) and superoxide (B) and as visualized by reactive oxygen species (ROS) staining in the leaves after 40 days
Scale bar = 1 cm; ABA –abscisic acid

drought stress, but less in comparison to the control. Either priming or non-priming did not affect the protein content in leaves under drought stress (Table 4).

DISCUSSION

Seed priming has emerged as a promising method to enhance the tolerance of peanut crops to stress conditions, as well as to improve seed yield and quality. The selection of priming agents is critical for achieving desirable outcomes (Marthandan et al. 2020). Among the various priming agents studied, it was found that SNP demonstrated significant positive effects on the number of pods, seeds, and their weight (Figure 1). Similarly, priming with ABA resulted in positive changes in peanut yield or quality under drought stress conditions, as evidenced in Table 1. However, compared to SNP, the efficacy of ABA priming seems to be limited in improving peanut yield or quality under drought stress. These differential outcomes obtained from SNP and ABA priming underscore the importance of selecting the appropriate priming agents for specific crops and stress conditions. Notably, the benefits of SNP priming are not limited to peanut crops alone. For instance, Farouk et al. (2020) found that supplementing marjoram herb with 20-60 μM SNP led to improved development and yield. Similarly, even lower doses of SNP significantly increased the growth rate and

Table 3. Effects of sodium nitroprusside (SNP) and abscisic acid (ABA) priming on the content of ascorbic acid and α-tocopherol, the activity of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and guaiacol peroxidase (GPX) in peanut leaves under drought stress after 40 days

Treatment	Control	Drought	ABA + drought	SNP + drought
Ascorbic acid (mg/g FW)	0.21 ± 0.02^{d}	0.71 ± 0.02^{c}	0.78 ± 0.05^{b}	0.96 ± 0.02^{a}
α-tocopherol (mg/g FW)	0.05 ± 0.01^{c}	0.08 ± 0.01^{b}	0.08 ± 0.01^{b}	0.15 ± 0.02^{a}
SOD (UI/mg protein)	0.10 ± 0.01^{ns}	0.12 ± 0.02^{ns}	0.11 ± 0.03^{ns}	0.11 ± 0.02^{ns}
CAT (UI/mg protein)	0.10 ± 0.01^{ns}	0.15 ± 0.01^{ns}	0.12 ± 0.01^{ns}	0.30 ± 0.39^{ns}
APX (UI/mg protein)	2.13 ± 0.12^{c}	2.32 ± 0.06^{b}	2.49 ± 0.07^{a}	2.60 ± 0.08^{a}
GPX (UI/mg protein)	0.14 ± 0.01^{ns}	0.15 ± 0.02^{ns}	0.15 ± 0.02^{ns}	0.14 ± 0.01^{ns}

FW – fresh weight
$^{a–d}$Values in the same row followed by different letters indicate statistical difference at $P < 0.05$

Table 4. Effects of sodium nitroprusside (SNP) and abscisic acid (ABA) priming on the content of starch, soluble sugar, protein and proline in peanut leaves under drought stress after 40 days

Treatment	Control	Drought	ABA + drought	SNP + drought
Starch (mg/g DW)	49.85 ± 4.58^{a}	28.13 ± 3.84^{d}	37.60 ± 1.45^{c}	42.61 ± 2.82^{b}
Sugar (mg/g DW)	22.75 ± 1.07^{c}	32.18 ± 0.97^{a}	27.91 ± 2.28^{b}	27.53 ± 1.79^{b}
Protein (mg/g DW)	13.82 ± 2.06^{b}	16.29 ± 1.01^{a}	16.37 ± 1.05^{a}	16.84 ± 0.76^{a}
Proline (mg/g DW)	0.18 ± 0.03^{c}	2.14 ± 0.37^{b}	2.38 ± 0.36^{ab}	2.74 ± 0.18^{a}

DW – dry weight

$^{a-d}$Values in the same row followed by different letters indicate statistical difference at $P < 0.05$

yield of cotton and tomato (Jangid, Dwivedi 2017). The biomass of kiwifruit seedlings was also observed to increase with SNP treatments (Xia et al. 2022). These findings suggest that the use of SNP as a priming agent can effectively enhance the growth and yield of various crops under stress conditions. From a mechanism perspective, seed priming triggers distinct metabolic changes during the imbibition process. Rehydration during seed priming regulates crucial cellular activities such as protein and nucleic acid synthesis, ATP generation, and antioxidant activation (Puppala et al. 2023). Moreover, priming treatments lead to the upregulation of tubulin subunit proteins, which play a critical role in cell signaling (Pagano et al. 2023).

This research discovered that priming the seeds with ABA or SNP significantly enhanced RWC and CEC while reducing EL, EWC, and MDA in leaves when exposed to drought stress, as shown in Table 2. The increase in RWC indicates that primed plants have a higher ability to retain water within their tissues. This enhanced water retention capacity allows the plants to maintain turgor pressure, cell hydration, and overall physiological functions, even under water-limited conditions (Liu et al. 2023). Moreover, the increase in CEC suggests an improved ability of the plant roots to retain and exchange essential nutrients. CEC is a measure of the soil's capacity to hold and release cations, such as potassium, calcium, and magnesium. Priming with ABA or SNP enhances the plant's capacity to absorb and retain these nutrients, which are crucial for maintaining proper metabolic functions under drought stress. Furthermore, the lower levels of EL and MDA in the primed plants suggest improved membrane integrity and reduced oxidative damage, allowing the plants to maintain their normal physiological processes and cellular functions even under drought conditions (Nimbolkar et al. 2023). The harmful impact of drought was reduced by SNP priming, which increased chlorophyll content, respiration, and photosynthesis rate. These increases were comparable to the control's (Figures 2 and 3). The intensification of photosynthesis acted as a source of carbohydrates for the seeds. As a result, priming with SNP notably enhanced the quality of the grains but decreased the soluble sugar content in the leaves (Table 4). Areas with brown polymerization pigment and formazan deposits showed that both ABA and SNP priming significantly reduced the accumulation of H_2O_2 and superoxide in mesophyll tissue compared to non-priming leaves, as shown in Figure 4. The free radicals may have been degraded by the action of antioxidants and the ROS-degrading enzyme system (Rai, Kaushik 2023). The results showed that ascorbic acid and a-tocopherol content increased strongly by priming the seeds with ABA or SNP. In addition, the activity of CAT was also noted to increase significantly (Table 3). Ascorbic acid and α-tocopherol are potent antioxidants. These compounds have the ability to scavenge and neutralize ROS generated during oxidative stress. By increasing their content, seed priming with ABA or SNP helps to bolster the plant's antioxidant defense system. Furthermore, the increased activity of CAT enhances the plant's ability to efficiently detoxify accumulated H_2O_2, thereby reducing oxidative damage (Zafar et al. 2024).

CONCLUSION

The results suggested that priming with SNP had a greater impact compared to ABA. SNP priming increased the chlorophyll content, gas exchange capacity, antioxidant activities, and decreased lipid peroxidation. The findings of the present study demonstrated that SNP priming improved the yield and quality of peanuts under drought stress.

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