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Assessing the Effects of Seed Priming on the Tolerance of Sugar beet Varieties to Salt and Drought Stress Using Plant Phenotyping Methods

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ABSTRACT

Sugar beet (*Beta vulgaris L.*) is a vital global crop, with Türkiye being the fifth-largest producer, contributing about 10% of the world's supply. The Konya Basin accounts for 35% of Türkiye's production. This region faces significant drought and salt challenges. In a study, six commonly grown sugar beet varieties in Konya ('Lider', 'Libellule', 'Lizard', 'Mohican', 'Bison', and 'Rodeo') were subjected to NaCl and PEG priming under salt and drought stress. 'Lizard' had the highest germination rate of 75.5% for NaCl-primed seeds, while 'Bison' reached 80.5% for PEG-primed seeds. The varieties varied in their germination rates, morphological traits, and photosynthetic parameters. NaCl-priming slightly increased leaf area under salt stress, PEG-priming improved stomatal conductance in 'Bison' under drought conditions. Overall, priming had limited effectiveness in alleviating stress impacts on sugar beet varieties, indicating a need for further research on the efficacy of priming methods and their integration with other mitigation strategies.

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Introduction

Sugar beet (*Beta vulgaris* L.), a biennial species within the *Amaranthaceae* family, is cultivated in temperate and subtropical regions worldwide (Biancardi et al., 2010). It plays a crucial role in the global sugar industry, contributing approximately 280 million tons of the annual sugar production, which was approximately 30% of world sugar production in 2023, after sugar cane production (FAO, 2024a). Türkiye was the fifth leading country for sugar beet production in 2023, with around 10% of total global sugar beet output (FAO, 2024a). Sugar beet also serves as a valuable source of raw materials for the production of bioethanol, and has applications in the health, pharmaceutical, animal feed, and food industries (Duraisam et al., 2017; Ptak et al., 2021; Yolcu et al., 2021).

The world population is projected to increase by 1 billion people by 2030 and reach 9.8 billion in 2050. This will create an increased demand for food production (UN, 2019; Van Dijk et al., 2021). The scope of this challenge will be made greater by a decrease in the availability of arable land, largely due to the adverse effects of soil salinization and drought, which are intensified by climate change, and adversely affect agricultural productivity and global food security (FAO, 2024b). Plants are subjected to a variety of stress factors throughout their life cycle, which can significantly impact their development, growth, and overall performance (Killi et al., 2017; Leufen et al., 2016). Among the various stress factors, salinity and drought are prominent abiotic constraints that can lead to a significant reduction in crop yield and agricultural productivity (Killi & Haworth, 2017; Mahajan & Tuteja, 2005). Additionally, the combined effects of soil or water salinity in drought-prone and semi-arid regions result in more severe damage to plants (Reynolds et al., 2005; Sabagh et al., 2019). Soils are considered saline when the electrical conductivity (EC) exceeds 4 dS m^{-1} in a saturated soil solution (approximately 40 mM NaCl) and 15 dS m^{-1} in the soil itself (Munns & Tester, 2008). Approximately 1.5 million

hectares of land are affected by salinity and alkalinity in Türkiye, the largest area affected by salinity in Türkiye is located in the Konya Basin (Dindaroğlu & Elmaz, 2024). Li et al. (2007) previously demonstrated that sugar beet can grow in soils containing 85–140 mM NaCl, and it is therefore considered moderately tolerant to salt stress. However, higher salt concentrations, typically above 70 mM, negatively affect growth parameters such as leaf area, dry biomass, indole-3-acetic acid (IAA) and gibberellic acid (GA) activity, while simultaneously increasing antioxidant activity as well as abscisic acid (ABA) levels (Wang et al., 2017). Therefore, understanding the osmotic regulation, ion transport mechanisms, and stress-related biochemical responses of sugar beet under salinity is a critical step for developing effective breeding strategies aimed at improving salt tolerance.

Droughts are predicted to become more frequent, severe, and prolonged in many regions of the Mediterranean. Konya province has an arid to semi-arid climate in the Central-Anatolian part of Türkiye, its total arable land is about 2.6 million ha, which corresponds to 65% of the total area of the province (Amarkai & Süheri, 2024). Thirty-nine percent of the soils in Konya are medium and high saline soils (Taş et al., 2013) Excess soil salts impede water uptake by plant roots causing crops to suffer osmotic stress, nutritional disorders and ion toxicity, and poor soil physical conditions leading to reduced crop yields and lower crop quality (Munns et al., 2020; Shabala & Munns, 2017; Yadav et al., 2011). Efforts to either desalinize soils or mitigate the deleterious effects of salinity will be required to sustain current levels of sugar beet production in the Konya region. An increase in the production of sugar beet to meet rising global demand will require the identification of more productive and salt and drought tolerant sugar beet genotypes through effective phenotyping and breeding programs (Costa et al., 2019).

Salinity and drought stress are major limitations to global crop production. Soil salinity and drought stress adversely affect physiological and metabolic processes, diminishing growth and yield (Alkharabsheh et al., 2021; Iyengar & Reddy, 1996). Excessive salt accumulation decreases soil water potential, reducing water availability for plant growth and impairing root uptake of essential nutrients (Okon, 2019). Consequently, this induces stomatal closure and restricts CO_2 uptake, resembling the physiological effects of drought stress. The nutritional deficiency resulting from ionic imbalance caused by salinity and drought leads to a decline in various metabolic activities (Grattan & Grieve, 1998; Hu & Schmidhalter, 2005). Under stress conditions, the photosynthetic activity of plants is often impacted as a result of the adjustment in the level and the activity of various photosynthetic enzymes such as Rubisco (Killi & Haworth, 2017; Salvucci & Crafts-Brandner, 2004). Salinity can also cause ion toxicity, where Na^+ disrupts metabolic functions, particularly by inhibiting enzymes involved in photosynthesis (Djanaguiraman & Prasad, 2013; Hussain et al., 2021).

Stomatal closure is a characteristic response to salt stress and drought. Lower stomatal conductance (G_{sw}) results in reduced transpirative water loss, but also restricts the entry of CO_2 into the leaf leading to a decline on the rate of photosynthesis(Haworth et al., 2024) (Killi & Haworth, 2017). The effect of reduced water availability and lower photochemical energy usage can result in photooxidative stress. The thylakoid membranes within the chloroplast envelope are the site of photosystem II (PSII) and are particularly sensitive to photooxidative stress (Killi et al., 2020; Tuna, 2014). Photosystem II can be gauged by chlorophyll fluorescence (ChlF) analysis of electron transport. Photosystem II is a crucial pigment system in photosynthesis; however, salinity disrupts its structure and function (Yan et al., 2013; Lu & Vonshak, 2002; Kalaji et al., 2011) and impairs the activity of its reaction centers (Kalaji et al., 2018). When excess energy accumulates in PSII and the plant fails to dissipate effectively, this can lead to oxidative damage of the photosystem (Gilmore & Govindjee, 1999; Walters & Horton, 1993). Chlorophyll fluorescence analysis of the impact of salinity and drought stress is non-destructive and can be performed rapidly, making it a potentially useful tool in high-throughput phenotyping of large numbers of plant genotypes to stress conditions (Haworth et al., 2023).

Seed priming is a strategic technique for enhancing seed germination and plant growth, resulting in enhanced productivity under various environmental conditions and stress factors (Cayuela et al., 1996; Darwin, 1855). Plant life initiates with seed germination, which is crucial for the survival of plant species and their growth, particularly within agricultural ecosystems for future food sustainability (Dhankher & Foyer, 2018; Reed et al., 2022). Seed germination and subsequent seedling development are significantly influenced by environmental factors, particularly temperature, moisture, drought, and salinity (Llanes et al., 2016; Uçarlı, 2020). Priming could be an effective technique to enhance germination and seedling establishment, optimizing the utilization of soil moisture and solar radiation, enables plants to complete their early stage of growth before the onset of environmental stresses. Seed priming shows mainly positive effects on germination (Dolu et al., 2025; Nawaz et al., 2013; Paparella et al., 2015; Şahin, 2024); however, some contrasting priming studies show that it did not improve germination rate (Ashraf & Iram, 2002; Brocklehurst & Dearman, 1983; Sun XiaoFang et al., 2000). The overall evidence suggests that while priming techniques can enhance seed germination and seedling emergence in certain plant species, its effectiveness is not universal. Further research is required to assess the impact of priming techniques on seed germination, seedling emergence and growth across a broader range of plant species.

The development of mitigation strategies such as seed priming alongside the effective phenotyping of salt and drought tolerant varieties of sugar beet are vital due to its role as an economically important crop in central Türkiye. This is particularly important in the Konya basin that produces about 35% of total sugar beet production in Türkiye (Topak et al., 2010) where water shortage is a critical problem. In this research we investigated six diverse genotypes of sugar beet under salt and water deficit stress towards effective phenotyping of traits associated with photosynthetic performance and resilience to salinity and reduced water availability. This study aims to; i) investigate the effects of NaCl and PEG seed-priming technics on seed germination, ii) assess the effect of NaCl-seed priming on the resilience of early stage sugar beet

seedling development and photosynthetic parameters under salt stress condition, iii) investigate the effect of PEG-seed priming on the tolerance of sugar beet seedling development and photosynthetic parameters under drought conditions, and iv) characterize the sugar beet genotypes to identify those most suited to future cultivation under conditions of high soil salinity and low soil water availability.

Materials and Methods

The seeds of six commonly cultivated sugar beet varieties in the Konya region were obtained from Beta Agriculture and Trade Inc., which are: 'Lider', 'Libellule', 'Lizard', 'Mohican', 'Bison', and 'Rodeo'

Seed Priming

The priming process using NaCl (halo-priming) was conducted in a 0.9% NaCl solution (~150 mM, equivalent 30% seawater salinity) with a seed-to-solution ratio of 1:5 (w/v) (Chen et al., 2021). The seeds were incubated for 16 hours at 18 ± 1°C in a cooled incubator under dark conditions (Senturk & Sivritepe, 2016). Osmo-priming was performed using a 20% (~-0.8 bar) PEG-6000 solution with the same seed-to-solution ratio (1:5 w/v) for 16 hours at 18 ± 1°C in the dark (Zhang et al., 2015). After priming, seeds were rinsed with distilled water and air-dried at room temperature. Untreated seeds served as the control group for germination and experimental studies.

Seed Germination Test

The germination test was conducted in accordance with the rules of the International Seed Testing Association (ISTA, 2018) to compare the germination percentage between non-primed (control), halo-primed (NaCl-primed), and osmo-primed (PEG-primed) sugar beet seeds. Each treatment was replicated four times with 50 seeds per replicate.

Germination was caried out at 20°C ± 1°C in a cooled incubator with 16-hour of light and 8-hour of dark photoperiod for 14 days. Germinated seeds were recorded daily from the 4th to the 14th day of the experiment. The total germination rate was determined by calculating the proportion of seeds that germinated normally for each variety and each treatment.

Greenhouse Experimental Set-Up

A pot experiment was conducted in a greenhouse at Konya Food and Agriculture University, Konya, Türkiye from February to April in 2024. The pot experiment was designated to test any potential ameliorative effect of halo-priming with NaCl against salinity stress, and osmo-priming with PEG-6000 against drought stress in six sugar beet varieties. In total, the experiment consisted of 18 treatments (six varieties × three stress conditions), each with eight replications (See Figure 1).

Primed and non-primed seeds were sown in 9x5 seedling trays (~300 mL per cell) filled with compost (Klasmann-Deilmann GmbH, Geeste, Germany). All trays, including the stress groups, were irrigated equally (50 mL per cell) every two days for five weeks until germination. Stress treatments were initiated on 5-week-old seedlings and continued for three weeks. At the end of this period, 8-week-old seedlings were evaluated for physiological and morphological parameters. Halo-primed seedlings were subjected to salt stress every two days with a 0.9% NaCl solution equivalent to 80% of the field capacity (FC). Osmo-primed seedlings were irrigated every two days with a reduced water supply to 30% FC. Control (non-primed) seedlings were irrigated every other day with water equivalent to 80% FC.

The field capacity (FC) was determined through the saturation of compost in five replicate seedling tray cells, followed by a 48-hour drainage period, where the residual moisture was designated as 100% FC and used to calibrate daily watering schedules.

Plant Morphological Measurements

At the end of the experiment, plant heights, fresh shoot weights, and fully developed leaves were recorded. Leaf areas (LA) were analyzed from the second uppermost fully developed leaf using ImageJ (Rasband, 1997; Schneider et al., 2012).

Stomatal Conductance and Light-Adapted Chlorophyll Fluorescence Parameters

At the end of the experiment, stomatal conductance of water vapour (G_{sw}) and light-adapted chlorophyll fluorescence parameters were measured using a Li-600 porometer and fluorimeter using a light flash intensity of 7000 µmols $m^{-2}s^{-1}$ and a flow rate of 150 µmols s^{-1} (Li-Cor Inc., Lincoln, NE, USA). Measurements were taken in the morning between 9 to 11 am. The quantum sensor on the Li-600 was used to measure ambient photosynthetic photon flux density (PPFD) at the time of the measurement – these values ranged from 400 to 1000 µmol m^{-2} s^{-1}, with a mean PPFD of 625 µmol m^{-2} s^{-1}.

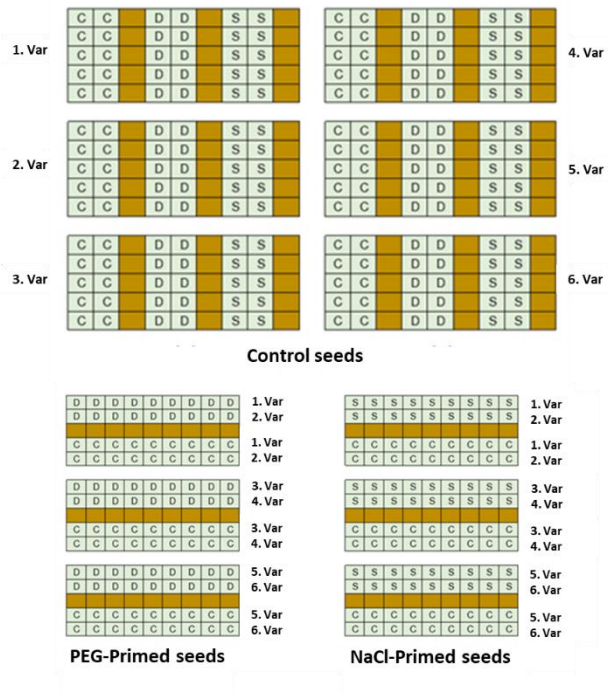

Figure 1. Experimental design of sugar beet varieties; *Lider, Libellule, Lizard, Mohican, Bison,* and *Rodeo* under control, drought and salt stress condition with Control, PEG-Primed and NaCl-Primed seeds, n=9

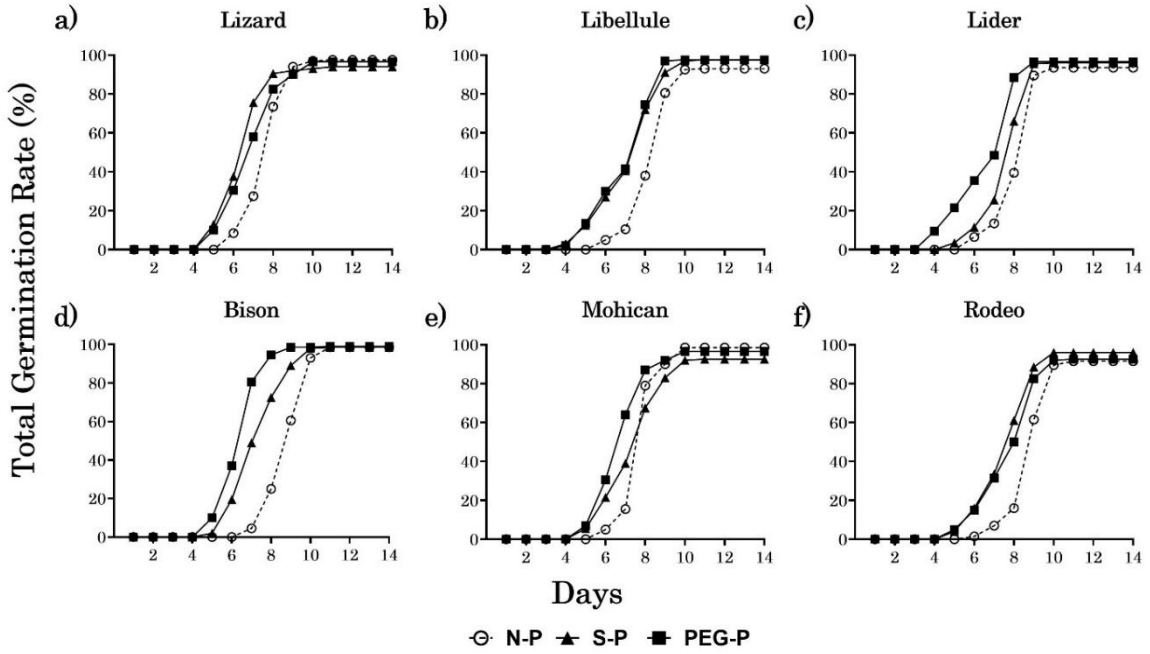

Figure 2. Time course of total germination rate of different varieties of sugar beet seeds over a period of 14 days. Non-Primed Seeds (N-P, ○), NaCl-Primed Seeds (S-P, ▲), PEG-Primed Seeds (PEG-P, ■), n=8

Stomatal conductance to water vapor (G_{sw}, mmol/m^{2}s) was determined by measuring the rate of water vapour released by a leaf inside a chamber. This transpiration rate is calculated based on the difference in water vapour concentration between the air entering and exiting the chamber. Quantum efficiency in light (ΦPSII) reflects the proportion of light energy captured by PSII that drives electron transport (Genty et al., 1989). Electron transport rate (ETR, µmol/m^{2}s) reflects the linear rate of electron flow through the photosynthetic electron transport chain. Derived from chlorophyll fluorescence measurements, it is reported as the rate of electron transport per unit leaf area per unit time (Rascher et al., 2000)..

Dark-Adapted Chlorophyll Fluorescence

A Pocket Plant Efficiency Analyzer (PEA, Hansatech Instruments Ltd., King's Lynn, UK) was used to measure dark-adapted chlorophyll fluorescence parameters. Measurements were taken approximately one hour after dark (in the evening) after dark adaptation of the plants. The data were utilized for OJIP curve analysis, a polyphasic chlorophyll *a* (Chl *a*) fluorescence transient plotted logarithmically. It reflects photosystem II (PSII) dynamics following a saturating light pulse (3500 µmol m^{-2}s^{-1}, 627 nm). The phases—O (30 µs, F_o), J (2 ms, F_j), I (30 ms, F_i), and P (1 s, F_m)—correspond to fluorescence intensities at distinct time points (Strasser et al., 2004). Parameters derived from the curve provide insights into the efficiency of the PSII function (Kalaji et al., 2016; Strasser et al., 2004) (, Figure 14).

Effective absorption flux per reaction center (ABS/RC) reflects the light absorbed by functional reaction centers. The electron transport rate (ETR) beyond plastoquinone-A (ET_O/RC) reflects the electron transport activity beyond plastoquinone-A per reaction center. Performance index on an absorption basis (PI_{ABS}) provides a comprehensive assessment of PSII functionality, incorporating photochemical and non-photochemical processes.

Statistical Analysis

Statistical differences between treatment groups were evaluated through post-hoc comparisons, specifically Duncan's multiple range test and the least significant difference (LSD) test. All statistical analyses were carried out with SPSS 25.0 (IBM Corp., Armonk, NY, USA) or GraphPad Prism 10.2 (GraphPad Software, San Diego, CA, USA).

Results

Seed Germination and Plant Morphological Results

Primed seeds exhibited more rapid germination for all varieties than their non-primed seed counterparts. PEG-primed (PEG-P) seed germination was faster and higher in most of the varieties such as Lider, Bison and Mohican (Figure 2). After one week, non-primed (N-P) seed germination was 4.5%, 7%, 10.5%, 13.5%, 15.5%, 27.5% for Bison, Rodeo, Libellule, Lider, Mohican and Lizard respectively, while NaCl-primed (S-P) seed germination was 49%, 33.5%, 40.5%, 25.5%, 39% and 75.5% for Bison, Rodeo, Libellule, Lider, Mohican and Lizard respectively. These results indicate that salt priming increased seed germination by 2-10 times across different varieties, with the smallest increase observed in Lider and Mohican, where germination approximately doubled after one week. In terms of PEG-primed (PEG-P), the germination rates of seeds were as follows: 80.5%, 31.5%, 41.5%, 48.5%, 64%, and 58% for Bison, Rodeo, Libellule, Lider, Mohican, and Lizard, respectively (Figure 3). The greatest improvements in germination rates were observed in Bison and Lizard when seeds were primed with either NaCl or PEG, compared to their non-primed counterparts.

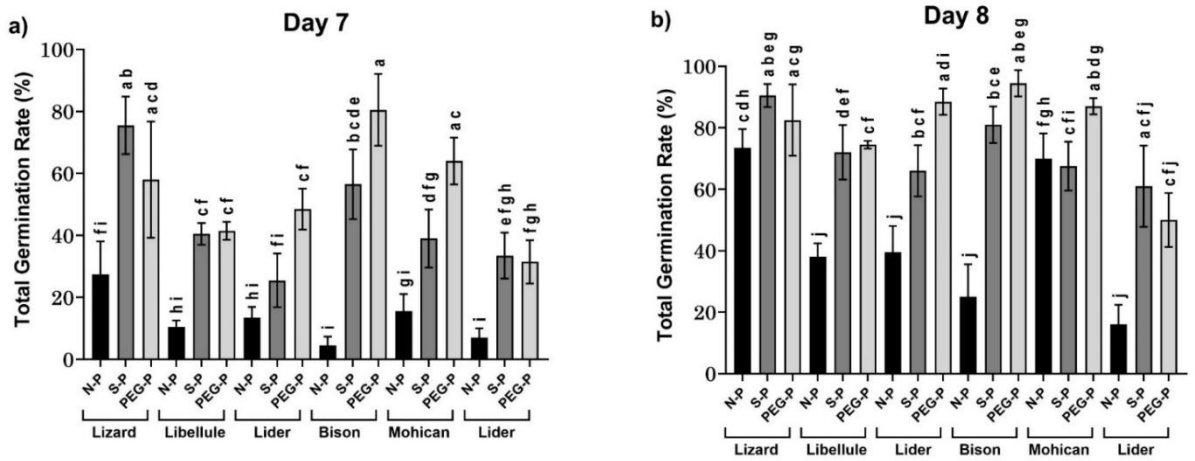

Figure 3. Total germination rates of six sugar beet varieties under three priming conditions: Non-Primed (N-P), NaCl-Primed (S-P), and PEG-Primed (PEG-P). Results are shown for the 7th (a) and 8th (b) days of the germination test (n=8)

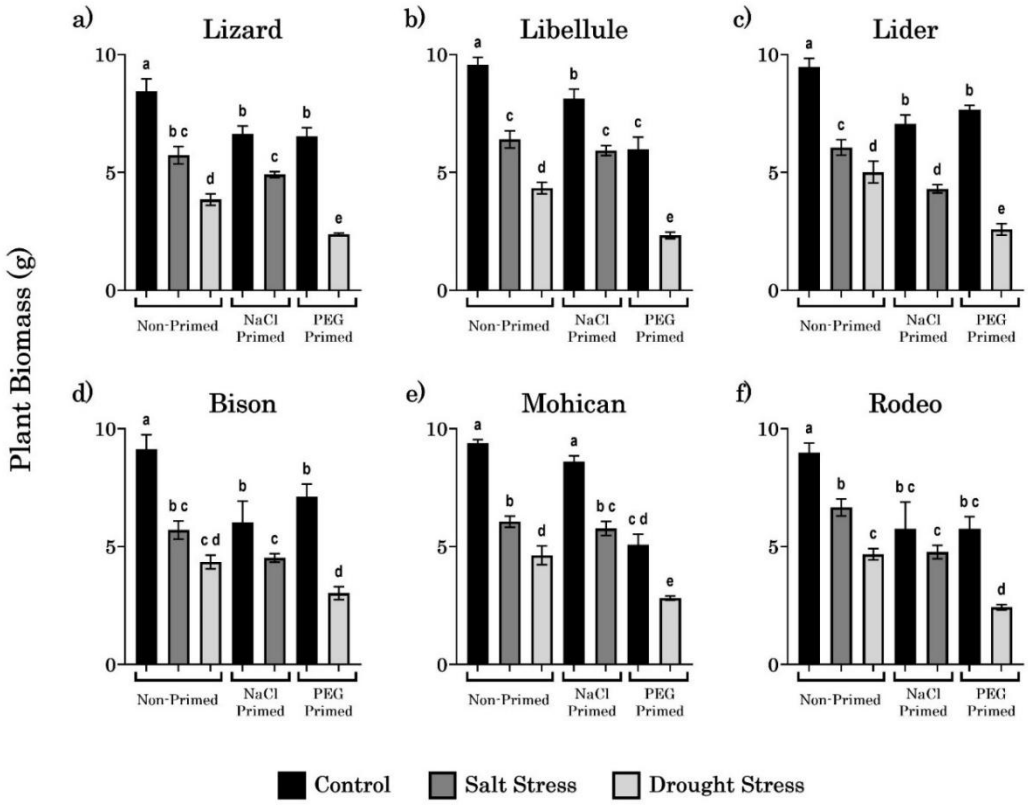

Figure 4. Plant Biomass of different sugar beet varieties with Non-Primed (N-P) Seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.
Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

Seedlings from non-primed seeds generally exhibited the highest biomass under control conditions across all varieties, except for Mohican. NaCl priming enhanced biomass only in the Mohican variety, reaching a level comparable to that of non-primed seeds (Figure 4e). NaCl priming had no significant effect on plant biomass under salt stress conditions, except for Rodeo and Lider, which exhibited negative effects (Figure 4c and 4f). PEG priming reduced seedling biomass under both control and drought conditions compared to non-primed seeds (Figure 4).

Under control conditions seedlings from non-primed (N-P) seeds generally exhibited greater height across all varieties (Figure 5). However, this is quite variable and there are no patterns supported by significance. PEG-P seeds under control condition showed plant height statistically similar ($p>0.05$) to N-P control plants except Libellule, Mohican and Rodeo which were statistically lower than N-P control plants. NaCl-primed (S-P) seeds did not significantly improve plant height under salt stress conditions (Lizard, Libellule and Mohican as high as N-P seeds under salt stress), similar to PEG-primed (PEG-P) seeds, which showed no statistically significant increase in plant height under drought conditions ($p > 0.05$) (Figure 5).

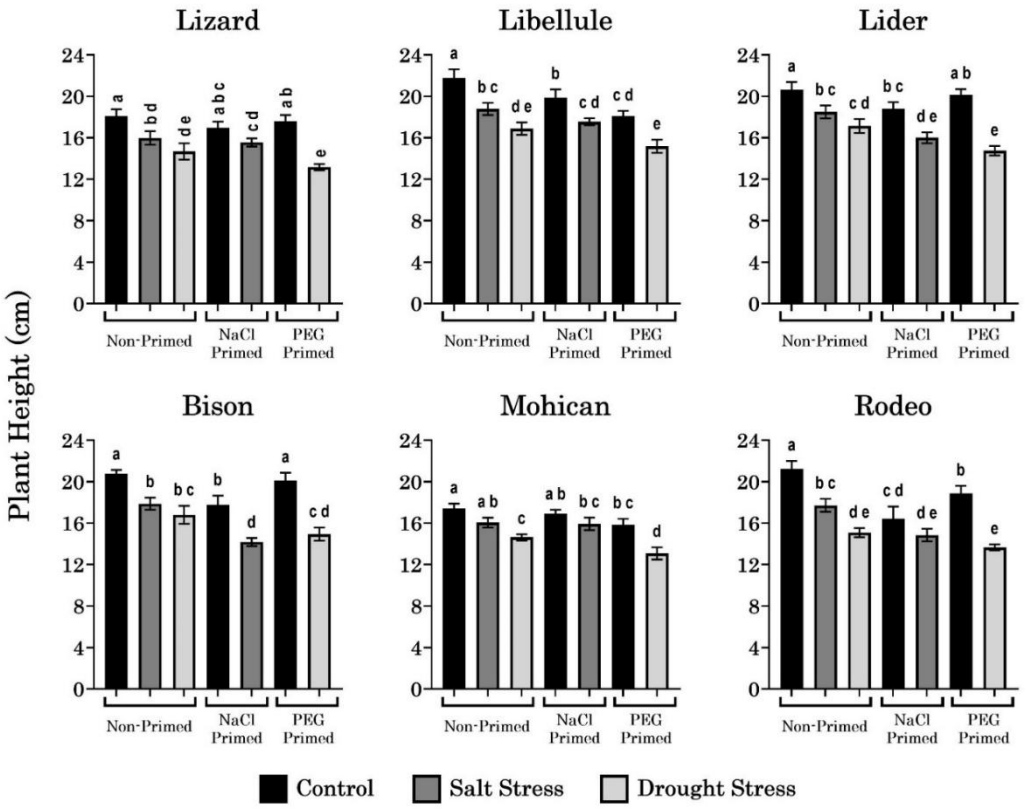

Figure 5. Plant Height of different sugar beet with Non-Primed (N-P) Seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.

Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

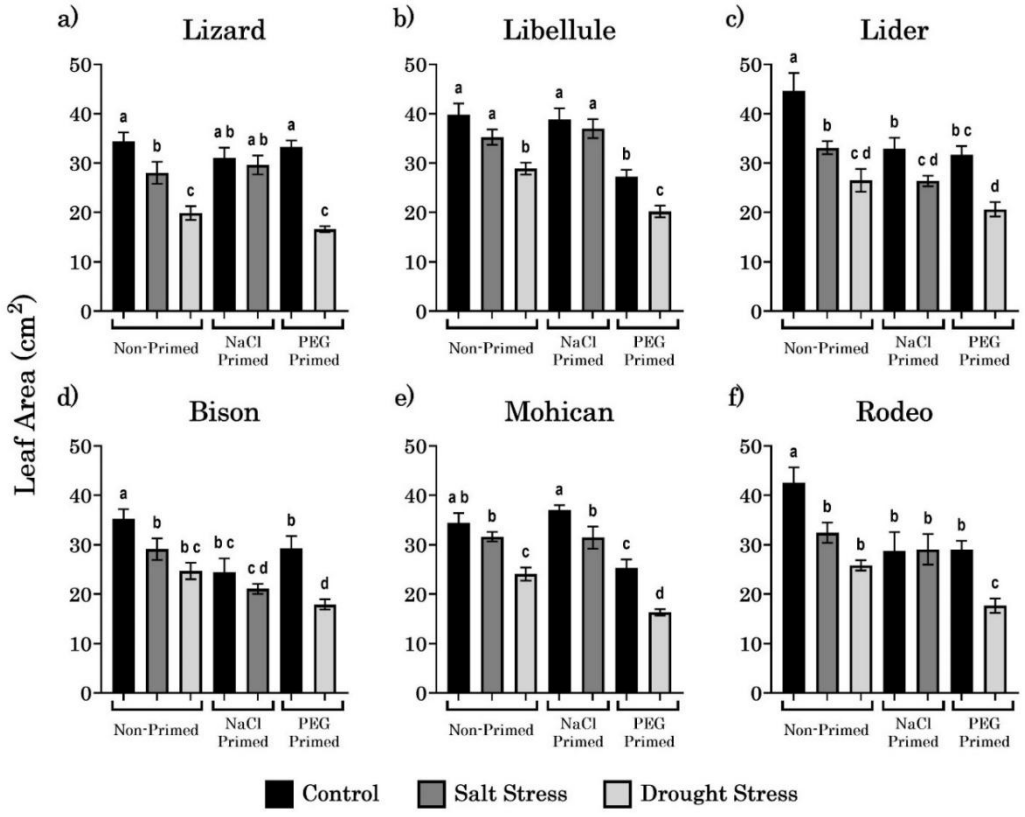

Figure 6. Leaf Area of different sugar beet varieties with Non-Primed (N-P) Seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.

Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

Under control growth conditions, the leaf area was reduced under salt stress and was lowest under drought stress across all varieties (Figure 6). NaCl priming (S-P) resulted in a slightly higher leaf area under salt stress conditions; however, the difference was not statistically significant ($p > 0.05$) for the Lizard, Mohican and Libellule varieties (Figure 6a, b and e). PEG priming (PEG-P) significantly reduced leaf area under drought stress conditions (Figure 6).

NaCl-primed (S-P) seeds did not significantly improve plant leaf number under salt stress condition, similar to PEG-primed (PEG-P) seeds, which showed no statistically significant increase in plant leaf number under drought conditions ($p > 0.05$) (Figure 7). Under control conditions, priming with NaCl and PEG generally resulted in a leaf number similar to that of non-primed (N-P) seeds (Figure 7).

Stomatal Conductance and Light-Adapted Chlorophyll Fluorescence Results

Non-primed seedlings exhibited higher stomatal conductance of water vapour (G_{sw}) under control growth conditions compared to salt or drought stress. The highest G_{sw} reduction due to salt and drought stress occurred on Bison, Rodeo and Libellule (Figure 8). However, PEG priming (PEG-P) significantly increased G_{sw} under drought conditions just for Bison compared to non-primed (N-P) plants subjected to drought stress (Figure 8d). NaCl-primed (S-P) and PEG-primed (PEG-P) plants showed increased G_{sw} under control conditions, particularly in the Lizard, Libellule, Lider, and Mohican varieties ($p < 0.05$) (Figure 8a, b, c and e).

Under control growth conditions the actual quantum efficiency of PSII (ΦPSII) was unaffected by seed priming, similar to N-P seedlings (Figure 9). Salt and drought stress did not reduce ΦPSII in Lizard, Mohican, and Rodeo with non-primed (N-P) seeds (Figure 9a, e, and f). NaCl priming (S-P) increased ΦPSII under salt stress conditions only in Libellule and Lider compared to N-P seeds under salt stress, however this difference was not statistically significant (Figure 9b and c). PEG priming did not have a statistically significant positive or negative effect on ΦPSII.

Salt stress did not reduce Electron Transport Rate ETR in non-primed (N-P) seeds, nor did NaCl priming (S-P) positively affect ETR under salt stress conditions (Figure 10). Under drought stress, ETR was only reduced in Lizard at the end of the experiment, while other varieties showed no significant reduction. PEG priming (PEG-P) negatively affected ETR in certain varieties, including Lider, Bison, and Rodeo (Figure 10c, d and f). Similarly, NaCl priming (S-P) had a negative impact on ETR in Lizard and Bison (Figure 10a and d).

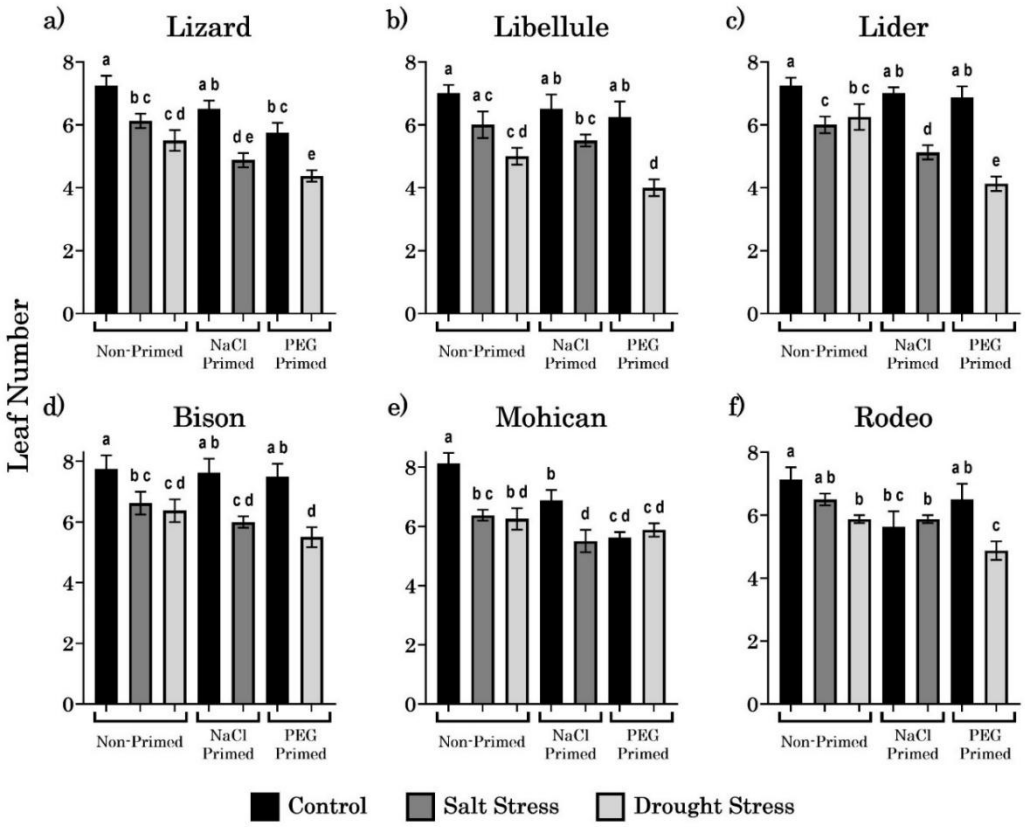

Figure 7. Leaf Number of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.

Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

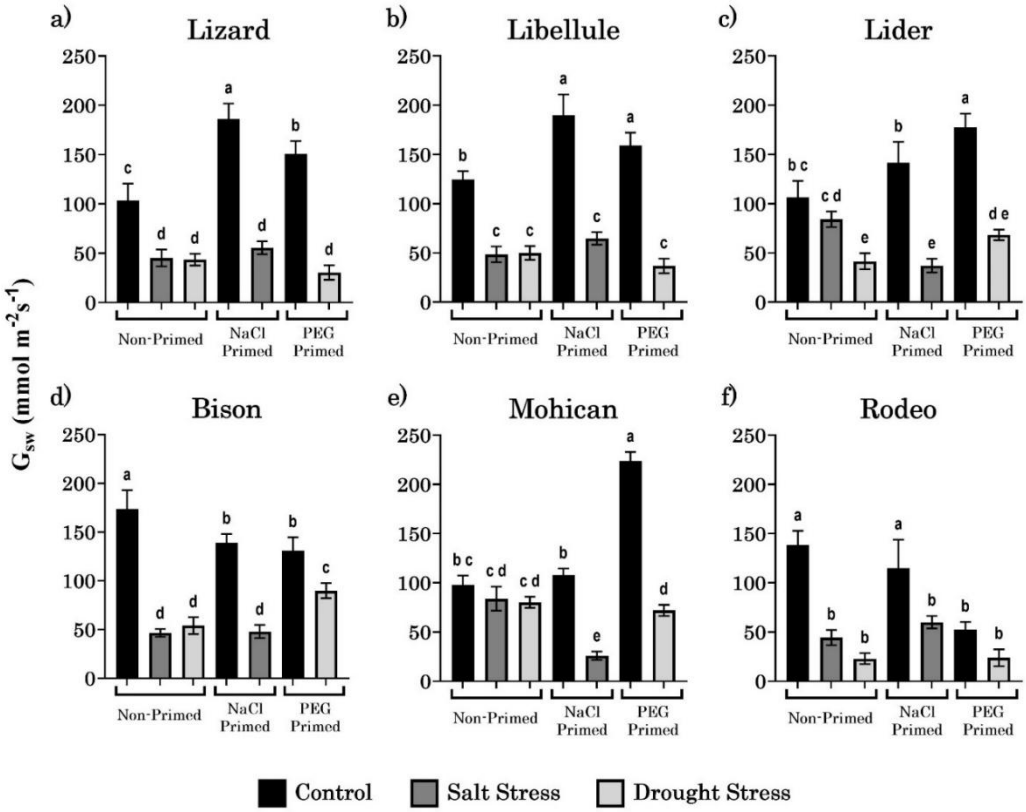

Figure 8. Stomatal Conductance of water vapor (G_{sw}) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.
Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

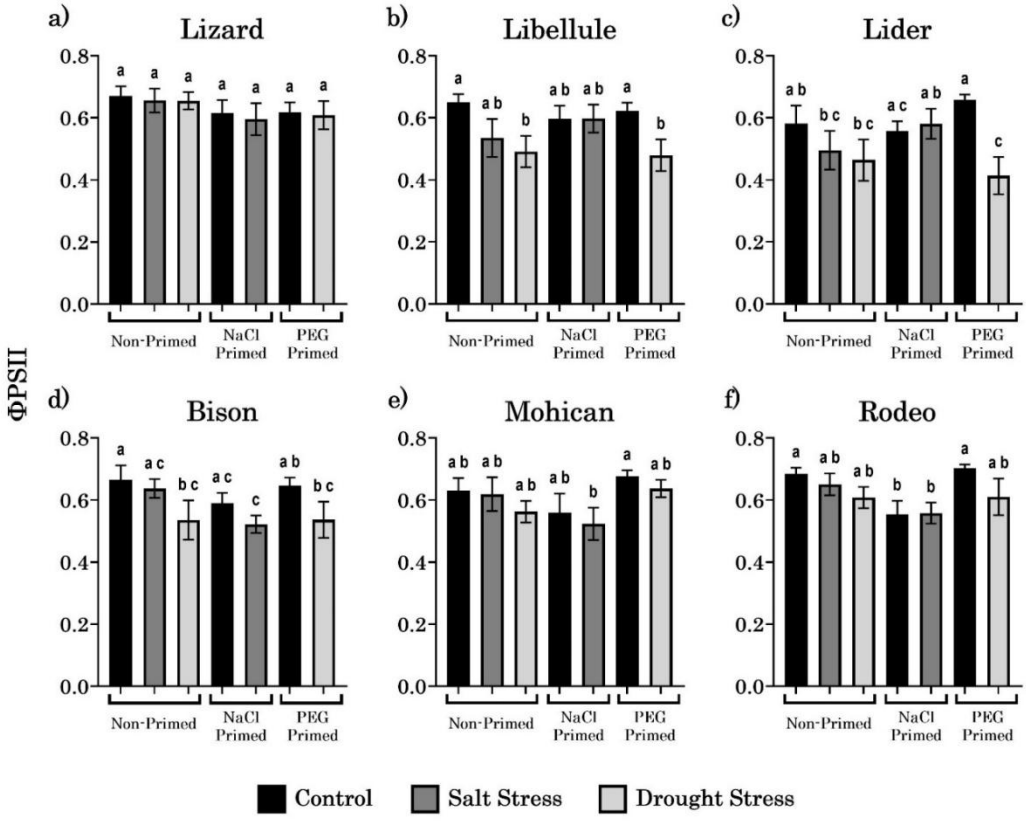

Figure 9. Actual quantum efficiency of PSII (ΦPSII) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.
Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

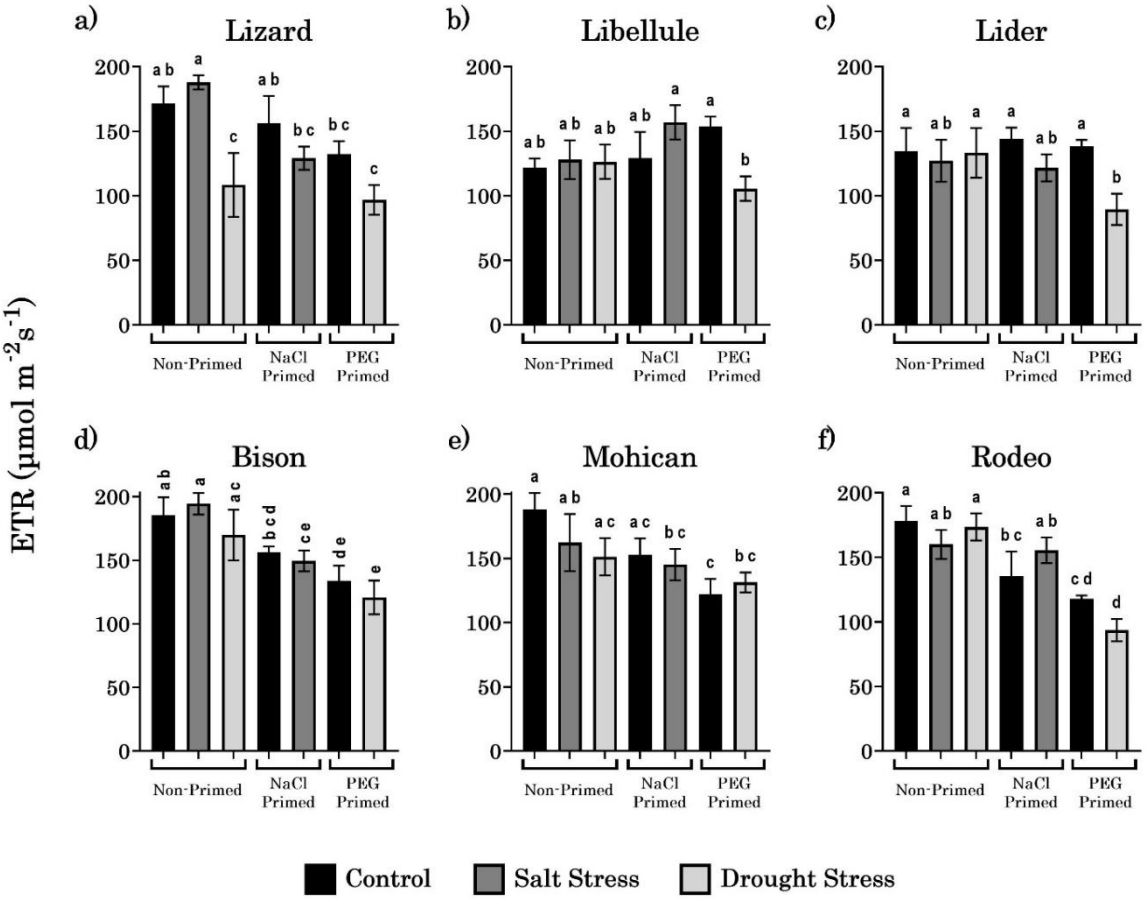

Figure 10. Electron Transport Rate (ETR) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.
Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

Dark-Adapted Chlorophyll Fluorescence Results

The effective absorption flux per reaction center (ABS/RC) is calculated based on the light absorbed by functional reaction center-associated chlorophyll (Chl_{RC}) relative to the total chlorophyll content (Chl_{tot}). *ABS/RC*, with N-P seeds mainly did not change with salt or drought stress (Figure 11a, b, c, d and e). NaCl-priming (S-P) increased ABS/RC, but this change was not statistically significant under control and salt stress condition (Figure 11a, c, d, e and f) except Libellule. PEG-priming statistically increased ABS/RC under drought conditions for Lizard, Libellule, Bison and Rodeo, but not for Lider and Mohican (Figure 11).

Seed priming and growth conditions did not significantly affect the electron transport rate beyond plastoquinone-A (ETo/RC) except PEG-Priming increased ETo/RC for Lizard, Libellule and Bison under drought stress conditions (Figure 12a, b and d).

Drought stress increased the performance index on an absorption basis (PI_{ABS}) with non-primed (N-P) seeds (Figure13a and f, also b, d and e had relatively small increases); however, seed priming (both S-P and PEG-P) had no significant effect on the performance index on an absorption basis (PI_{ABS}) (Figure 13).

In the OJIP curve (Figure 14), at point O, which reflects the LHCII health, no significant differences were observed among treatments or varieties. However, in 'Lizard' and 'Libellule', NaCl priming exerted a positive effect on PSII performance at the J phase under both control and stress conditions (Figure 14a and b, blue lines). In contrast, for the other varieties and treatments, no clear effect of priming or stress on PSII was detected.

Discussion

In the study, results indicate that Lizard exhibited the highest germination rates among N-P, S-P, and PEG-P seeds, with 27.5%, 75.5%, and 58% and Bison demonstrated 49.5% and 80.5% with S-P and PEG-P seeds, respectively (Figure 2). PEG-priming enhanced seed germination by accelerating the process and increasing the overall germination rate (Figure 3). The high molecular weight of PEG limits its diffusion into the seed, preventing cytotoxic effects while simultaneously reducing the solute potential (Marthandan et al., 2020). Brocklehurst and Dearman (1983) found that PEG priming enhanced the germination rate, particularly in poorly emerging carrot and celery seeds; however, it had no significanteffect on onion seed germination. In this study, seedlings from non-primed seeds generally exhibited the highest biomass under control conditions across all varieties. NaCl-priming and PEG-priming did not statistically increase plant biomass and plant height (Figure 4 and Figure 5).

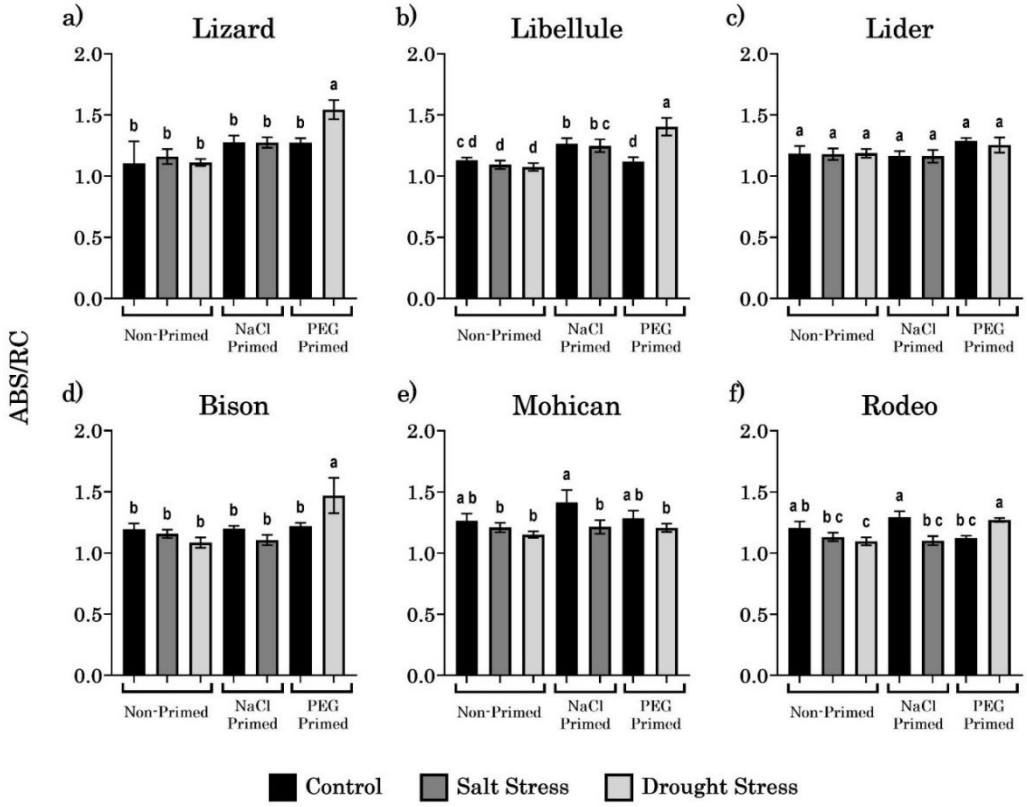

Figure 11. Absorbance per Reaction Center (ABS/RC) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.

Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

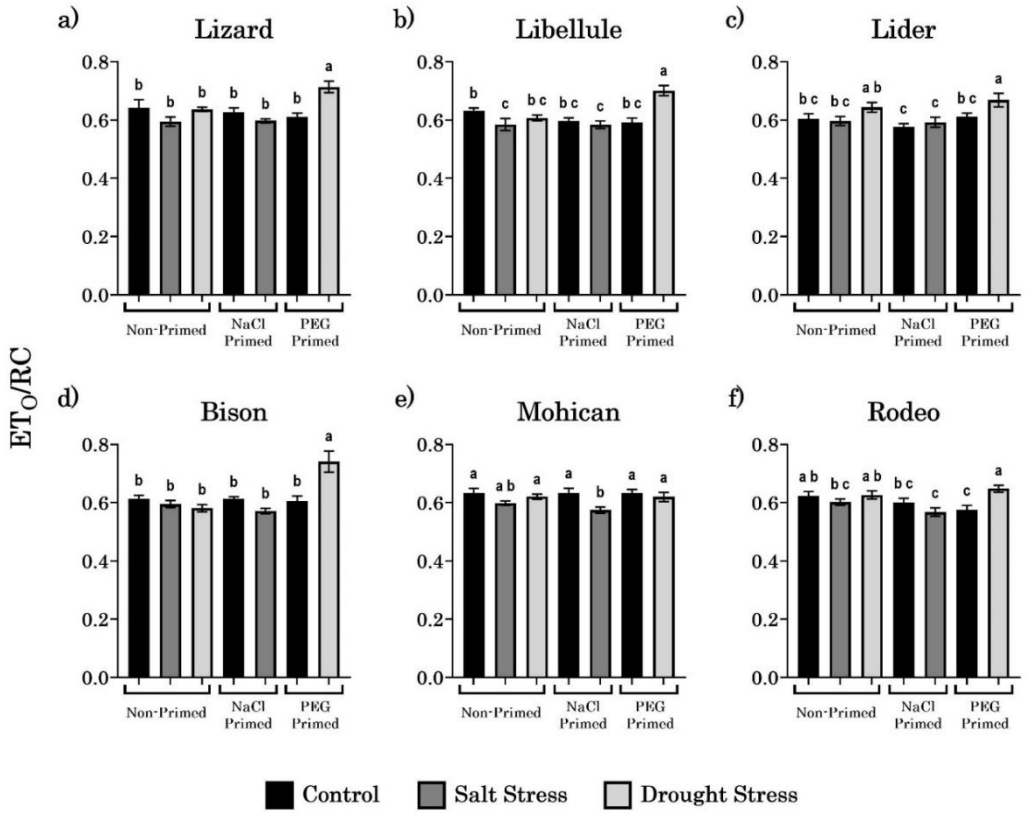

Figure 12. The electron transport rate beyond plastoquinone-A (ETo/RC) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition.

Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

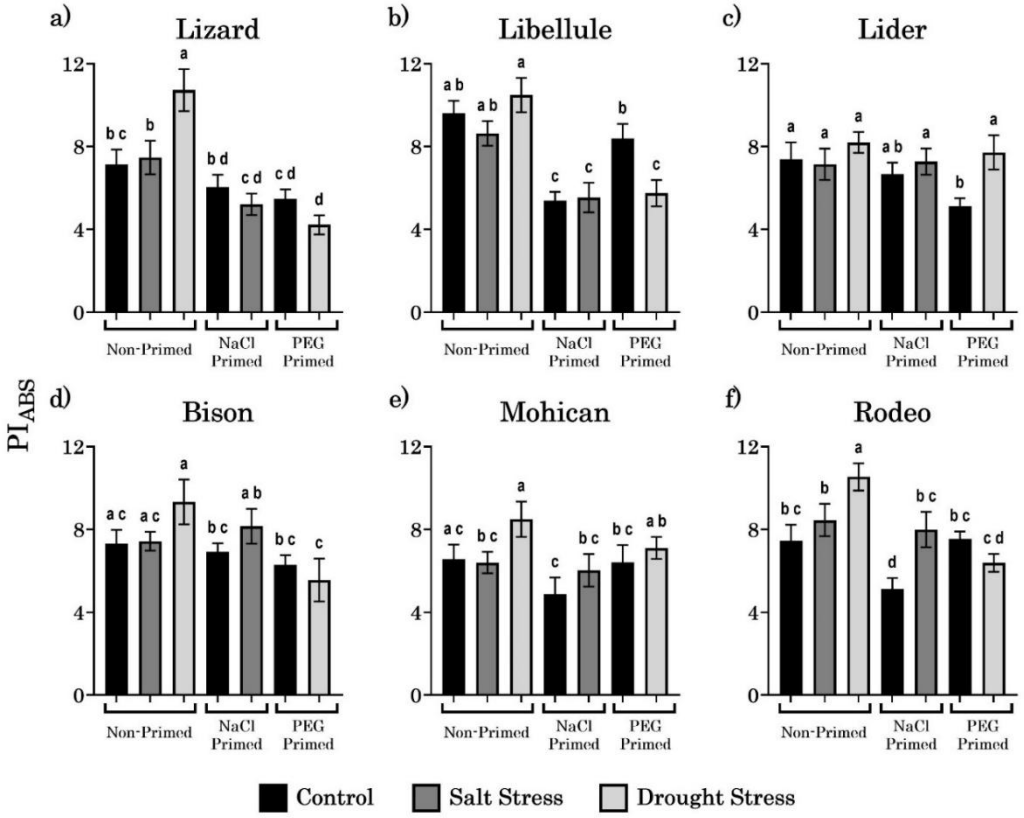

Figure 13. The performance index on an absorption basis (PI_{ABS}) of different sugar beet varieties with Non-Primed (N-P) seeds, NaCl-Primed (S-P) seeds and PEG-Primed (PEG-P) seeds, at the end of 3 weeks of control, salt stress and drought stress condition. Values are means of 8 replicates. Different and identical small letters above histograms indicate significant ($p < 0.05$) and no significant differences ($p > 0.05$), respectively, between the means according to Duncan's test, n=8

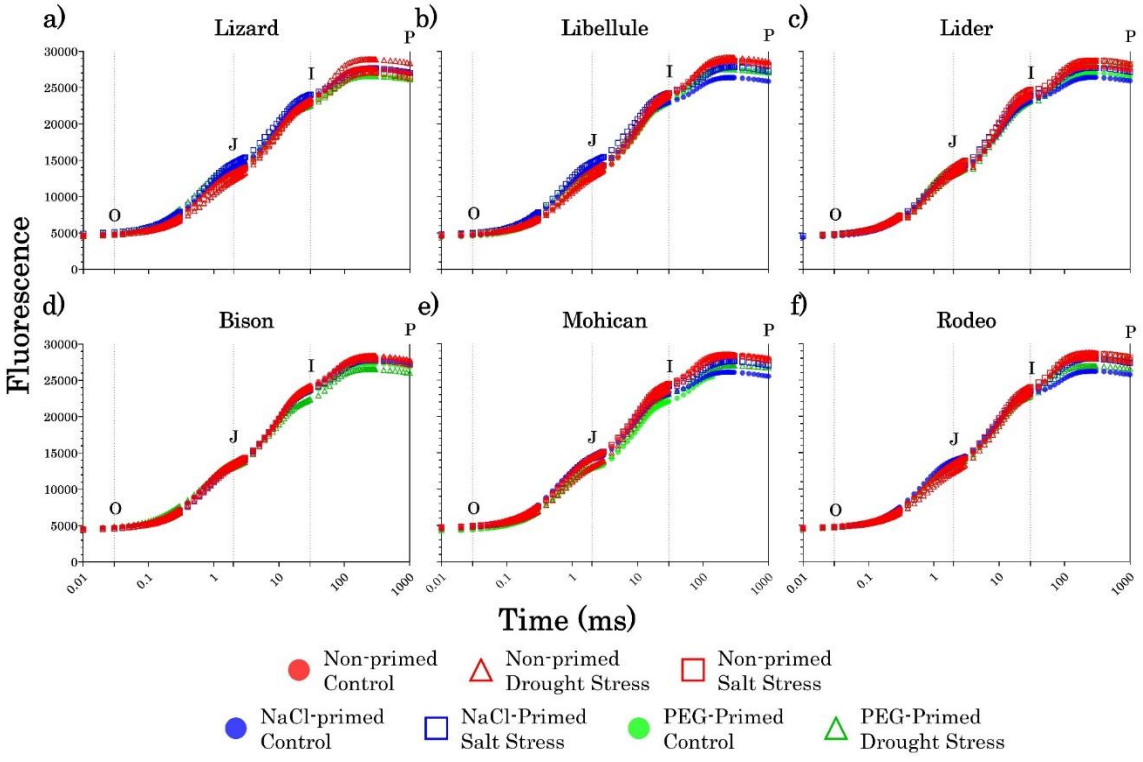

Figure 14. Average OJIP fluorescence transient curves for six sugar beet varieties (a-f) illustrating the effects of different priming and stress treatments (n=8). Data points represent the average fluorescence intensity (arbitrary units) over time (milliseconds). Key inflection points of the OJIP transient are labeled (O, J, I, P)

Şahin (2024) reported that various priming techniques significantly enhanced the germination rate of different sugar beet varieties. However, these priming methods did not consistently increase seedling fresh biomass compared to the control. Instead, seedling fresh biomass was significantly influenced by the duration of seed priming. Thus, the duration of seed priming in this study may have been a determining factor in obtaining this result. Similarly, a study by Ashraf and Iram (2002) indicated that neither different priming durations, nor varying salt concentration, effectively induced salt tolerance in two spring wheat cultivars, as reflected by the lack of significant improvements in germination percentage, germination rate, or rudimentary shoot dry weight also observed in this study.

Previous research has demonstrated that NaCl seed priming activates protective mechanisms within the seeds, thereby improving their capacity to withstand and adapt to salt stress more effectively (Sen & Puthur, 2020; Sivritepe et al., 2003). Sivritepe et al. (2003) observed that NaCl priming in melon seedlings led to an increase in the accumulation of total sugars and proline, which in turn helped alleviate the toxic effects of salinity. Primed seeds promote germination rate and seedling growth through the activation of enzymes, repair of cellular structures, synthesis of proteins, and enhancement of antioxidant defense mechanisms, in contrast to non-primed seeds (Afzal et al., 2008; Jafar et al., 2012; ur Rehman et al., 2015). Osmopriming is one of the priming technique involving osmotic solutions including KH_2PO_4, KNO_3, $CaCl_2$, $MgSO_4$, NaCl, KCl, and PEG. These different priming solutions are widely used to enhance the drought and salinity tolerance in many crop plants. Although all these techniques have a common feature, i.e., partial pre-hydration and earlier activation of germination events in seeds, the efficiency highly depends on the treated plant species and the chosen priming technique (Marthandan et al., 2020). The findings of Cayuela et al. (1996) support the hypothesis that different levels of NaCl seed priming induce physiological modifications in plants, with these effects becoming more evident at later growth stages. Thus, the results of this study may have been affected by the duration of seedling growth or level of NaCl and PEG. Sorghum seeds primed with 50 mM NaCl exhibited the highest relative shoot fresh weight and shoot length compared to those primed with 100 mM and 150 mM NaCl. Similarly, 10% PEG priming resulted in the greatest relative shoot fresh weight and shoot length in sorghum seedlings compared to 20% and 30% PEG priming treatments (Chen et al., 2021).

Leaf area generally remained similar to the control in NaCl-primed seeds under salt stress, except for Lider and Bison, which exhibited reductions. In contrast, PEG-priming was less effective in maintaining leaf area under drought stress compared to non-primed seeds (Figure 6). Notably, the Lizard variety was the only one that maintained leaf area under both salt and drought stress conditions with both priming techniques (Figure 6a). Primed sugar beet exhibited increased leaf area index (LAI) between 60 and 120 days after sowing under field conditions (Chomontowski et al., 2020). Mohajeri et al. (2015) reported statistically higher leaf area index (LAI) with PEG-primed seeds in bean crops than control (non-primed seeds) under field experiment. In the same experiment, NaCl-priming was also statistically identical to control plants ($p>0.05$). NaCl priming at 0.5 M and 1 M significantly reduced shoot length and leaf area in maize seedlings compared to non-primed seeds under varying levels of salt stress (Farahbakhsh & Shamsaddin, 2011). Mohajeri et al. (2015) found that six hours of PEG priming in bean seeds significantly increased seedling height in a field experiment, compared to non-primed seedlings. Although in this study, PEG-primed seedlings exhibited relatively greater plant height than NaCl-primed seedlings, this difference was not statistically significant. These results show that duration of priming, different level of osmolytes and also different plant growth stages may change germination rates and plant morphologic parameters. Research into the later stages of sugar beet cultivation showed that seed priming increased sugar beet root yield by approximately 10–11% in field trials compared to non-primed seeds (Chomontowski et al., 2020). Michalska-Klimczak et al. (2018) reported that priming significantly enhanced the average sugar beet root mass in a two-year field experiment, although no statistically significant increase was observed in total root and leaf yield per hectare. Similarly, Brocklehurst and Dearman (1983) found that plant fresh weights after 9, 7, and 12 weeks of sowing were consistently higher in carrot, celery, and onion grown from PEG-primed seeds, with increases of up to 33%, 182%, and 47%, respectively, compared to controls. However, contrasting findings indicate that distilled water priming and KNO_3 priming did not significantly enhance cotton shoot and root biomass, plant shoot length under varying salinity conditions (Rezaee et al., 2015).

Drought tolerance mechanisms function by regulating various morphological and physiological traits that help plants mitigate osmotic stress. These mechanisms include enhanced root growth, reduced stomatal density and conductance, decreased leaf area, leaf thickening, increased biosynthesis of cuticular wax, and leaf folding, all of which contribute to minimizing evapotranspiration (Haworth et al., 2024; Killi et al., 2017; Lee SaetBuyl & Suh MiChung, 2013; Liu et al., 2017). Non-primed seedlings exhibited higher G_{sw} under control growth conditions compared to salt or drought stress. PEG-priming increased G_{sw} under control conditions, particularly in Lider and Mohican, while under drought conditions, only Bison showed increased G_{sw} with PEG-priming. Additionally, only Lizard and Libellule seedlings from S-P and PEG-P seeds showed increased G_{sw} under control conditions (Figure 8). These findings suggest that seed priming positively influenced plant physiology, but its effects were primarily observed under control conditions. Khalequzzaman et al. (2023) observed that various priming techniques reduced G_{sw} in cotton by 20–40% under drought stress conditions (50% of field capacity). Even though net photosynthesis was increased by some of the priming techniques under drought conditions, some priming techniques, such as silicon and proline, did not increase photosynthesis under drought conditions in comparison to non-primed seedlings under the same drought treatment (Khalequzzaman et al., 2023). Zaid et al. (2022) found that different priming techniques and varying concentrations of priming agents can reduce photosynthesis and stomatal conductance.

Seed priming had no effect on the actual quantum efficiency of PSII (ΦPSII) under control conditions. NaCl priming (S-P) enhanced ΦPSII under salt stress conditions only in Libellule and Lider compared to non-primed (N-P) seeds under salt stress (Figure 9b, 9c). PEG priming did not exhibit any statistically significant impact on ΦPSII. Salt stress did not decrease the Electron Transport Rate (ETR) in non-primed (N-P) seeds, nor did NaCl priming (S-P) enhance ETR under salt stress conditions (Figure 10). Nouairi et al. (2019) found that calcium chloride priming in faba bean enhanced F_v/F_m (maximum quantum yield of PSII), ΦPSII (actual efficiency of PSII), and ETR (photosynthetic electron transport rate), while reducing NPQ (non-photochemical quenching) under cadmium (Cd) stress. Osmopriming with PEG 6000 improved drought tolerance in *Medicago sativa* by enhancing PSII efficiency. As a result, osmoprimed plants exhibited greater plant height, leaf area, and overall growth compared to non-primed plants under drought stress (Mouradi et al., 2016).

The effective absorption flux per reaction centre (ABS/RC) increased only in the Lizard, Libellule, and Bison varieties under drought stress with PEG-primed seeds, indicating a reduced number of active reaction centers. This trend was also observed in the electron transport rate beyond plastoquinone-A (ETo/RC) which is determined based on the specific electrical conductivity across the thylakoid membrane and the relative volume of the active electron transport chain (Figure 11 and 12). This suggests that salt stress with PEG-primed seeds, predominantly impair reaction centers (RCs). This response may be attributed to lower antioxidant production in these varieties with PEG-priming seeds under drought stress, leading to reduced protection of the photosystem against reactive oxygen species (ROS). In this study, drought stress led to an increase in the Performance index on an absorption basis (PI_{ABS}), of the seedlings with non-primed (N-P) seeds, whereas seed priming (both S-P and PEG-P) showed no significant impact on PI_{ABS} (Figure 13). Dolu et al. (2025) found that the first twelve days after stress application, PI_{ABS} experienced a reduction under salt-stress condition comparison to unstress groups, indicates a breakdown in these protective mechanisms, resulting in reduced photosynthetic efficiency. In another study examining six sweet sorghum varieties under incremental salt stress from 0 to 250 mM, certain varieties showed higher PI_{ABS} values at 100 mM salt stress relative to the control (Rastogi et al., 2020).

The results indicate that salt priming (S-P) and PEG priming (PEG-P) significantly enhanced germination rates, particularly in certain sugar beet varieties. Additionally, morphological and photosynthetic parameters varied among different varieties depending on the priming technique and stress conditions. This variation may be attributed to genetic differences among varieties, influencing germination rates and physiological responses to priming under varying levels of salt and drought stress. Studies suggest that factors such as priming duration, osmolyte concentration, plant growth stage, and genetic variation can all impact germination rates, as well as morphological and photosynthetic traits. Further research on varying levels and durations of NaCl and PEG priming, as well as different intensities of salt and drought stress, will help clarify the effects of these factors on different plant growth stages. Understanding these interactions will contribute to enhancing food security in the context of climate change and environmental degradation.

Declarations

Author Contributions

Conceptualization, methodology, supervision, project administration, D.K.; software, H.D., Z.S.G, D.K.; validation, D.K, H.D., Z.S.G.; formal analysis, H.D., Z.S.G., D.K.; investigation, D.K, H.D., Z.S.G.; writing—original draft preparation, D.K.; writing—review and editing, D.K.; All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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