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Exploring salt sensitivity in berseem (*Trifolium alexandrinum*) through analysis of ROS-scavenging attributes

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ABSTRACT

Berseem (*Trifolium alexandrinum* L.) serves as an excellent fodder source, yet its limited salt tolerance restricts its cultivation. This study was carried out during 2022 and 2023 at Indian Institute of Technology, Ropar, Punjab to examine the impact of salinity stress (2.5, 5.0, and 6.5 dS/m) imposed at different growth stages (2-leaf, 6-leaf, and flowering) on berseem in a sensor-based lysimeter system. The control group was irrigated with tap water in and completely randomised block (CRD) design was followed. Growth attributes and antioxidative potential were assessed. The results revealed that salt stress significantly reduced plant height (by up to 33%), biomass (by up to 68%), and root length (by up to 59%), with the most severe decline observed at 6.5 dS/m at the 6-leaf stage. Pearson's correlation matrix indicated a strong positive correlation between H_2O_2 content and MDA ($r = 0.78$) and a moderate positive correlation with SOD ($r = 0.58$). The activities of antioxidative enzymes, peroxidase and superoxide dismutase, exhibited a significant up-regulation by 525% and 71%, respectively as salinity increased from control to 6.5 dS/m. Principal component analysis confirmed that the 6-leaf stage was the most salt-sensitive. The critical damage threshold for berseem was identified at salinity levels exceeding 5 dS/m.

Keywords: Antioxidative potential, Correlation analysis, Growth stages, Principal component analysis, Salinity stress

Environmental factors can significantly disrupt plant development and productivity (Parihar *et al.* 2015), with salt stress being a major abiotic constraint. Salinity affects around 6% of the world's land area, including 20% of arable and 33% of irrigated land (Kuang *et al.* 2019) leading to estimated yield losses of about 20% globally (Pirasteh-Anosheh *et al.* 2015). This issue is particularly pronounced in arid and semi-arid regions, where it causes substantial agricultural decline (Hasanuzzaman *et al.* 2014). In India, approximately 5.95 million hectares are impacted by salinity, with Haryana, Punjab, Rajasthan, Gujarat, and Andhra Pradesh accounting for nearly 48% of the affected soils (Mandal *et al.* 2010).

Legumes, in particular berseem (*Trifolium alexandrinum* L.), is notably sensitive to salt, with a narrow threshold tolerance of about 1.5 dS/m (Abd el-naby *et al.* 2019). Berseem is a vital fodder crop cultivated across nearly 2 million hectares in India (Boelt *et al.* 2014), yielding approximately 85 t/ha and containing 20% protein and a high digestibility (up to 65%), making it an optimal choice as a fodder crop (Singh *et al.* 2020). High salinity levels hinder its growth, particularly affecting root length during critical growth stages of 2 leaf, 6 leaf and flowering, leading to reduced yields (Kazemeini *et al.* 2018). Salt toxicity triggers the accumulation of reactive oxygen species (ROS) (Pakar *et al.* 2016) including singlet oxygen (O_2^1), hydrogen peroxide (H_2O_2), superoxide ($O^{2\cdot -}$) and hydroxyl radical (OH.), which can damage DNA, protein structure and peroxidation of the lipids in the cell membrane.

In response to salt stress, plants activate various defense mechanisms, including the upregulation of antioxidative enzymes like catalase and peroxidase, to mitigate ROS damage (Ashraf and Harris 2005). Understanding the effects of salinity at different growth stages of berseem is crucial for developing strategies to enhance its resilience in salt-prone areas, ultimately improving crop productivity. Therefore, this study was carried out in berseem to examine the effect of salt concentrations imposed at different growth stages and to screen the most sensitive developmental stage.

MATERIALS AND METHODS

Trial location and experimental procedure: The lysimetric study was carried out during the year 2022 and 2023 at the Indian Institute of Technology, Ropar (30.97°N, 76.47°E), Punjab (Fig. 1). The experiment was conducted

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to investigate the effects of salinity stress on berseem plants at three salinity levels (2.5, 5 and 6.5 dS/m NaCl) taken as treatments in a completely randomised block design (CRBD). The berseem cultivar (BL 43) used in the experiment was procured from the Department of Agronomy, Punjab Agricultural University, Ludhiana, Punjab and was sown in a completely randomised block design. Each PVC lysimeter (acrylic column) constituted one experimental unit, and each treatment was replicated three times (n=3). A single replication consisted of 15 seeds each. Later on, the plants in each PVC pipe were trimmed to seven per pipe to provide the maximum surface area for the growth of the cultivar. Lysimeters were constructed using acrylic columns with dimensions of 18 cm in diameter and 120 cm in height and were equipped with excess water collectors at the bottom (Fig. 1). Each lysimeter was filled with a mixture of air-dried soil and sand in a 3:1 ratio, with a *p*H of 7.4 and electrical conductivity (EC) of 0.48 dS/m. Soil *p*H and EC were measured using a Mettler Toledo *p*H meter (FP 20 bio kit) and an SSI-23 ABS Auto Digital Conductivity Meter, respectively. Seeds were sown in each lysimeter and initially irrigated with tap water for 15 days to avoid any osmotic shock. After this acclimatisation period, the lysimeters were treated with saline water as per the respective treatment, while one lysimeter received only tap water and served as a control. Three sensors were placed at heights of 10 cm, 45 cm and 65 cm to regularly monitor water content and EC.

Morphological parameters: The growth parameters, including plant height (cm), root length (cm), and the dry weight of roots and shoots (g) were recorded at 2-leaf, 6-leaf and flowering stages of the berseem crop. The plant height and root length were manually measured at each stage, while the dry weight was determined by placing the samples (in triplicates) in a hot air oven at temperature 65±5°C for 72 h with proper air circulation.

Biochemical parameters: To assess the antioxidative potential at three key stages namely 2-leaf, 6-leaf, and flowering, whole plant samples were collected, and the activities of peroxidase (POD) and superoxide dismutase (SOD) were analysed. For enzyme extraction, 100 mg of plant tissue was homogenized in 2000 µl of 0.1 M sodium phosphate buffer. The homogenate was centrifuged at 15,000 rpm for 15 min, and the supernatant was used for further analysis. POD and SOD activities were measured according to the protocols of Malik and Singh (1980) and Beauchamp and Fridovich (1971), respectively. Additionally, the extent of membrane damage due to salt stress was evaluated by measuring malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) levels, according to protocols by Heath and Packer (1968) and Velikova *et al.* (2000), respectively.

Statistical analysis: The experimental data from two consecutive years were pooled for analysis, with each treatment comprising three biological replications per year (total n=6). The effects of Salinity (T) and Growth Stage (S) and their interaction (T×S) on all measured parameters were assessed using a two-way Analysis of Variance (ANOVA) in the R statistical environment. Treatment means were considered significantly different at a probability level of $p \leq 0.05$. The Critical Difference (CD) at the 5% significance level is reported for comparing means within the significant interaction term. To integrate and visualize the complex relationships between the physiological and biochemical variables under the influence of salinity and growth stage, a multivariate Principal Component Analysis (PCA) was performed.

RESULTS AND DISCUSSION

Effect of salt stress on the physiological attributes: The experiment demonstrated a clear disruption in ionic homeostasis as salt concentration increased from 2.5–6.5 dS/m, leading to significant ($p \leq 0.05$) declines in key physiological attributes (Table 1). The decline in plant height at 6.5 dS/m became more pronounced across developmental stages, with reductions of 27%, 33%, and 22% at the 2-leaf, 6-leaf, and flowering stages, respectively, compared to the control. This trend aligns with the established understanding that high salinity adversely affects plant growth by disrupting cellular processes and reducing water availability (Munns and Tester 2008, Van Zelm *et al.* 2020). The severity of salt stress was most evident in root architecture, a critical system for nutrient and water uptake (Zhu 2016). At 6.5 dS/m, root length declined by 27%, 27%, and 30% across the three stages, while root dry weight suffered even more drastic reductions of 77%, 75%, and 57%, respectively (Table 1). These findings are consistent with the work of Ashraf and Harris (2005), who reported that salinity-induced osmotic stress severely impairs root function and development. Under control conditions, dry matter accumulation increased predictably as the plant matured from the 2-leaf to the flowering stage. However, salt stress severely inhibited this process. At 6.5 dS/m, shoot dry weight exhibited declines of 63%, 59%, and 56% at the three respective stages (Table 1). This

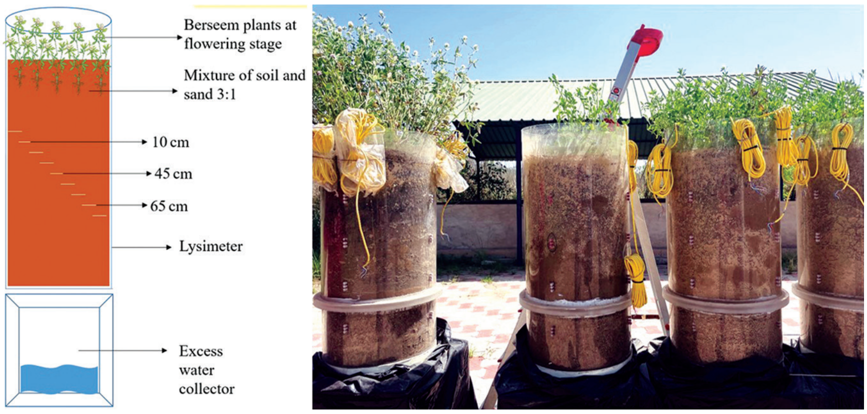

Fig. 1 Pictorial representation of lysimetric set up at IIT Ropar, Punjab, India containing berseem plants exposed to NaCl concentrations.

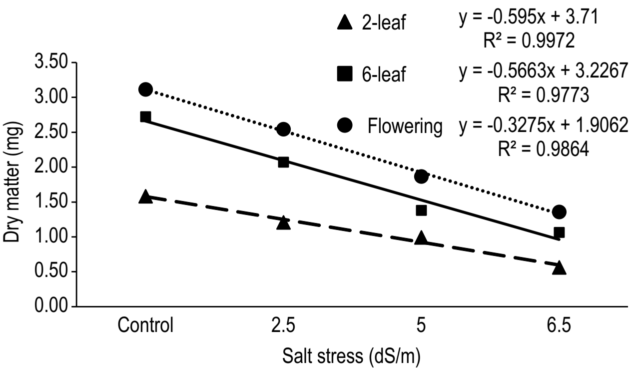

Fig. 2 Relationship between total dry matter (mg) with increasing concentration of NaCl.

significant inhibition of dry matter accumulation under salt stress corroborates findings by Gupta and Huang (2014), who emphasised that salinity induces oxidative stress, damaging cellular structures and impairing photosynthesis. The sensitivity of berseem varied with its developmental stage. The slope of reduction in total dry matter was steepest at the 2-leaf stage (-0.59), followed by the 6-leaf stage (-0.56), and was mildest at the flowering stage (-0.32) (Fig. 2). This variation suggests that early vegetative stages are particularly vulnerable, likely because the initial establishment of ionic and osmotic homeostasis is critical for subsequent growth (Flowers and Colmer 2015, Kumar *et al.* 2023).

Effect of salt stress on the biochemical parameters: The biochemical response to salinity involved a marked accumulation of reactive oxygen species (ROS) and a concomitant activation of the plant's antioxidative defense system (Table 2). As NaCl levels increased, the defense system was triggered, resulting in the significant upregulation of key antioxidative enzymes, superoxide dismutase (SOD) and peroxidase (POD), which work in concert to detoxify ROS (Gill and Tuteja 2010, Hasanuzzaman *et al.* 2020). The antioxidative potential increased dramatically as salinity levels rose to 6.5 dS/m. POD activity increased by 304%, 521%, and 419% at the 2-leaf, 6-leaf, and flowering stages, respectively. Similarly, SOD activity was upregulated by 71%, 37%, and 70% at the same stages (Table 2). These findings aligned with studies by Mittler (2002) and Foyer and Noctor (2005), who reported that plants enhance their antioxidative defense mechanisms as a primary strategy

Table 1 Effect of salt stress on morphological parameters of berseem at different growth stages

Salt stress (dS/m)	Plant height (cm)			Root length (cm)			Shoot Dry weight (g)			Root dry weight (g)		
	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering
Control	39.98 ± 0.91	56.25 ± 0.50	70.37 ± 1.03	21.14 ± 0.56	24.05 ± 0.15	27.58 ± 0.72	1.45 ± 0.01	2.40 ± 0.01	2.56 ± 0.04	0.13 ± 0.01	0.32 ± 0.02	0.56 ± 0.04
2.5	37.47 ± 0.17	49.31 ± 0.60	67.17 ± 1.25	19.43 ± 0.25	20.33 ± 0.25	22.60 ± 0.01	1.14 ± 0.03	1.88 ± 0.04	2.09 ± 0.05	0.07 ± 0.02	0.20 ± 0.01	0.46 ± 0.03
5	30.90 ± 0.02	46.64 ± 0.18	59.94 ± 1.11	17.87 ± 0.23	18.90 ± 0.21	20.41 ± 0.04	0.83 ± 0.01	1.23 ± 0.01	1.56 ± 0.02	0.33 ± 0.01	0.15 ± 0.01	0.30 ± 0.01
6.5	29.44 ± 0.23	37.85 ± 0.51	54.93 ± 0.18	15.44 ± 0.14	17.64 ± 0.14	19.29 ± 0.15	0.53 ± 0.01	0.98 ± 0.01	1.12 ± 0.01	0.03 ± 0.01	0.08 ± 0.01	0.24 ± 0.03
CD (p=0.05)	T=0.95; S=0.82; T×S=1.65			T=0.43; S=0.37; T×S=0.74			T=0.034; S=0.030; T×S=0.060			T=0.007; S=0.006; T×S=0.011		

T, Salinity treatments; S, Stages of Berseem. Values are mean ± SE.

Table 2 Variations in POD activity, SOD activity, MDA content and H_2O_2 content at different growth stages in berseem crop on exposure to different levels of salt stress

Salt stress (dS/m)	POD (kat/sec/mg of protein)			SOD (mg/g FW protein)			H_2O_2 content (moles/g FW)			MDA content (moles/g FW)		
	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering	2-leaf	6-leaf	Flowering
Control	0.27 ± 0.01	0.24 ± 0.01	0.21 ± 0.01	7.34 ± 0.03	9.60 ± 0.05	6.40 ± 0.23	35.35 ± 0.69	24.88 ± 0.37	24.52 ± 0.09	0.15 ± 0.01	0.25 ± 0.02	0.22 ± 0.01
2.5	0.41 ± 0.02	0.38 ± 0.01	0.33 ± 0.02	8.51 ± 0.10	11.27 ± 0.09	7.96 ± 0.16	39.04 ± 0.17	36.19 ± 0.58	36.42 ± 0.61	0.18 ± 0.02	0.31 ± 0.03	0.25 ± 0.04
5	0.62 ± 0.02	0.59 ± 0.01	0.62 ± 0.01	9.34 ± 0.06	12.49 ± 0.26	9.72 ± 0.07	57.50 ± 1.58	45.47 ± 0.41	57.38 ± 1.36	0.31 ± 0.05	0.34 ± 0.02	0.41 ± 0.01
6.5	1.09 ± 0.02	1.49 ± 0.05	1.09 ± 0.03	12.56 ± 0.28	13.16 ± 0.35	10.91 ± 0.16	82.62 ± 1.85	72.61 ± 2.27	92.38 ± 0.89	0.38 ± 0.02	0.44 ± 0.01	0.41 ± 0.03
CD (p=0.05)	T= 0.026; S=0.023; T×S=0.046			T= 0.25; S=0.22; T×S=0.44			T=1.56; S=1.35; T×S=2.70			T= 0.009; S=0.008; T×S=0.016		

T, Salt treatments; S, Stages of Berseem crop; POD, Peroxidase; SOD, Superoxide Dismutase; H_2O_2, Hydrogen peroxide; MDA, Malondialdehyde.

r value	SOD	POD	H_2O_2	MDA	PH	RL	SDW	RDW
SOD	1.00							
POD	0.73^{**}	1.00						
H_2O_2	0.58^{*}	0.89^{**}	1.00					
MDA	0.77^{**}	0.82^{**}	0.78^{**}	1.00				
PH	-0.43^{NS}	-0.44^{NS}	-0.42^{NS}	-0.11^{NS}	1.00			
RL	-0.62^{*}	-0.71^{**}	-0.75^{**}	-0.54^{NS}	0.82^{**}	1.00		
SDW	-0.52^{NS}	-0.71^{**}	-0.78^{**}	-0.45^{NS}	0.85^{**}	0.95^{**}	1.00	
RDW	-0.65^{*}	-0.52^{NS}	-0.45^{NS}	-0.22^{NS}	0.80^{**}	0.80^{**}	0.75^{**}	1.00

Fig. 3 Pearson's correlation matrix illustrating the relationships among physiological and growth parameters under different salinity levels.
** denotes significance at the 0.01 probability level, * denotes significance at the 0.05 probability level, and NS indicates a non-significant correlation. SOD, Superoxide dismutase; POD, Peroxidase; H_2O_2, Hydrogen peroxide; MDA, Malondialdehyde content (a marker for lipid peroxidation), PH, Plant height; RL, Root length; SDW, Shoot dry weight; and RDW, Root dry weight.

to mitigate the damaging effects of ROS under stress. Conversely, the stress indices, malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), showed a linear increase with rising NaCl concentration. H_2O_2, a key ROS and signaling molecule (Saxena *et al.* 2016), accumulated significantly, with increase of 134%, 192%, and 277% at 6.5 dS/m across the three stages. This oxidative burst leads to lipid peroxidation, reflected in the increased MDA content (153%, 76%, and 86% increase, respectively) (Table 2). This is consistent with studies confirming that elevated ROS levels under salt stress cause oxidative damage to cellular components (Apel and Hirt 2004, Gill and Tuteja 2010). The Pearson's correlation matrix (Fig. 3) powerfully illustrates the interplay between these physiological and biochemical changes. The correlation between MDA content and plant height (r = -0.11, non-significant) suggests a weak relationship between membrane damage and growth retardation under the tested conditions. The positive correlation between MDA and H_2O_2 content (r = 0.78) underscores that ROS accumulation directly leads to oxidative damage. The positive correlation between SOD activity and H_2O_2 content (r = 0.58, $p \leq 0.05$) suggests that increased SOD activity may be associated with higher H_2O_2 levels, potentially indicating a complex interplay in the ROS-scavenging mechanism under salt stress.

Multivariate analysis of salt sensitivity across stages: The Principal Component Analysis (PCA) provided a holistic view of how all parameters contributed to salt stress tolerance across different growth stages. The analysis effectively reduced the multidimensional data into two principal components that together explained 87.3% of the total variation (Fig. 4). PCA 1, which accounted for the majority of the variance, was primarily loaded with physiological parameters i.e. plant height, root dry weight, and root length. The strong negative loading of these traits on PCA 1 visually confirms that increasing salinity levels directly cause a reduction in growth and biomass (Table 1). PCA 2 was loaded with biochemical parameters i.e. MDA, H_2O_2, POD, and SOD activities. The positive loading of these traits indicates that the biochemical response comprising both oxidative damage and antioxidative defense is a major, distinct dimension of the plant's stress response. The score plot (Fig. 4) clearly segregated the treatments based on salinity and, most importantly, identified the 6-leaf stage clusters as the most distinct under high salt stress. This multivariate finding confirms that the 6-leaf stage is the most sensitive, a conclusion supported by the univariate data showing the

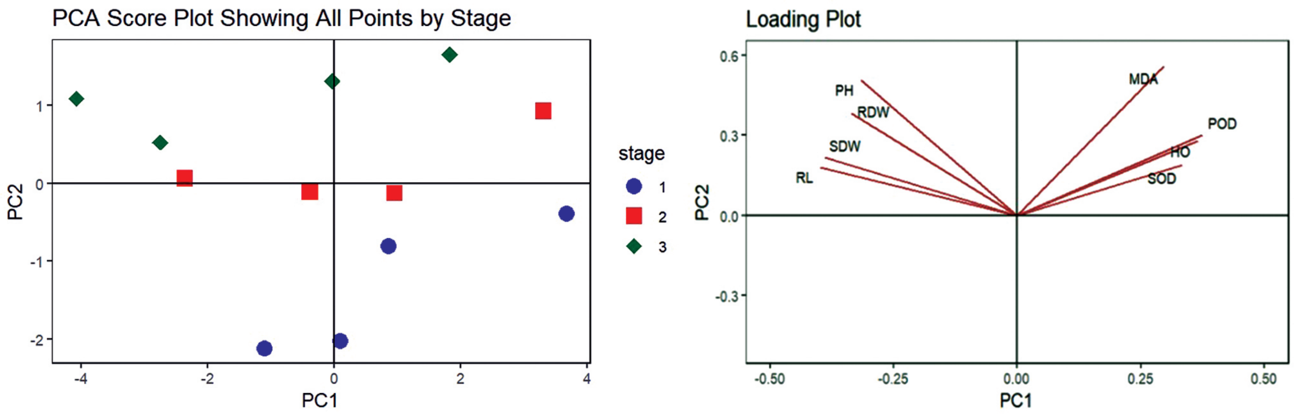

Fig. 4 Principal Component analysis (PCA) biplot illustrating the multivariate relationships among physiological, growth, and oxidative stress-related biomarkers across experimental samples.
(A) Score plot depicting the ordination of individual samples along the first two principal components colour-coded by developmental stage {stage 1: 2 leaf (red squares); stage 2: 6 leaf (blue circles); stage 3: Flowering green triangles)}. (B) Corresponding loading plot (vector biplot) showing the contributions of 8 key variables to PC1 and PC2, with arrow length proportional to loading magnitude and direction indicating positive/negative correlations. PH, Plant height; RDW, Root dry weight; SDW, Shoot dry weight; RL, Root length; SOD, Superoxide dismutase activity; MDA, Malondialdehyde content; POD, Peroxidase activity; HO, Hydrogen peroxide content.

greatest percentage reductions in growth (Table 1) and the most pronounced upregulation of POD activity at this stage (Table 2). The sensitivity of this stage may be attributed to its high metabolic activity and rapid vegetative growth, which are highly vulnerable to ionic and osmotic imbalance (Parihar *et al.* 2015). While the flowering stage showed damage, the 6-leaf stage emerged as the critical period where salt stress inflicts the most severe and comprehensive damage on the plant system.

The study concluded that contrary to the initial focus, the 6-leaf stage was identified as the most sensitive, not the flowering stage. A critical damage threshold was established at NaCl concentrations exceeding 5 dS/m. This heightened sensitivity was characterised by a significant increase in oxidative stress markers (MDA and H_2O_2) and a strong upregulation of antioxidative enzymes (SOD and POD). The findings elucidate the complex relationship between antioxidative capacity and morpho-physiological attributes under salt stress. These insights are crucial for developing targeted strategies to enhance Berseem cultivation in saline environments, thereby contributing to improved fodder security and sustainable agricultural practices in affected regions.

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