



TISSUE-SPECIFIC SALINITY TOLERANCE MECHANISMS IN LEAVES AND STEMS OF PEARL-MILLET NAPIER (PMN) HYBRIDS (*Pennisetum glaucum* L.R. BR.) × (*Pennisetum purpureum* K. SCHUM)

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ABSTRACT

Salinity stress is one of the major abiotic constraints limiting crop productivity and productive use of saline soils. Cultivation of salt-tolerant fodder grasses is a practical solution for saline marginal lands, and Pearl millet Napier hybrids (PMN) are promising candidates due to their high biomass potential, adaptability, and nutritive value. A pot culture experiment was conducted to study the salinity tolerance mechanisms in five PMN hybrids, namely BNH14, DHN6, IGFR17, Phule Yashwant, and NB21, under four salinity levels: 0, 4, 8, and 12 ECe. Salinity was imposed using a mixture of salts (NaCl, Na₂SO₄, MgCl₂, and CaSO₄) in the ratio 13:7:1:2. The genotypes varied significantly in their morphological, physiological, and biochemical responses under saline conditions. Of the genotypes studied, BNH14 showed an increasing trend in plant height (146.67 cm) with higher biomass production (249.67 g plant⁻¹) even at higher salinity levels, indicating better adaptability. Membrane stability decreased in both leaf and stem tissues across all genotypes as salinity increased, but the reduction was more pronounced in DHN6. The total antioxidant activity was always higher in leaves than in stems across all genotypes, with the difference more evident in BNH14. The amount of sodium was stored more in stems than in leaves, and BNH14 had the highest Na⁺ concentration in stem tissue as well as K⁺ content. These results suggest that tissue-specific mechanisms regulate salinity tolerance in PMN hybrids. These include sequestration of sodium in stem tissues, maintenance of membrane stability under stress in both leaf and stem tissues, and enhanced antioxidant defence in leaves, along with morphological adaptations, thereby supporting sustained growth and biomass production under saline conditions.

Key words: Salinity, membrane stability, antioxidants, sodium accumulation.

Introduction

Soil salinity is one of the major abiotic stresses that limit agricultural productivity worldwide and is increasing rapidly in many cultivated regions. About 6.73 million hectares of land in India are affected by salinity, of which nearly 40% are saline soils, and 60% are sodic soils (Dheeravathu *et al.*, 2021). The increase in salt-affected lands is due to uncontrolled irrigation, monocropping, excessive fertiliser application, poor-quality irrigation water, and inadequate drainage, leading to extensive salt accumulation. Soil salinisation adversely affects plant

growth, reduces crop productivity, declines product quality, and threatens food security and sustainable agriculture (Cansev and Ozgur, 2010). A large proportion of salt-affected lands are underutilised because they are not suitable for conventional crop cultivation. Therefore, identifying and cultivating salt-tolerant crops suitable for these marginal environments is essential.

Establishing salt-tolerant perennial fodder grasses on saline degraded lands is a practical and sustainable approach for improving land productivity while ensuring year-round forage availability. Compared with annual

crops, perennial fodder grasses generally require less input and are more adaptable to adverse environmental conditions. Although considerable progress has been made in understanding salinity tolerance in annual crops, relatively less attention has been given to perennial fodder grasses (Roy and Chakraborty, 2014; Munns *et al.*, 2020; Rahimi *et al.*, 2021). A better understanding of the physiological mechanisms regulating salinity tolerance in perennial grasses is essential for selecting suitable cultivars and developing effective management strategies for the reclamation and productive utilisation of salt-affected lands.

Among perennial fodder grasses, the Pearl Millet–Napier (PMN) hybrid is among the most promising and high-yielding for tropical and subtropical regions. It is an interspecific hybrid developed by crossing Napier grass [*Pennisetum purpureum* (K.) Schum.] with Pearl millet [*Pennisetum glaucum* (L.) R. Br.]. The hybrid is triploid (AAB genome; $2n = 3x = 21$). PMN is a perennial, multi-cut forage grass that grows up to 3–4 m in height and is characterised by profuse tillering, abundant leaf production, rapid regrowth, and high biomass yield. It combines the leafiness of Pearl millet with the vigorous growth habit of Napier grass, producing superior fodder compared with its parents (Gupta and Mhere, 1997). The fodder contains 8.2% crude protein, 34% crude fibre, and 10.5% ash, with calcium and phosphorus in a balanced proportion, making it highly nutritious and palatable for livestock. Consequently, PMN hybrids are widely cultivated across tropical and subtropical regions, including several Indian states such as Uttar Pradesh, Odisha, Gujarat, West Bengal, Punjab, Haryana, and Assam (Karforma, 2018).

During the period from 1989 to 2000, several forage breeding programmes developed numerous Pearl-millet Napier hybrids with improved biomass production and superior agronomic performance. However, despite these advances, most released hybrids have not been systematically evaluated for salinity tolerance. Information on the physiological mechanisms underlying salt tolerance in these hybrids also remains limited. Therefore, evaluating the salinity tolerance of PMN hybrids and understanding the associated physiological responses are essential for identifying resilient genotypes suitable for cultivation on salt-affected soils. Such information will facilitate the efficient utilisation of marginal lands, contribute to sustainable fodder production, and support future breeding programmes aimed at improving salinity tolerance in perennial forage grasses.

Material and Methods

Experimental details

A pot culture experiment was conducted at ICAR-SRRS-IGFRI, Dharwad (15° 29' 5" N, 74° 58' 35" E, 720 m, AMSL) to investigate the tolerance mechanisms of Pearl-millet Napier (PMN) hybrids under different levels of salinity stress. The primary objective of the experiment was to elucidate the morphological, physiological and biochemical tolerance mechanisms functioning in different tissues of PMN hybrids exposed to varying salinity levels. Five PMN hybrids, namely BNH14, DHN6, IGFR1 7, Phule Yashwant, and NB21, were selected for the study. The hybrids were grown at four levels of artificially induced soil salinity: 0 ECe (control), 4 ECe, 8 ECe, and 12 ECe. Salinity treatments were imposed using different combinations of salts, following the methodology described by Dheeravathu *et al.*, (2018). The experiment was conducted in a Factorial RBD with three replications. Observations were recorded on growth, biomass accumulation, physiological responses, biochemical traits, and tissue-specific tolerance mechanisms under salinity stress.

Morphological observations

Morphological parameters were recorded to evaluate the growth performance of PMN hybrids under varying salinity levels. Plant height was measured from the basal portion of the plant to the tip of the terminal leaf using a meter scale and expressed in centimetres (cm). The number of tillers per plant was determined by manual counting. Internodal length was measured using a ruler and expressed in centimetres (cm). Fresh biomass accumulation was estimated by separately recording the fresh weights of leaves and stems. The total fresh biomass per plant was calculated by adding the leaf and stem fresh weights and expressed in g plant⁻¹.

Leaf and stem membrane stability index (%)

The membrane stability index (MSI) was calculated from the electrical conductivity (EC) of leaf samples in double-distilled water at 40°C and 100°C, following the method of Sairam (1994). Mature leaves and the middle portion of the stem were cut into small pieces, and 0.5g of the sample was placed in a test tube containing 10ml of double-distilled water. The test tubes were placed in a water bath at 40°C for 60 minutes, and the electrical conductivity (C1) was measured. Another set of test tubes containing 10ml of distilled water and 0.5 g samples was heated in a 100°C water bath for 10 minutes, and the electrical conductivity (C2) was measured with a

Table 1: Salinity-Induced Changes in Internodal length (cm) of PMN Hybrids.

Genotypes	0ECe	4ECe	8ECe	12ECe	Mean
BNH14	8.89±0.51	8.67±0.58	9.00±1.00	10.00±1.00	9.14
DHN6	7.33±0.58	7.00±0.87	6.33±0.58	4.67±0.58	6.33
IGFRI7	7.00±1.00	7.33±1.15	7.00±1.00	4.33±0.58	6.42
Phule Yashwant	6.33±0.58	7.00±1.00	6.67±1.15	6.00±1.00	6.50
NB21	6.78±0.39	7.33±0.58	7.00±1.00	5.67±0.58	6.69
Mean	7.27	7.47	7.20	6.13	
	SEM±		CD at 5%		
Genotype	0.23		0.66		
Salinity	0.21		0.59		
Genotype × Salinity	0.46		1.32		
The values of Internodal length are presented as mean±SD,					

conductivity meter. Then the membrane stability index was calculated by using the formula,

$$\text{Membrane stability index (MSI)} = 1 - \frac{C_1}{C_2} \times 100$$

Where C1 is the conductivity at 40°C and C2 is the conductivity at 100°C

Estimation of total antioxidant activity

Total antioxidant activity was measured by ferric reducing antioxidant power (FRAP) assay of Benzie and Strain (1999). Sample (250 µl) (leaf/stem extract) was mixed with 3 ml of working FRAP reagent, and absorbance (593 nm) was measured at 0 minutes. Thereafter, samples were placed in a water bath at 37 °C, and absorption was measured again after 4 minutes. Ascorbic acid standards (100µM-1000µM) were processed in the same way. Antioxidant activity was calculated by using the formula,

$$\text{FRAP value of sample (}\mu\text{g g}^{-1}\text{ FW)} = \left(\frac{\text{Change in absorbance of the sample from 0 to 4 mins}}{\text{Change in absorbance of standard from 0 to 4 mins}} \right) \times \text{FRAP value of standard (1000}\mu\text{M)}$$

Sodium and Potassium content in different tissues

Potassium and sodium contents in leaf and stem samples were estimated by using a flame photometer (Systronics 128, India) after triacid digestion with HNO₃, H₂SO₄, and HClO₄ (10:1:4). About 0.5 g of dried sample was digested, filtered, and made up to 100 mL before reading Na and K separately using the appropriate filters and standards. Element concentrations were calculated from the standard curve and expressed as mg g⁻¹ DW. Jackson (2005).

Statistical Analysis

The data collected from the experiment were subjected to statistical analysis using the RAISINS (R and AI Solutions for Inferential Statistics) statistical package (<http://www.raisins.live>; Hisham M, M *et al.*, (2025). The

levels of significance used in the ‘F’ test were p < 0.05. The least significant difference (LSD) was calculated whenever the ‘F’ test was significant.

Results and Discussion

Morphological Adaptations of PMN Hybrids under Salinity Stress

Salinity stress significantly influenced the morphological characteristics of PMN hybrids. Plant height increased under mild salinity stress (4 ECe) in all genotypes; however, a gradual decline was observed at higher salinity levels (8 ECe and 12 ECe), except in BNH14. Among the genotypes, BNH14 recorded the highest plant height at 12 ECe (146.67 cm), whereas DHN6 recorded the lowest at 12 ECe (73.67 cm). (Fig. 1). Similarly, internodal length increased in BNH14 under higher salinity levels, while a reduction was observed in the remaining genotypes (Table 1). The ability to increase plant height under mild to severe salinity stress represents a key morphological adaptive response associated with salinity tolerance in PMN hybrids, as reported by Rakshata *et al.*, (2023) and Amulya *et al.*, (2025). Plant height exhibited a strong positive and significant correlation with internodal length (0.97**), indicating that increased internodal elongation contributed considerably to increased plant height under salinity stress.

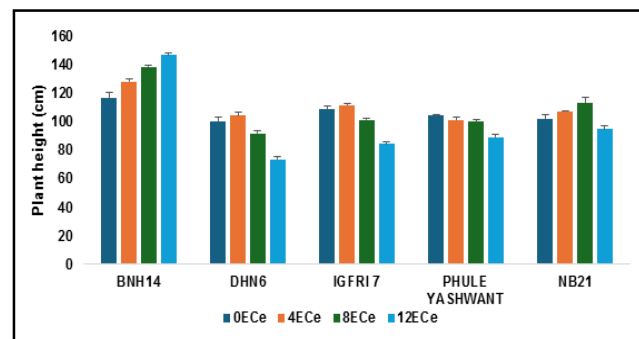


Fig. 1: Salinity-Induced Changes in Plant height (cm) of PMN hybrids.

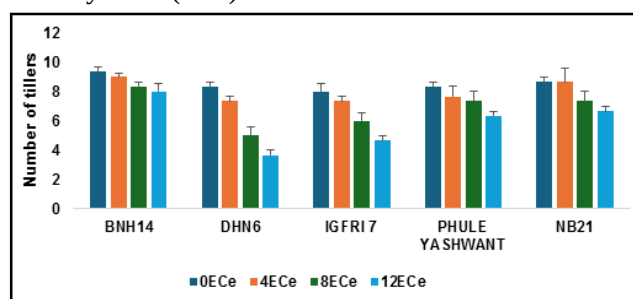
Table 2: Impact of salinity on total antioxidants ($\mu\text{g g}^{-1}$ FW) in leaves of PMN hybrids.

Genotypes	0ECe	4ECe	8ECe	12ECe	Mean
BNH14	0.95±0.06	1.07±0.07	4.15±0.11	3.28±0.06	2.36
DHN6	0.82±0.09	1.36±0.10	1.33±0.01	1.38±0.03	1.22
IGFRI7	0.88±0.09	1.34±0.08	1.71±0.17	1.91±0.31	1.46
Phule Yashwant	0.76±0.10	1.16±0.04	1.98±0.07	2.93±0.30	1.71
NB21	0.79±0.09	1.19±0.02	2.41±0.17	3.03±0.11	1.86
Mean	0.84	1.22	2.31	2.51	
	SEM±		CD at 5%		
Genotype	0.04		0.11		
Salinity	0.03		0.10		
Genotype × Salinity	0.08		0.22		

The number of tillers decreased gradually with increasing salinity levels in all the genotypes. The maximum reduction in tiller number was observed in DHN6 at 12 ECe (3.67), followed by IGFRI 7 (4.67) (Fig. 2). Total fresh biomass also declined significantly at higher salinity levels (8 ECe and 12 ECe) across all genotypes. However, BNH14 maintained the highest fresh biomass under 12ECe (249.67 g plant⁻¹), whereas the lowest biomass was recorded in DHN6 at 12 ECe (171.00 g plant⁻¹) (Fig. 3). Rakshata *et al.*, (2023) also reported a significant reduction in biomass production in DHN6 and IGFRI 7 under 12 ECe salinity stress. Yield is a complex phenomenon influenced by various agronomic traits, including plant height, number of tillers, leaf area, and Internodal length, as stated by Ghaffar *et al.*, (2022). A significant positive correlation was observed between the number of tillers and total fresh biomass at 12 ECe (0.95*), suggesting that tiller production played a crucial role in maintaining biomass under saline conditions. Higher salinity levels induced adverse effects on growth and biomass, whereas moderate salinity levels compensated for the cumulative effect compared to the control, as reported by Kumar *et al.*, (2023).

Changes in the membrane stability index of leaf and stem tissues under different salinity levels in PMN hybrids

Salinity stress significantly regulated the membrane stability index (MSI) of both leaf and stem tissues in PMN

**Fig. 2:** Effect of salinity on the number of tillers in PMN hybrids.

hybrids at 25 days after salinity stress. A gradual decline in MSI was observed with increasing salinity across all genotypes, indicating salinity-induced membrane damage. However, the extent of reduction varied among the genotypes.

In leaf tissues, the highest MSI was recorded in BNH14 under 12 ECe treatment (80.39%), whereas the lowest MSI was observed in DHN6 under 12 ECe treatment (68.33%). Under severe salinity stress (12 ECe), tolerant genotypes such as BNH14 and NB21 maintained higher MSI values than sensitive genotypes (Fig. 4a), suggesting better membrane integrity and cellular stability under salt stress. A similar pattern of membrane stability was reported in *Megathyrsus maximus* genotypes under salinity stress (Anusree *et al.*, 2025). In this study, leaf MSI showed a positive association with biomass accumulation (0.91*), suggesting that maintaining membrane stability contributed to improved growth and increased fresh biomass production under salinity stress.

Similarly, stem MSI decreased progressively with increasing salinity levels across all the genotypes. The reduction in 12 ECe was more pronounced in DHN6 (21.8%) than in 0 ECe, whereas in BNH14 (11.6%) and NB21 (9.8%), stem MSI reduction was less under saline conditions (Fig. 4b). Stem MSI showed a positive correlation with tiller number and total fresh biomass, suggesting that improved membrane stability in stem

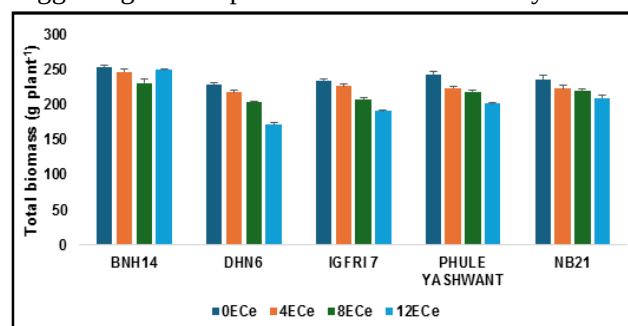
**Fig. 3:** Effect of salinity on total biomass in PMN hybrids.

Table 3: Impact of salinity on total antioxidants ($\mu\text{g g}^{-1}$ FW) in the stem of PMN hybrids.

Genotypes	0ECe	4ECe	8ECe	12ECe	Mean
BNH14	0.27±0.04	0.37±0.04	0.56±0.07	0.71±0.04	0.48
DHN6	0.24±0.05	0.34±0.06	0.44±0.03	0.22±0.05	0.31
IGFRI7	0.22±0.05	0.35±0.05	0.47±0.10	0.37±0.18	0.35
Phule Yashwant	0.25±0.06	0.37±0.02	0.40±0.05	0.44±0.18	0.36
NB21	0.27±0.06	0.41±0.01	0.50±0.10	0.56±0.07	0.43
Mean	0.25	0.37	0.47	0.46	
	SEM±		CD at 5%		
Genotype	0.01		0.03		
Salinity	0.01		0.03		
Genotype × Salinity	0.02		0.05		
The values of total antioxidants in leaf and stem are presented as mean±SD,					

tissues plays a crucial role in maintaining tiller production and biomass accumulation under salinity stress. The cell membrane is the primary site of vulnerability to abiotic stresses, which are targeted by reactive oxygen species produced under salinity stress. This leads to lipid peroxidation, disrupting the bilayer structure and causing electrolyte leakage. Mahdavi *et al.*, (2023). The higher membrane stability observed in tolerant genotypes may be attributed to enhanced osmotic adjustment and antioxidant defence mechanisms that protect cellular membranes from oxidative damage induced by salt stress.

Impact of different salinity levels on total antioxidants in the leaf and stem of PMN hybrids

Total antioxidant activity in leaf tissues increased with increasing salinity levels in all PMN hybrids, indicating enhanced antioxidant defence under salt stress. Among the genotypes, BNH14 recorded the highest antioxidant activity at 8 ECe ($4.15 \mu\text{g g}^{-1}$ FW), whereas DHN6 showed comparatively lower activity at 12 ECe ($1.38 \mu\text{g g}^{-1}$ FW) (Table 2). The tolerant genotypes, particularly BNH14 and NB21, maintained higher antioxidant activity under saline conditions, suggesting better oxidative stress tolerance. Total antioxidant activity showed positive correlations with the membrane stability index (0.86) and total biomass (0.79), indicating the role of antioxidants in maintaining membrane integrity and supporting growth under salinity stress.

Total antioxidant activity in stem tissues increased with increasing salinity levels across all PMN hybrids (Table 3), indicating enhanced antioxidant defence under salt stress. Among the genotypes, BNH14 recorded the highest antioxidant activity at 12 ECe ($0.71 \mu\text{g g}^{-1}$ FW), followed by NB21 ($0.56 \mu\text{g g}^{-1}$ FW), whereas the lowest activity was observed in DHN6 at 12 ECe ($0.22 \mu\text{g g}^{-1}$ FW). The overall mean antioxidant activity increased from $0.25 \mu\text{g g}^{-1}$ FW under control conditions to $0.46 \mu\text{g g}^{-1}$ FW at 12 ECe, suggesting increased production of

antioxidant compounds in response to salinity-induced oxidative stress. Total antioxidant activity in stem tissues showed a positive and significant correlation with stem membrane stability index (0.94*) and total biomass (0.98**), indicating the importance of antioxidant defence in maintaining membrane integrity and biomass production under saline conditions. An effective antioxidant defence system that mitigates damage caused by excess ROS is essential for salinity tolerance. Hasanuzzaman *et al.*, (2021).

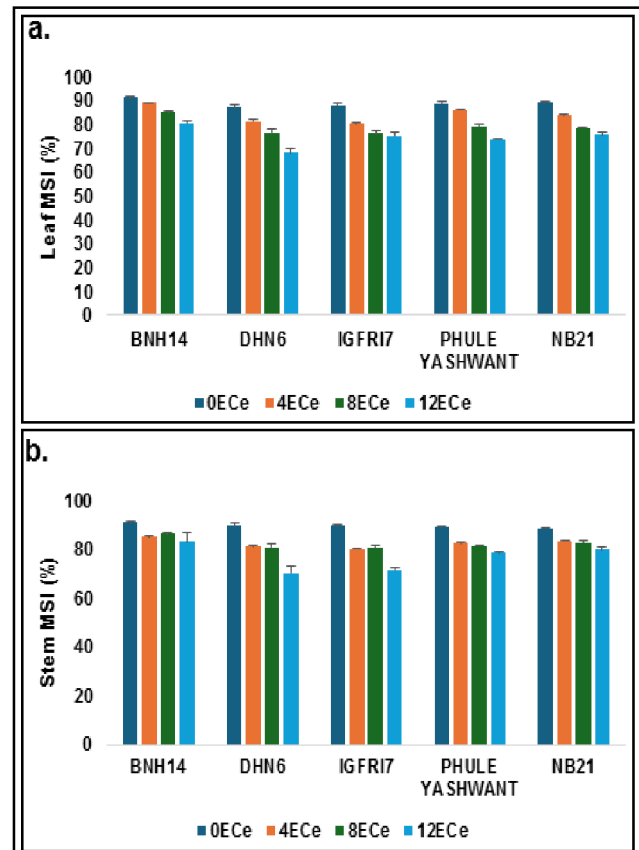


Fig. 4: Changes in the membrane stability index of leaf (a) and stem (b) tissue at different salinity levels in PMN hybrids.

Table 4: Effect of salinity stress on sodium accumulation (mg g^{-1} DW) and K: Na ratio in leaf and stem tissues of PMN hybrids.

	Na ⁺ content in leaf		Na ⁺ content in the stem		K ⁺ content in the leaf		K ⁺ content in the stem		K:Na ratio in leaf		K:Na ratio in stem	
	0ECe	12ECe	0ECe	12ECe	0ECe	12ECe	0ECe	12ECe	0ECe	12ECe	0ECe	12ECe
BNH14	0.57±0.03	8.52±0.25	1.51±0.33	16.60±0.47	50.27±0.35	47.84±0.32	73.80±0.51	82.51±0.93	87.99±6.04	5.61±0.18	48.92±1.03	4.97±0.19
DHN6	0.98±0.02	7.13±0.54	1.24±0.02	11.79±0.07	57.87±2.23	38.29±0.49	91.52±1.60	50.56±0.81	59.05±3.79	5.37±0.35	73.68±0.25	4.29±0.08
IGFRI7	0.54±0.01	4.95±0.41	1.76±0.03	7.49±0.25	3.90±3.73	35.85±3.73	56.55±0.58	41.90±0.57	63.25±8.28	7.25±0.70	32.16±0.25	5.60±0.15
Phule Yashwant	0.97±0.46	4.76±0.45	1.69±0.02	8.10±0.17	51.03±0.98	42.05±1.16	50.22±0.24	38.20±0.96	52.43±2.29	8.84±0.60	29.77±0.41	4.72±0.11
NB21	0.59±0.01	4.85±0.22	1.16±0.03	9.48±1.05	46.66±0.15	30.59±1.22	67.13±3.71	34.18±0.83	78.55±1.05	6.31±0.07	57.77±2.60	3.61±0.45
Mean	0.73	6.04	1.47	10.69	47.94	38.92	67.84	49.49	68.25	6.68	48.46	4.64
	SEM±	CD at 5%	SEM±	CD at 5%	SEM±	CD at 5%	SEM±	CD at 5%	SEM±	CD at 5%	SEM±	CD at 5%
Genotype	0.13	0.39	0.16	0.47	0.57	1.69	0.61	1.80	3.15	9.37	1.31	3.89
Salinity	0.08	0.24	0.10	0.3	0.36	1.07	0.38	1.14	1.99	5.93	0.83	2.46
Genotype × Salinity	0.18	0.55	0.23	0.67	0.80	2.39	0.86	2.55	4.46	13.25	1.82	5.42

The values of sodium-potassium in leaf and stem are presented as mean±SD,

Sodium and potassium content in different tissues of PMN hybrids

Salinity stress significantly increased sodium accumulation in both leaf and stem tissues of all PMN hybrids (Table 4). Leaf sodium content increased from a mean value of 0.73 mg g^{-1} DW under control conditions to 6.04 mg g^{-1} DW at 12 ECe, while stem sodium content increased from 1.47 mg g^{-1} DW to 10.69 mg g^{-1} DW under salinity stress. Among the genotypes, BNH14 recorded the highest sodium content in both leaf (8.52 mg g^{-1} DW) and stem tissues (16.60 mg g^{-1} DW) under 12 ECe. In contrast, comparatively lower sodium accumulation was observed in Phule Yashwant and IGFRI 7 under saline conditions. A higher amount of Na^+ was stored in the stem, reducing its toxicity in the leaf. Na^+ exclusion from the leaf blade is important for stress adaptation to preserve important metabolic processes such as photosynthesis, as reported by Rizk *et al.*, (2024)

The potassium content recorded in stems was higher than in the leaves under both control and saline conditions. The K^+ content of both the leaf and stem was significantly decreased at 12ECe compared to the control across all genotypes (Table 4). The decrease in K^+ content in leaves was low in BNH14 at 12ECe (4.83%), whereas a sharp decline was recorded in DHN6 (33.83%) at 12ECe. In stems of PMN hybrids, BNH14 increased K^+ content even at 12ECe conditions, unlike in other genotypes. The greatest decrease in K^+ content in the stem was also observed in DHN6 at 12ECe.

The K: Na ratio decreased drastically at 12ECe in both leaf and stem tissues across all the genotypes, indicating ionic imbalance caused by excessive sodium uptake. In leaf tissues, the mean K: Na ratio decreased from 68.25 under control conditions to 6.68 at 12 ECe, whereas the stem K: Na ratio decreased from 48.46 to 4.64. Maintaining a higher K: Na ratio under saline conditions is considered an important tolerance mechanism, as it helps maintain ion homeostasis, osmotic balance, and normal metabolic activity under salt stress. However, in our study, the accumulation of both sodium and potassium at higher concentrations resulted in a low K: Na ratio in BNH14. Instead of excluding Na^+ ions, BNH14 accumulated a significantly large amount of Na^+ and K^+ ions in both leaf and stem tissues. According to Munns *et al.*, (2020), Na^+ ions are compartmentalised into vacuoles to prevent cytoplasmic toxicity, and the accumulation of these ions may help in osmotic adjustment, which is less energy-consuming than the production of organic osmolytes.

Conclusion

This study demonstrated that PMN hybrids differ in their tolerance to salinity, with leaves and stems showing distinct tissue-specific responses. At mild salinity, the genotypes showed little or no visible damage, suggesting they could initially cope with stress. However, at higher salinity levels, clear differences in tolerance emerged, with tolerant genotypes maintaining better growth, membrane stability, and antioxidant activity than sensitive genotypes. Among the tested hybrids, BNH14 was the most tolerant, as it showed better plant height increase, maintained membrane stability in both leaf and stem tissues, accumulated sodium mainly in stem tissues, and exhibited stronger antioxidant activity in leaves. These responses helped to protect the photosynthetic machinery and support biomass production under stress. In contrast, DHN6 was the most sensitive genotype, showing poor morphological adaptation and reduced membrane stability, especially under higher salinity. Overall, the study highlights that salinity tolerance in PMN hybrids is expressed more strongly under severe stress and depends on coordinated morphological, physiological, and biochemical adaptations.

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