Plant Ecology and Evolution 158 (3): 325–336, 2025
https://doi.org/10.5091/plecevo.161947

PLANT ECOLOGY EVOLUTION

RESEARCH ARTICLE

Inter-population variation in salinity tolerance of *Vigna marina* var. *marina* (Fabaceae) seedlings in Sri Lanka

D. Jithmi M. De Silva[1], B.D. Punsara Dharaka[1], K.M.G. Gehan Jayasuriya[1,2], Filip Vandelook[3,4]

1 Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka
2 Postgraduate Institute of Science, University of Peradeniya, Peradeniya, Sri Lanka
3 Meise Botanic Garden, Meise, Belgium
4 Plant Conservation and Population Biology, Department of Biology, University of Leuven, Belgium

Corresponding author: Jithmi De Silva (jithmid@sci.pdn.ac.lk)

Academic editor: Sergey Rosbakh ♦ **Received** 13 June 2025 ♦ **Accepted** 28 July 2025 ♦ **Published** 8 September 2025

Abstract

Background and aims – Climate change is a significant global challenge affecting soil health and agriculture, including increased soil salinity levels. Certain salt-tolerant wild species can be considered for crop improvement and provide a solution to increasing salinization. We studied the inter-population variation in salt tolerance of *Vigna marina* seedlings, to explore the potential use of these wild resources to improve cultivated *Vigna* and for better conservation decisions.
Material and methods – Inter-populational variation in salinity tolerance of seedlings of four different *V. marina* populations growing in different regions in Sri Lanka (Unawatuna, Mahamodara, Negombo, and Thalpe) was studied. Seedlings from seeds collected from these populations were grown under 0, 100, 1000, 2000, 10,000, and 20,000 ppm NaCl concentrations, following standard salinity tolerance test procedures. The plant performance was evaluated by measuring biomass, root: shoot ratio, height, growth rate, and chloride ion accumulation in leaves, stems, and roots. Finally, the performance of the *V. marina* populations was compared with two commercial varieties of *Vigna radiata* (MI6 and Ari), one of which was considered salt-tolerant.
Key results – All seedlings showed reduced growth at 10,000 and 20,000 ppm NaCl concentrations. The Negombo population showed the highest total dry mass at 20,000 ppm, and seedlings from all populations survived at 20,000 ppm salt concentration, except those from the Mahamodara population. Overall, the Thalpe population performed best at 20,000 ppm. The highest salt accumulation was recorded in leaves and stems rather than in roots. Commercial *V. radiata* varieties did not survive the highest salt concentrations (10,000 and 20,000 ppm).
Conclusion – Given that *V. marina* populations collected in different locations show considerable inter-populational variation in salinity tolerance, we recommend conserving multiple *V. marina* populations to cover the range in variability in salinity tolerance traits. Natural populations of *V. marina* exhibited better survival at high salinity levels as compared to the commercial salt-tolerant *V. radiata* varieties, highlighting the halophytic nature of *V. marina*, and its putative importance in developing *Vigna* varieties that can be cultivated in more saline conditions.

Keywords

conservation, crop wild relatives, inter-population variation, salinity, *Vigna marina*

INTRODUCTION

Climate change will pose major challenges for agriculture in the coming decades, as it is expected to affect plant productivity in certain regions (Leisner 2020). Temperature stress and a limited water supply due to drought can directly impact crop yields. In addition, the effects of climate change on soil functions will also impact crop productivity globally (Hamidov et al. 2018). There is convincing evidence showing that human-induced climate change has already affected global crop productivity (Lone et al. 2017). These effects, combined

Copyright D. Jithmi M. De Silva, B.D. Punsara Dharaka, K.M.G. Gehan Jayasuriya, Filip Vandelook. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Plant Ecology and Evolution is published by Meise Botanic Garden and the Royal Botanical Society of Belgium.

with a growing human population, will make ensuring food security during the coming decades very challenging (Lobell and Gourdji 2012; Lone et al. 2017).

Soil salinization is the result of the accumulation of soluble salts in the soil due to saltwater intrusion, mineral deposition, irregular precipitation patterns, and increased evaporation, often exacerbated by intensive agriculture (Nachshon 2018; Eswar et al. 2021; Atta et al. 2023). Salinization is an often-overlooked effect of climate change (Rahman et al. 2017; Eswar et al. 2021). Saline soils can contain NaCl levels up to as high as 40 mM (~2300 ppm), as compared to standard soils that have NaCl levels between 0 and 20 mM (~1170 ppm) (Mohamad Yunus et al. 2024b). Nonetheless, farmers still attempt to utilize high-salinity soils for agriculture by cultivating salt-tolerant species (Septiana and Analuddin 2019; Mohamad Yunus et al. 2024a). Salt-tolerant species, or halophytes, can exhibit different patterns of salt accumulation in plant tissues (Noda et al. 2022). Most of the halophytes generally accumulate salts in high concentrations in leaves, which gives evidence for a tissue tolerance mechanism (Shabala 2013).

Crop wild relatives (CWRs) are wild plant taxa that are genetically closely related to crop species (Maxted et al. 2006). Since different CWRs are adapted to growing in different habitat conditions and exhibit diverse ecological strategies, they may harbour important characteristics to cope with diverse stress conditions. Exploiting the diversity of these characteristics is one of the main solutions to develop climate resilience in crops to ensure global food security (Satori et al. 2022). CWRs have evolved traits to cope with different climatic conditions, pest outbreaks, diseases, and abiotic stresses (Castañeda-Álvarez et al. 2016). This genetic diversity has been partially lost in modern cultivated varieties due to years of selective breeding (Dempewolf et al. 2017). Recent advances in plant molecular biology have opened new opportunities for breeding to incorporate these valuable traits of CWRs into crops by overcoming the barriers of traditional breeding programs (Bohra et al. 2022).

The genus *Vigna* Savi (Fabaceae) comprises a wide range of economically important food legumes, distributed in tropical and subtropical regions, including Sri Lanka (Tomooka et al. 2002; Buddenhagen 2014; Yoshida et al. 2020). Different *Vigna* species show tolerance to various abiotic stresses, allowing them to thrive in sandy saline soils, limestone rocks, waterlogged lands, mountain tops, and shaded ecosystems (Tomooka et al. 2014a). Moreover, their ability to fix nitrogen, even under abiotic stress conditions, is significant and enables them to grow in low-resource environments (Tomooka et al. 2014b). Soil salinity tolerance has evolved multiple times independently within the *Vigna* genus, as is shown by the different mechanisms that evolved to cope with salinity (Noda et al. 2022). Shankar et al. (2023) identified 12 potentially salt-tolerant wild *Vigna* species growing in coastal ecosystems. *Vigna marina* (Burm.) Merr., also known as the Beach bean, is the *Vigna* species showing the highest salt tolerance (Yoshida et al. 2020). This species resides in coastal ecosystems and can cope with high salt concentrations and low nutrient levels (Mohamad Yunus et al. 2024a, 2024b). Similar to all other *Vigna* species, *V. marina* is a CWR of *Vigna* crop species like *Vigna radiata* (L.) R.Wilczek and *Vigna unguiculata* (L.) Walp. (Horton et al. 2024). Most *Vigna* crops are sensitive to high salinity in the root environment (Lawn and Cottrell 2016). However, Yoshida et al. (2020) describe unique responses of *V. marina* to high salinity levels, such as the ability to maintain physiological activity, increased stomatal pore opening, increased transpiration, and tolerating salt inside its tissues. The salt tolerance characteristics of *V. marina* can be utilized to cultivate this useful food legume (Padulosi and Ng 1993; Chankaew et al. 2014; Septiana and Analuddin 2019) as a cover crop in saline soils (Yoshida et al. 2020; Mohamad Yunus et al. 2024a).

Although the capacity for salt tolerance of *Vigna marina* and the underlying mechanisms have been well documented (Noda et al. 2022; Wang et al. 2024), there is limited understanding of how different populations of this species respond to salinity stress. This knowledge gap is particularly relevant in Sri Lanka, an island nation with a highly diverse and unique coastal ecosystem. *Vigna marina* occurs across a range of habitats in Sri Lanka, which possibly have varying salinity levels (Bandara 1989). It is therefore reasonable to hypothesize that different populations of *V. marina* may exhibit varying degrees of salinity tolerance in response to local environmental conditions. Despite its ecological importance, *V. marina* has received limited conservation attention in Sri Lanka, even though it is listed as an endangered species in the National Red List of Sri Lanka (Biodiversity Secretariat 2020). Consequently, understanding inter-population variation in salinity tolerance is essential for conservation planning and for identifying populations with valuable phenotypic traits for potential breeding programs.

For plants in particular, inter-population variation and phenotypic plasticity are critical adaptive responses to climate change, given that plants are generally less mobile than animals and cannot easily escape rapidly changing environmental conditions (Lazaridi et al. 2017; Henn et al. 2018; Roybal and Butterfield 2018). For instance, Lazaridi et al. (2017) examined inter-population variation in agro-morphological traits of wild *Vigna unguiculata* populations and highlighted the presence of a valuable gene pool that can be utilized for crop improvement. Similarly, exploring the genetic and phenotypic diversity of *V. marina* populations in Sri Lanka could provide essential information for both conservation and sustainable utilization efforts.

The main objective of this study is to determine the inter-population variation in salt tolerance of *V. marina* seedlings. We assess this by studying the salt tolerance of four wild populations of *V. marina* from the wet coastal zone in Sri Lanka. In addition, we compared the salt tolerance of the *V. marina* populations with two commercially available *V. radiata* populations, one

considered salt-tolerant and the other not. Specifically, we studied: (i) the growth response of the different *V. marina* populations in 100, 1000, 2000, 10,000, and 20,000 ppm salinity levels, and (ii) the amount of accumulation of NaCl inside different plant tissues (roots, shoots, and leaves). We expect that *V. marina* populations show considerable variation in seedling salt tolerance, as the local habitat conditions of these populations differ substantially. Further, we hypothesized that populations occurring in highly saline locations have evolved a greater salinity tolerance, as natural selection tends to favour such traits under prolonged salt stress. Accordingly, we predict that halophytic *V. marina* seedlings will outperform their domesticated relative, *V. radiata* whose seedlings typically inhibit non-saline agricultural soils, when both are subjected to saline conditions.

MATERIAL AND METHODS

Study materials

Mature pods (brown-coloured dry pods) of *Vigna marina* were collected from ten to 20 plants of four selected populations in four different locations in Sri Lanka (Mahamodara (28 Sep. 2023), Unawatuna (29 Sep. 2023), Negombo (22 Sep. 2023), and Thalpe (29 Sep. 2023)) during the peak fruiting period of each population (Suppl. material 1). Pods were collected into labelled polythene bags and transported to the Department of Botany, University of Peradeniya, Sri Lanka. Seeds were extracted from dry pods and stored in labelled plastic bottles under ambient laboratory conditions (at ca 25°C) until used for experiments. Two varieties of *Vigna radiata*, one salt-tolerant (MI6) and one non-salt-tolerant (Ari), provided by the Field Crop Research and Development Institute (FCRDI), Mahailluppallama, Sri Lanka, were used for a comparative study.

Growth conditions and experiment design

Vigna marina seeds were germinated in laboratory conditions on 2 Oct. 2023, and seeds with 1 cm radicle were transplanted to the respective experiments. Three hundred seeds from each population were sterilized first by soaking them in 1% Clorox (Liquid Bleach) three times for 30 s and subsequently washing them in distilled water. Seeds were then manually scarified with a scalpel blade and placed in tissue papers (Flora multi-fold paper towel 1PLY), moistened with distilled water in Petri dishes, and incubated under ambient laboratory temperature (ca 25°C) and light conditions (diffused sunlight and white fluorescent light during the day (8 h) and dark at night) for five days. After five days, six to eight germinated seeds with a 1 cm radicle were selected randomly and transplanted at 1.5 cm depth in 9 cm diameter pots containing four holes at the bottom and filled up with 300 g of silica sand (washed silica sand from Jayalath Silica Sand Suppliers). Paper (unbleached sack craft paper 90 GSM) was placed at the bottom of each pot to prevent the soil medium from leaking during irrigation. Three hundred sterilized intact seeds from two varieties of *V. radiata* were germinated as mentioned above and transplanted after two days of incubation as described above. Experiments were conducted under uncontrolled glasshouse conditions at an average 27°C and under ambient light (diffuse sunlight and white fluorescent light during the day and complete darkness at night) in the glasshouse of the Department of Botany, University of Peradeniya, Sri Lanka. Following seedling emergence, four vigorous and uniform plants were kept in each pot. One week after seedling emergence, plants were fertilized by adding 50 mL of nutrient solution (Albert solution) to each pot. The same fertilizer treatment was applied weekly to all pots until the end of the experiment. Salt (NaCl) treatment began when the first trifoliate leaf began to expand (Ravelombola et al. 2019). Salt concentrations of 0, 100, 1000, 2000, 10,000, and 20,000 ppm were selected for treatments based on the possible salinity concentrations observed in the natural habitats of *V. marina* (Rhoades 1996). Soil samples collected from these habitats were analysed for salinity using standard protocols. The 20,000 ppm concentration, however, was included based on values reported in the literature. Each concentration was replicated three times, and the pots were placed randomly on a glasshouse bench (on average, 27°C temperature and ca 110,000 lux light conditions during the daytime). Pots were placed on rectangular plastic trays and irrigation was performed by supplying either distilled water or salt solutions to the plastic trays. Irrigation was done by soaking the pots in the respective solution up to one-third of the pot height for 2 h every day (Ravelombola et al. 2019). The treatment was conducted for one month after trifoliate leaf emergence and the growth of the plants in each salt concentration was measured.

Plant performance parameters

Plant height was measured using a string and a ruler calibrated with cm and mm. Measurements started 14 days after the transplant and were repeated in one-week intervals for 28 days. In addition, deceased plants and morphological changes were recorded at weekly intervals. Leaf injury scores were determined and reported every week. Leaf injury was assessed based on a 1 to 7 scale (1 = healthy plants, 2 = first sign of leaf chlorosis, 3 = expansion of chlorosis on leaf surface, 4 = totally chlorotic leaf, 5 = first sign of necrosis, 6 = expansion of necrosis on leaf surface, and 7 = completely dead plants) (Ravelombola et al. 2019). The biomass of leaves, stems, and roots was determined using the oven-dry method. At the end of the experiment, each plant was harvested separately and separated into components; leaves, stems, and roots. Samples were properly labelled and oven-dried at 120°C for 3 h and the dry mass of each component from every plant was measured using a digital chemical balance to the nearest 0.001 g (USDA NRCS 2001).

Tissue ion analysis to test NaCl accumulation in leaves, stems, and roots

Oven-dried samples of various tissues (leaves, stems, and roots) of the same sampled plants were ground to a fine powder and analysed for chloride content following the dilute acid extraction method in Munns et al. (2010). Ground plant tissues (100 mg) were extracted in 0.5 M HNO_3 (10 mL) by shaking for 48 h in darkness at room temperature. Diluted samples of the extracts were then analysed for Cl^- with an Ion Selective Electrode (ORION STAR A214, pH/ISE meter, Thermo Scientific).

Statistical analysis of data

Two-way ANOVAs were performed to analyse height difference, dry mass (leaf, stem, and root), and ANOVA Type III was performed to analyse chloride ion accumulation in plant tissues. Tukey's post-hoc test was utilized to test for significant differences between individual treatments. The Andersen-Darling test was used to assess the normality of data. Data analysis was conducted using Past v.4.03 and R v.4.4.2 statistical software and a probability level of 5% was used to compare means.

RESULTS

Seedling survival, height, and growth rate

All the seedlings of *Vigna marina* from the Unawatuna, Negombo, and Thalpe populations survived at all the studied salt concentrations (Fig. 1). Seedlings of the Mahamodara population all survived at 100, 1000, 2000, and 10,000 ppm NaCl, but none survived for more than three weeks at 20,000 ppm. None of the seedlings of the two varieties of *V. radiata* (salt-tolerant and salt-sensitive) survived at 10,000 and 20,000 ppm NaCl. Both varieties of *V. radiata* died within 2 days at the 20,000 ppm condition, while plants grown in 10,000 ppm NaCl died within one week (Fig. 1). Seedlings of *V. radiata* grown in 2000 ppm NaCl showed necrotic symptoms during the fourth week of the treatment.

A significant interaction effect ($F = 14.6$, $p < 0.001$) was observed between the salt concentration and the four *V. marina* populations and two varieties of *V. radiata* for the final height of the plants (Suppl. material 2). Seedlings of all the populations tested showed reduced height at 10,000 and 20,000 ppm concentrations compared to 0, 100, 1000, and 2000 ppm concentrations. The seedlings of all *V. marina* populations grew higher at 1000 ppm as compared to distilled water (Fig. 1). Plants from the Thalpe population showed the highest growth at 1000 and 2000 ppm, while the highest growth at 100 ppm was shown by seedlings from the Mahamodara population compared to 0 ppm NaCl. Furthermore, the seedling height of the two *V. radiata* varieties was lower at 100, 1000, and 2000 ppm as compared to the *V. marina* populations (Suppl. material 2).

A significant interaction effect ($F = 9.127$, $p < 0.001$) between salt concentration and four *V. marina* populations and two varieties of *V. radiata* was observed for the growth rate of the plants (Suppl. material 2). The highest growth rate at 10,000 and 20,000 ppm salt concentrations was observed in seedlings from the Negombo population. Seedlings of all the populations showed a reduced growth rate at 10,000 and 20,000 ppm concentrations compared to 0, 100, 1000, and 2000 ppm concentrations, while all the *V. marina* populations showed a higher growth rate at 1000 ppm than 0 ppm NaCl (Fig. 2). Salt-tolerant variety of *V. radiata* showed higher growth rate at 100, 1000, and 2000 ppm than distilled water in contrast salt-sensitive variety showing the highest growth rate at 0 ppm NaCl. Overall growth performance was highest in *V. marina* populations compared to the salt-tolerant variety of *V. radiata* seedlings at the highest salinity levels (2000, 10,000, and 20,000 ppm; Fig. 2).

Dry mass of leaves, stems, and roots

We observed a significant interaction effect on dry mass in leaf ($F = 12.99$, $p < 0.001$), stem ($F = 20.52$, $p < 0.001$), and root ($F = 9.658$, $p < 0.001$) between different *V. marina* and *V. radiata* (salt-tolerant and salt-sensitive) populations and salt concentrations. An increased leaf dry mass compared to the control condition was observed in all the *V. marina* populations at 100 ppm NaCl. Plants from the Mahamodara, Negombo, and Thalpe populations showed an increased leaf dry mass at 1000 and 2000 ppm NaCl, while those from Unawatuna did not. In contrast, leaf dry mass was lower at 10,000 and 20,000 ppm NaCl as compared to the control condition in the four studied *V. marina* populations, except for that of the Mahamodara population at 10,000 ppm (Suppl. material 3; Fig. 3A). The same trend was observed for stem and root dry mass (Fig. 3B, C). Leaf dry mass of both *V. radiata* varieties was lower at 100 and 2000 ppm NaCl than at 0 ppm. In contrast, leaf dry mass was higher at 1000 ppm NaCl. The salt-tolerance variety of *V. radiata* showed a higher leaf dry mass than the salt-sensitive one. Stem dry mass of *V. radiata* in both varieties grown at 100, 1000, and 2000 ppm NaCl was lower than that at distilled water (Fig. 3B). The root dry mass of the salt-sensitive variety of *V. radiata* was higher than the salt-tolerant one. Dry masses at each salt condition and in each population differed significantly.

Root: shoot ratio

There was no significant difference in root: shoot ratio of *V. marina* and *V. radiata* populations across different NaCl concentrations except for the Negombo population ($F = 4.154$, $p < 0.001$). Plants from the Negombo population showed a significantly higher root: shoot ratio at 20,000 ppm NaCl (Fig. 4). However, for most *V. marina* populations, there was no significant increase in root: shoot ratio at more saline conditions except for seedlings

of the Negombo population at 20,000 ppm. Salt-sensitive and salt-tolerant varieties of *V. radiata* showed the same trend in root: shoot ratio values (Fig. 4).

Leaf injury score

All the seedlings of *V. marina* from the Unawatuna, Negombo, and Thalpe populations remained healthy at all the studied salinity conditions (Suppl. material 4). While seedlings of Mahamodara at 20,000 ppm NaCl showed the first sign of necrosis in the third week and completely died during the fourth week. Seedlings of two varieties of *V. radiata* remained healthy at 100 ppm NaCl throughout the experimental period, while seedlings at 10,000 and 20,000 ppm NaCl completely died within the first week. Seedlings of the salt-sensitive *V. radiata* variety showed the first necrosis sign at 1000 ppm NaCl in the fourth week of the treatment, while seedlings of the tolerant *V. radiata* variety remained healthy until the end of the treatment (fourth week). Moreover, seedlings of the salt-sensitive variety in 2000 ppm showed the first sign of necrosis in

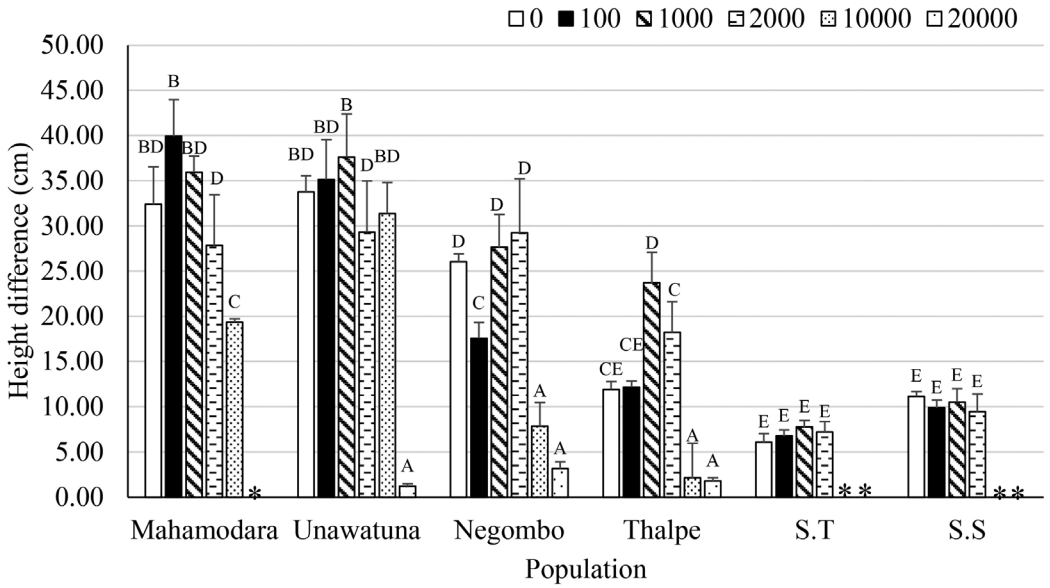


Figure 1. Height difference of seedlings of the four studied *Vigna marina* populations, and salt-tolerant (S.T) and salt-sensitive (S.S) *V. radiata* varieties after one month of salt treatments at 100, 1000, 2000, 10,000, 20,000 ppm concentrations. * Indicates 0% survival. Error bars are + SD. Different uppercase letters depict significant differences between treatments.

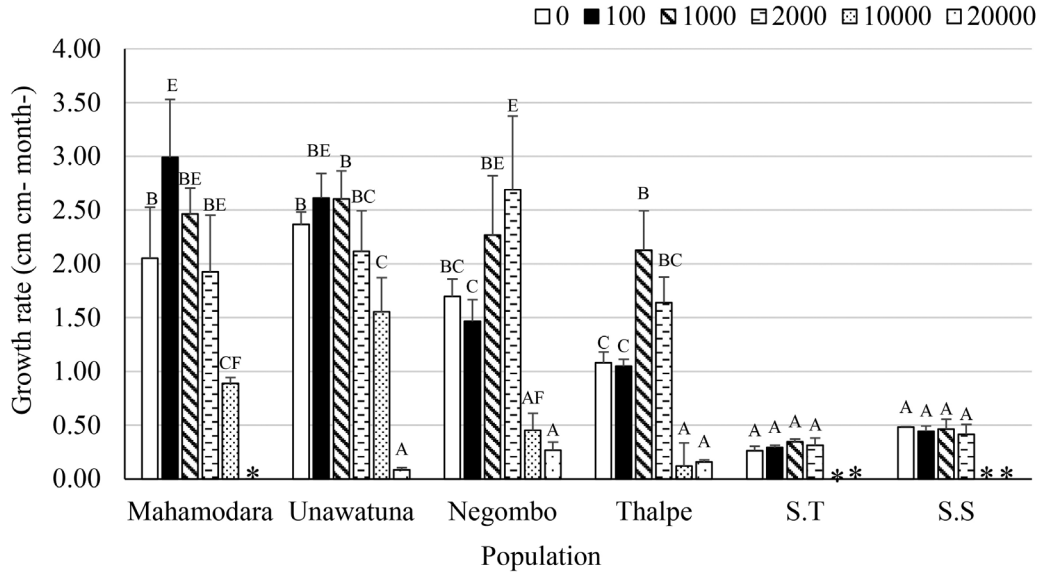


Figure 2. Growth rate of seedlings of the four studied *Vigna marina* populations, and salt-tolerant (S.T) and salt-sensitive (S.S) *V. radiata* varieties after one month of salt treatments at 100, 1000, 2000, 10,000, 20,000 ppm concentrations. * Indicates 0% survival. Error bars are + SD. Different uppercase letters depict significant differences between treatments.

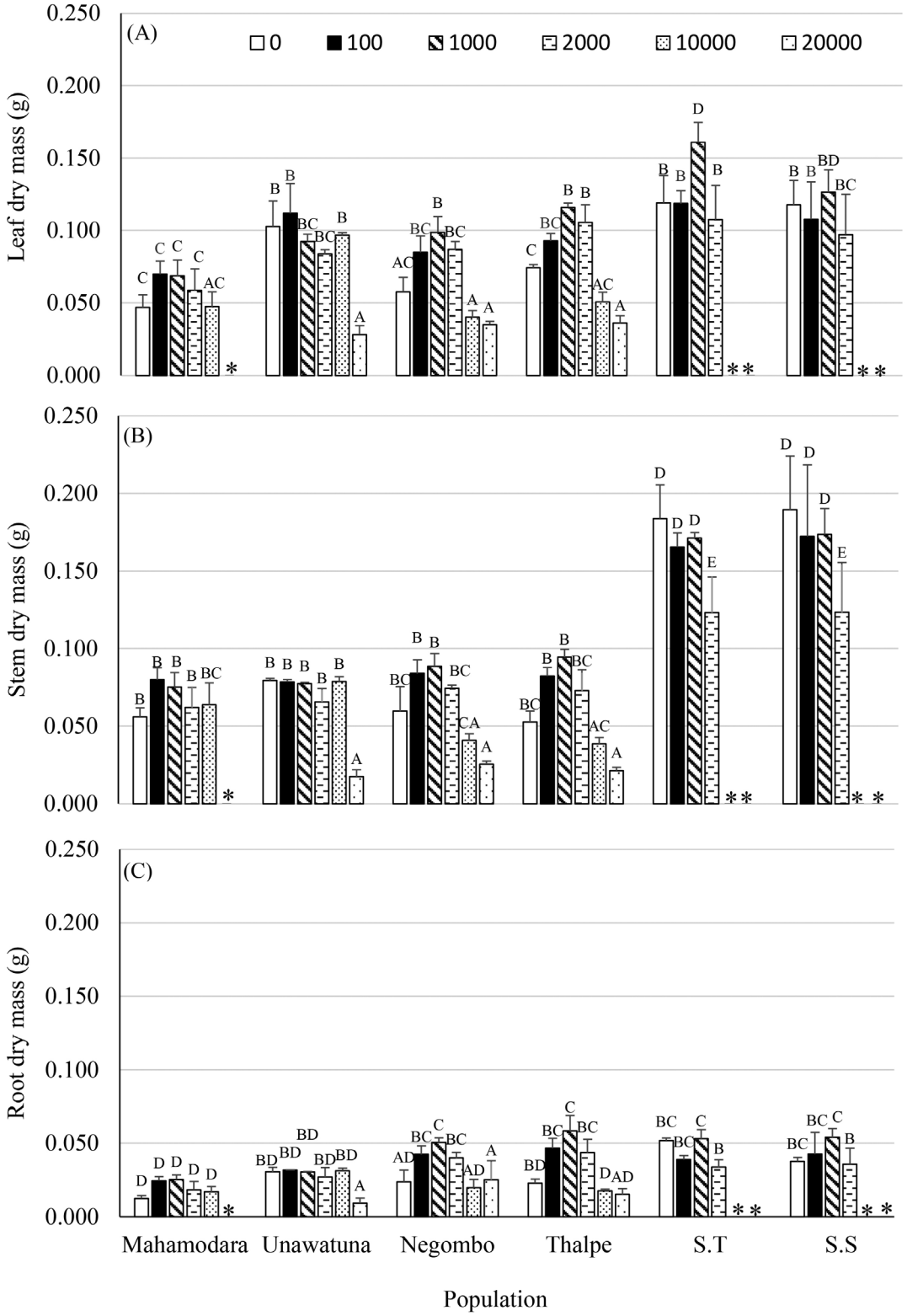


Figure 3. Dry mass of leaves (**A**), stems (**B**), and roots (**C**) of the four studied *Vigna marina* populations, and salt-tolerant (S.T) and salt-sensitive (S.S) *V. radiata* varieties seedlings grown in different salt concentrations after 30 days of growth. * Indicates 0% survival. Error bars are +SD. Different uppercase letters depict significant differences between treatments.

the third week of the treatment and the salt-tolerance variety had these signs by the fourth week. The intensity of necrotic patches was higher in the salt-sensitive variety of *V. radiata* than in the salt-tolerant variety.

Tissue ion analysis

There was a significant interaction effect for chloride ion accumulation in leaf ($F = 22.92$, $p < 0.001$), stem ($F = 13.22$, $p < 0.001$), and root ($F = 13.61$, $p < 0.001$) between different populations and salt concentrations (Suppl. material 3). The chloride accumulation in the leaves, stems, and roots differs significantly between treatments and between populations (Fig. 5). Most of the seedlings of *V. marina* accumulated low chloride content at the lowest salt concentrations, while a high chloride content was accumulated at high concentrations. The Unawatuna population accumulated the highest concentration of chloride ions in the leaves and stems when they were grown in 20,000 ppm NaCl. In contrast, the Negombo population accumulated the highest chloride ion content in the roots, which is significantly different from other populations (Fig. 5). The salt accumulation of *V. marina* was higher in the leaves and stems compared to the roots. When considering the *V. radiata* varieties, their chloride ion accumulation in the leaves significantly increased with increasing saline conditions. The same trend was observed in the stems and roots as well (Fig. 5).

DISCUSSION

High salinity concentrations had a strong impact on seedling growth parameters of both *Vigna marina* and *V. radiata*. Nonetheless, wild *V. marina* seedlings clearly performed better than cultivated *V. radiata* populations in high salt concentrations, even if one of the *V. radiata* populations was considered more tolerant to high salinity levels. From our results, it is also evident that *V. marina* populations growing in different locations in Sri Lanka show inter-populational variation for seedling salinity tolerance, which has implications for conservation efforts as outlined below (Table 1).

Seedling development of all the studied *V. marina* populations improved at slightly higher salt concentrations as compared to growth in distilled water. A similar observation has been made for other halophytes (Alhaddad et al. 2021; Abdellaoui et al. 2023) and confirms the true halophytic nature of *V. marina*. The growth performance of the four studied *V. marina* populations differed considerably between the populations, as shown by the different traits measured. The Thalpe and Negombo populations showed the overall best performance at 20,000 ppm NaCl. Given their better performance in saline conditions, these populations may contain salinity tolerance genes, which could be explored for genetic improvement of *Vigna* crop species. Our experiment showed that the chloride ion content in leaves, stems, and roots of the studied *V. marina* populations was significantly different among populations. This suggests that plants from different populations, which are exposed to varying salinity levels, have adapted differently to salinity stress, and these adaptations may be reflected in the traits studied. The highest chloride accumulation was recorded in the leaves and stems of *V. marina* compared to the roots. When the chloride content is higher in the soil solution, Cl^- ions influx into the roots and accumulate

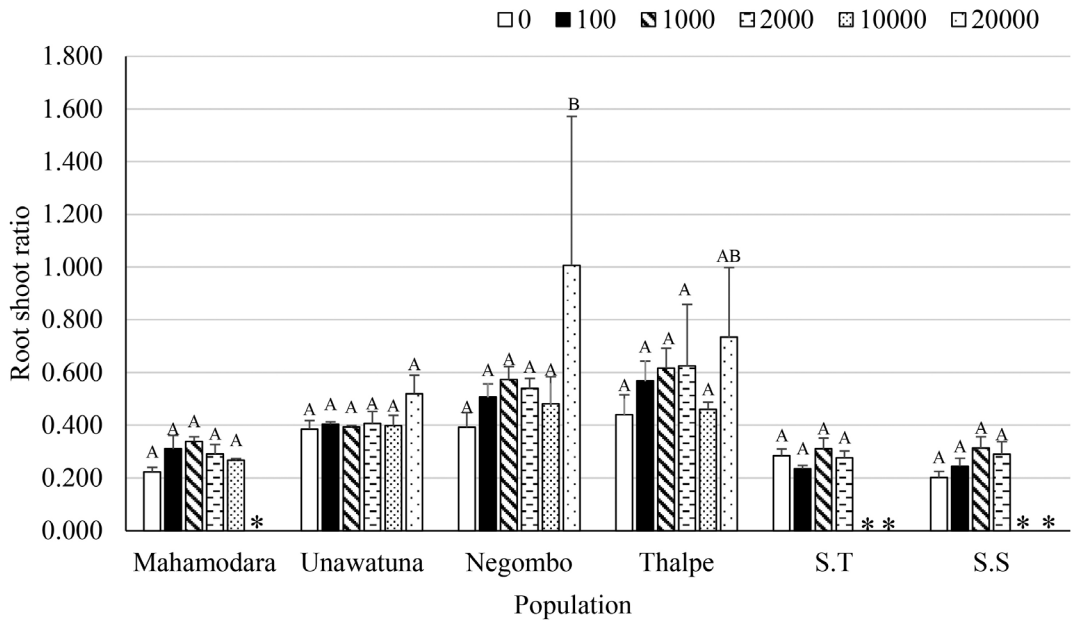


Figure 4. Root shoot ratio of seedlings of the four studied *Vigna marina* populations, and salt-tolerant (S.T) and salt-sensitive (S.S) *V. radiata* varieties after one month of salt treatments at 100, 1000, 2000, 10,000, 20,000 ppm concentrations. * Indicates 0% survival. Error bars are + SD. Different uppercase letters depict significant differences between treatments.

in the aerial parts of the plants, which reduces plant growth, while the first toxicity symptoms can be seen in leaves as chlorotic patches (Geilfus 2018). Yoshida et al. (2020) showed that the Na^+ concentration of *V. marina* also tended to be higher in the stems and leaves than in the roots (roots < stems = leaves). However, in contrast to this report, another study reported that *V. marina* mainly allocated Na+ to the roots but not to the shoot apex. Na^+ was significantly higher in the root than in the stem or the leaf (Noda et al. 2022). Noda et al. (2025) showed that *V.*

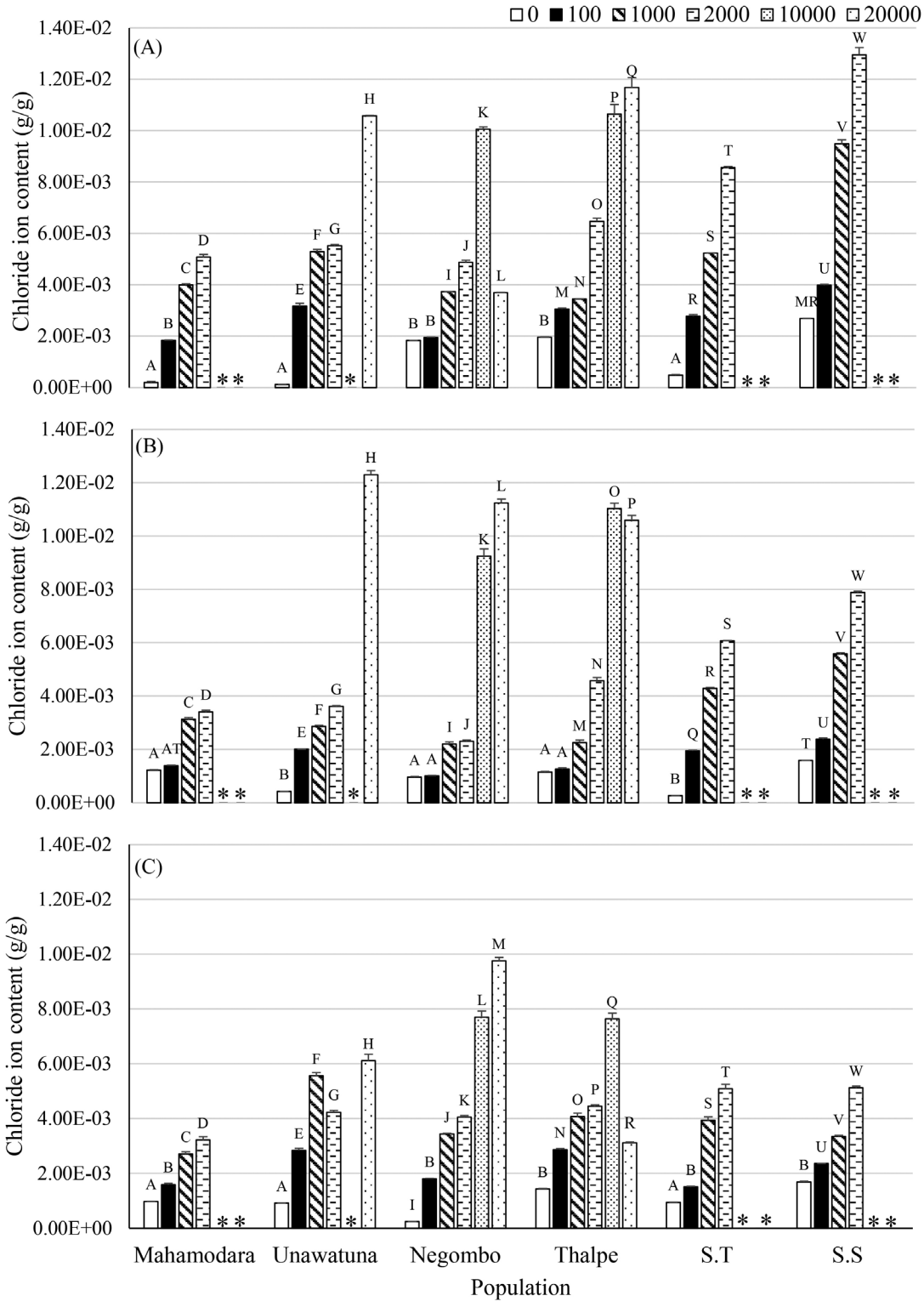


Figure 5. Chloride ion content of leaves (**A**), stems (**B**), and roots (**C**) of the four studied *Vigna marina* populations, and salt-tolerant (ST) and salt-sensitive (SS) *V. radiata* varieties seedlings grown in different salt concentrations after 30 days of growth. * Indicates 0% survival. Error bars are +SD. Different uppercase letters depict significant differences between treatments.

Table 1. Comparison of growth performance of seedlings of studied *Vigna marina* populations at 20,000 ppm saline condition. Growth performance rated from lowest (1) to highest (4), * 0% survival.

Growth Parameters	Studied *Vigna marina* populations			
	Mahamodara	Unawatuna	Negombo	Thalpe
Height (cm)	*	4	2	3
Leaf injury score	1	4	4	4
Total dry mass (g)	*	1	4	3
Root: shoot ratio	*	1	4	3

marina effectively restricted sodium uptake, maintaining low internal sodium allocation even at 300 mM NaCl. Notably, sodium accumulation was predominantly confined to the roots at higher salinity levels, particularly at 200 and 300 mM NaCl.

Recent studies showed that *V. marina* had the ability to suppress sodium (Na^+) uptake under salt stress by upregulating genes related to Casparian strip formation and developing a multi-layered, lignified apoplastic barrier around the endodermis. This structural adaptation significantly limits Na^+ allocation to the shoots. This reinforced endodermal barrier is a key factor in *V. marina*'s dominance in high-salinity environments and represents a promising trait for improving salt tolerance in crop plants (Wang et al. 2025). In our results, there was no significant difference in the root: shoot ratio at the highest NaCl concentration (20,000 ppm) and control (0 ppm NaCl). Further, the root dry mass was lower compared to the shoot dry mass at the 20,000 ppm salinity level. In contrast, Wang et al. (2024) reported that under salt stress conditions, *V. marina* exhibited a distinctive growth strategy by allocating more resources to root development than shoot growth. Specifically, the genotype produced a greater number of fine roots that were shorter in length, as well as fewer but longer thick roots. This adaptation led to a significant increase in root dry weight, even under saline conditions. Moreover, *V. marina* effectively limited sodium accumulation in the stems and leaves, instead retaining some sodium within the root tissues, indicating a potential mechanism for salt tolerance. This root-focused biomass allocation strategy was consistent with observations in *V. marina*, the most salt-tolerant species in the genus, which also prioritized root over shoot dry matter production under salt stress. These findings suggest a conserved adaptive response among salt-tolerant *Vigna* species, with implications for improving stress resilience in crop breeding programs.

Inter-population variation in plant traits and responses to environmental conditions can be caused by various factors (Moreira et al. 2012), with genetic variability (Nicotra et al. 2010; Cochrane et al. 2015), maternal effects (Roach and Wulff 1987), and environmental effects (Cochrane 2016) being the three main factors. Since we performed the experiment in standardized conditions, we can exclude variation due to environmental effects as a potential explanation. Any differences we observed between the populations are therefore related to genetic variation or maternal effects. Chankaew et al. (2014) reported that certain alleles, from *V. marina* and *V. luteola* (Jacq.) Benth., which are genetically closely related species, can increase salt tolerance. Further, they also observed that the salinity tolerance of *V. marina* is controlled by the same QTL at the seedling and vegetative stages. Iseki et al. (2016) suggested that the genetic variability in a few genes can considerably affect the salt tolerance of *Vigna*. Besides genetic variation, plants can respond differently to high salt concentrations due to maternal effects. Seeds of *Glycyrrhiza uralensis* Fisch. ex DC. collected from plants growing in more saline conditions showed a higher germination rate as compared to seeds from plants growing in non-saline conditions (Gu et al. 2024). Further studies are required to determine whether the inter-population differences we observed are related to maternal effects, due to plants growing in different conditions, or whether there is a genetic background. This could be realized by growing plants from different populations in a common garden for at least one generation and testing the performance of these offspring in different salt conditions.

Understanding the sources of trait variation is not only important for basic ecological insight but also critical for conservation and breeding strategies. Preserving populations that represent the functional and agro-morphological diversity within a species is essential, as such variation underpins resilience to environmental stresses and potential use in crop improvement. *Vigna marina* has been reported to harbour valuable traits like salinity tolerance, that is absent in domesticated crop varieties (Maxted et al. 2012; Warschefsky et al. 2014). To develop a precise conservation plan for *V. marina*, a broader sampling effort covering its full distribution across Sri Lanka is necessary to capture local adaptations and rare traits (Vincent et al. 2013). Moreover, incorporating additional functional traits such as phenology, root architecture, and physiological response to stress can help identify ecotypes adapted to specific environmental conditions (Funk et al. 2017). Ultimately, determining whether observed trait variation has a genetic background is critical for prioritizing populations for conservation and utilization in breeding programs.

When comparing the performance parameters of *V. marina* with the two varieties of *V. radiata*, it was clear that *V. marina* performed much better. *Vigna marina* seedlings survived in high salt concentrations (10,000 and 20,000 ppm), while seedlings of both varieties of *V. radiata* died at these concentrations. *Vigna radiata* varieties showed necrotic patches during the salt treatment at 1000 and 2000 ppm saline conditions. This indicates that *V. marina* seedlings have a higher salt tolerance than the commercialized salt-tolerant variety of *V. radiata*. The root: shoot ratio of *V. radiata* was also higher than that of the *V. marina* populations, which indicates that they invested more energy in root formation, potentially indicating that *V. radiata* suffered more from drought stress in saline conditions than *V. marina*. The salt-tolerant variety of *V. radiata* did show a higher performance than the salt-sensitive variety in saline conditions. Hence, our study showed the potential of *V. marina* as a genetic resource to improve the salinity tolerance of crops such as *V. radiata*. *Vigna marina* is an edible plant that is used as a food crop in many places (Padulosi and Ng 1993; Chankaew et al. 2014). Our findings suggest that *V. marina* exhibits traits that may be valuable for cultivation in saline environments. While our study included only a limited number of populations, the observed inter-population variation in salt-related traits highlights the potential of this species as a genetic resource. With further research and broader sampling, *V. marina* could be considered for use in breeding programs aimed at improving salinity tolerance or even for neo-domestication. The use of crop wild relatives in improving cultivated varieties or in developing new crops is expected to increase with advancements in breeding tools and a growing understanding of species diversity (Tomooka et al. 2014b). However, realizing this potential depends on the conservation and accessibility of crop wild relatives, underscoring the need to safeguard germplasm in gene banks and facilitate access to it (Castañeda-Álvarez et al. 2016).

Studying the inter-population variation of a species is useful for understanding the potential resilience of a species to climate change and for informing in situ conservation strategies (Hudson et al. 2015; Henn et al. 2018; Samarasinghe et al. 2022). Species exhibiting high levels of inter-population variation may possess a greater adaptive capacity to cope with future climatic challenges. In our study, *V. marina* showed some inter-populational differences in seedling functional traits under salinity, which may indicate local adaptation. However, given the limited number of populations examined, it is suggested to study a wider range of populations and environmental gradients to confirm these findings. Conserving only a few *V. marina* populations may not capture the full extent of trait variability. Therefore, both in situ and ex situ conservation measures should be considered to protect the genetic and functional diversity of *V. marina*. This is particularly important as the populations studied were located in roadside habitats, which may be vulnerable to disturbance or development. Ex situ and in situ methods could be used to conserve the genetic diversity of *V. marina*. Seed banking is an important ex situ conservation method that can be used to preserve this species. For further steps, it is important to study more *V. marina* populations covering coastal areas around the country to evaluate the mechanisms underlying this species's tolerance to salinity.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge Ms. H.M.S. Herath, Assistant Director of Agriculture (Research), FCRDI, Mahaillupallama, Sri Lanka for providing the salt-tolerant and salt-sensitive varieties of *Vigna radiata*. Sincere thanks are also extended to the Department of Botany, University of Peradeniya and Analytical Chemistry Laboratory, Department of Chemistry, University of Peradeniya, for their valuable assistance and support in providing necessary materials for this study.

REFERENCES

Abdellaoui R, Elkelish A, El-Keblawy A, Mighri H, Boughalleb F, Bakhshandeh E (2023) Editorial: Halophytes: salt stress tolerance mechanisms and potential use. Frontiers in Plant Science 14: 1218184. https://doi.org/10.3389/fpls.2023.1218184

Alhaddad FA, Abu-Dieyeh MH, ElAzazi E-SM, Ahmed TA (2021) Salt tolerance of selected halophytes at the two initial growth stages for future management options. Scientific Reports 11: 10194. https://doi.org/10.1038/s41598-021-89462-3

Atta K, Mondal S, Gorai S, Singh AP, Kumari A, Ghosh T, Roy A, Hembram S, Gaikwad DJ, Mondal S, Bhattacharya S, Jha UC, Jespersen D (2023) Impacts of salinity stress on crop plants: improving salt tolerance through genetic and molecular dissection. Frontiers in Plant Science 14: 1241736. https://doi.org/10.3389/fpls.2023.1241736

Bandara CMM (1989) Environmental awareness among the most vulnerable communities in developing countries. International Social Science Journal 41(3): 441–448.

Biodiversity Secretariat (2020) The National Red List 2020: Conservation Status of the Flora of Sri Lanka. Biodiversity Secretariat, Ministry of Environment and the National Herbarium, Department of National Botanic Gardens, Sri Lanka, 1–254.

Bohra A, Kilian B, Sivasankar S, Caccamo M, Mba C, McCouch SR, Varshney RK (2022) Reap the crop wild relatives for breeding future crops. Trends in Biotechnology 40: 412–431. https://doi.org/10.1016/j.tibtech.2021.08.009

Buddenhagen CE (2014) *Vigna marina* (beach bean). CABI Compendium. https://doi.org/10.1079/cabicompendium.121982

Castañeda-Álvarez NP, Khoury CK, Achicanoy HA, Bernau V, Dempewolf H, Eastwood RJ, Guarino L, Harker RH, Jarvis A, Maxted N, Müller J V, Ramirez-Villegas J, Sosa CC, Struik PC, Vincent H, Toll J (2016) Global conservation priorities for crop wild relatives. Nature Plants 2: 16022. https://doi.org/10.1038/nplants.2016.22

Chankaew S, Isemura T, Naito K, Ogiso-Tanaka E, Tomooka N, Somta P, Kaga A, Vaughan DA, Srinives P (2014) QTL mapping for salt tolerance and domestication-related traits in *Vigna marina* subsp. *oblonga*, a halophytic species.

Theoretical and Applied Genetics 127: 691–702. https://doi.org/10.1007/s00122-013-2251-1

Cochrane A (2016) Can sensitivity to temperature during germination help predict global warming vulnerability? Seed Science Research 26: 14–29. https://doi.org/10.1017/S0960258515000355

Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? Global Ecology and Biogeography 24: 12–24. https://doi.org/10.1111/geb.12234

Dempewolf H, Baute G, Anderson J, Kilian B, Smith C, Guarino L (2017) Past and future use of wild relatives in crop breeding. Crop Science 57: 1070–1082. https://doi.org/10.2135/cropsci2016.10.0885

Eswar D, Karuppusamy R, Chellamuthu S (2021) Drivers of soil salinity and their correlation with climate change. Current Opinion in Environmental Sustainability 50: 310–318. https://doi.org/10.1016/j.cosust.2020.10.015

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews 92: 1156–1173. https://doi.org/10.1111/brv.12275

Geilfus C-M (2018) Chloride: from nutrient to toxicant. Plant and Cell Physiology 59(5): 877–886. https://doi.org/10.1093/pcp/pcy071

Gu J, Yao S, Ma M (2024) Maternal effects of habitats induce stronger salt tolerance in early-stage offspring of *Glycyrrhiza uralensis* from salinized habitats compared with those from non-salinized habitats. Biology 13: 52. https://doi.org/10.3390/biology13010052

Hamidov A, Helming K, Bellocchi G, Bojar W, Dalgaard T, Ghaley BB, Hoffmann C, Holman I, Holzkämper A, Krzeminska D, Kværnø SH, Lehtonen H, Niedrist G, Øygarden L, Reidsma P, Roggero PP, Rusu T, Santos C, Seddaiu G, Skarbøvik E, Ventrella D, Żarski J, Schönhart M (2018) Impacts of climate change adaptation options on soil functions: a review of European case-studies. Land Degradation & Development 29: 2378–2389. https://doi.org/10.1002/ldr.3006

Henn JJ, Buzzard V, Enquist BJ, Halbritter AH, Klanderud K, Maitner BS, Michaletz ST, Pötsch C, Seltzer L, Telford RJ, Yang Y, Zhang L, Vandvik V (2018) Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. Frontiers in Plant Science 9: 1548. https://doi.org/10.3389/fpls.2018.01548

Horton DM, Feleke Y, Pasquet RS, Javadi F, Melville KA, Delgado-Salinas A, Thulin M, Mithen RF, Gepts P, Egan AN (2024) Phylogenetic systematics of *Vigna* sensu stricto in the context of *Physostigma* and allies. American Journal of Botany 111: e16381. https://doi.org/10.1002/ajb2.16381

Hudson AR, Ayre DJ, Ooi MKJ (2015) Physical dormancy in a changing climate. Seed Science Research 25: 66–81. https://doi.org/10.1017/S0960258514000403

Iseki K, Takahashi Y, Muto C, Naito K, Tomooka N (2016) Diversity and evolution of salt tolerance in the genus *Vigna*. PLoS ONE 11: e0164711. https://doi.org/10.1371/journal.pone.0164711

Lawn RJ, Cottrell A (2016) Seeds of "*Vigna marina*" (Burm.) Merrill survive up to 25 years flotation in salt water. Queensland Naturalist 54: 3–13. https://search.informit.org/doi/10.3316/informit.174719815713738 [accessed 11.08.2025]

Lazaridi E, Ntatsi G, Fernández JA, Karapanos I, Carnide V, Savvas D, Bebeli PJ (2017) Phenotypic diversity and evaluation of fresh pods of cowpea landraces from Southern Europe. Journal of the Science of Food and Agriculture 97: 4326–4333. https://doi.org/10.1002/jsfa.8249

Leisner CP (2020) Review: climate change impacts on food security- focus on perennial cropping systems and nutritional value. Plant Science 293: 110412. https://doi.org/10.1016/j.plantsci.2020.110412

Lobell DB, Gourdji SM (2012) The influence of climate change on global crop productivity. Plant Physiology 160: 1686–1697. https://doi.org/10.1104/pp.112.208298

Lone B, Qayoom S, Singh P, Dar Z, Kumar S, Dar N, Fayaz A, Ahmad N, Lyaket, Bhat M, Singh G (2017) Climate change and its impact on crop productivity. British Journal of Applied Science & Technology 21: 1–15. https://doi.org/10.9734/BJAST/2017/34148

Maxted N, Ford-Lloyd BV, Jury S, Kell S, Scholten M (2006) Towards a definition of a crop wild relative. Biodiversity and Conservation 15: 2673–2685. https://doi.org/10.1007/s10531-005-5409-6

Maxted N, Kell S, Ford-Lloyd B, Dulloo E, Toledo Á (2012) Toward the systematic conservation of global crop wild relative diversity. Crop Science 52(2): 774–785. https://doi.org/10.2135/cropsci2011.08.0415

Mohamad Yunus AT, Bin Chiu S, Ghazali AH (2024a) *Vigna marina* as a potential leguminous cover crop for high salinity soils. Pertanika Journal of Tropical Agricultural Science 47: 481–494. https://doi.org/10.47836/pjtas.47.2.10

Mohamad Yunus AT, Chiu SB, Allen SC, Ghazali AHA (2024b) Establishment of potential leguminous cover crop, *Vigna marina* for high-salinity soil conditions. In: Sayyed RZ, Ilyas N (Eds) Plant Holobiome Engineering for Climate-Smart Agriculture. Sustainable Plant Nutrition in a Changing World. Springer, Singapore, 399–417. https://doi.org/10.1007/978-981-99-9388-8_21

Moreira B, Tavsanoglu Ç, Pausas JG (2012) Local versus regional intraspecific variability in regeneration traits. Oecologia 168: 671–677. https://doi.org/10.1007/s00442-011-2127-5

Munns R, Wallace PA, Teakle NL, Colmer TD (2010) Measuring soluble ion concentrations (Na^+, K^+, Cl^-) in salt-treated plants. In: Sunkar R (Ed.) Plant Stress Tolerance. Methods in Molecular Biology, vol. 639. Springer, New York, 371–382. https://doi.org/10.1007/978-1-60761-702-0_23

Nachshon U (2018) Cropland soil salinization and associated hydrology: trends, processes and examples. Water 10(8): 1030. https://doi.org/10.3390/w10081030

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15: 684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Noda Y, Sugita R, Hirose A, Kawachi N, Tanoi K, Furukawa J, Naito K (2022) Diversity of Na^+ allocation in salt-tolerant species of the genus *Vigna*. Breeding Science 72: 326–331. https://doi.org/10.1270/jsbbs.22012

Noda Y, Wang F, Chankaew S, Ariga H, Muto C, Iki Y, Ohashi H, Takahashi Y, Sakai H, Iseki K, Ogiso-Tanaka E, Suzui N, Yin Y-G, Miyoshi Y, Enomoto K, Kawachi N, Somta P, Furukawa J, Tomooka N, Naito K (2025) Diurnal regulation of SOS pathway and sodium excretion underlying salinity tolerance of *Vigna marina*. Plant, Cell and Environment 48: 3925–3938. https://doi.org/10.1111/pce.15402

Padulosi S, Ng NQ (1993) A useful and unexploited gerb, *Vigna marina* (Leguminosae-Papilionoideae) and the taxonomic revision of its genetic diversity. Bulletin du Jardin Botanique National de Belgique / Bulletin van de National Plantentuin van België 62: 119–126. https://doi.org/10.2307/3668270

Rahman A, Nahar K, Al Mahmud J, Hasanuzzaman M, Hossain MdS, Fujita M (2017) Salt stress tolerance in rice: emerging role of exogenous phytoprotectants. In: Li J (Ed.) Advances in International Rice Research. InTechOpen, London, 139–174. https://doi.org/10.5772/67098

Ravelombola W, Qin J, Weng Y, Mou B, Shi A (2019) A simple and cost-effective approach for salt tolerance evaluation in cowpea (*Vigna unguiculata*) seedlings. HortScience 54: 1280–1287. https://doi.org/10.21273/HORTSCI14065-19

Rhoades JD (1996) Salinity: electrical conductivity and total dissolved solids. In: Sparks DL (Ed.) Methods of Soil Analysis. Part 3 – Chemical Methods. Soil Science Society of America Book Series No. 5. ASA and SSSA, Madison, WI, 417–435.

Roach DA, Wulff RD (1987) Maternal effects in plants. Annual Review of Ecology and Systematics 18: 209–235. https://doi.org/10.1146/annurev.es.18.110187.001233

Roybal CM, Butterfield BJ (2018) Functional trait heritability and local climatic adaptation among grasses: a meta-analysis. Plant Ecology 219: 369–379. https://doi.org/10.1007/s11258-018-0801-y

Samarasinghe BRCP, Jayasuriya KMGG, Gunaratne AMTA, Senanayaka MC, Dixon KW (2022) Seed traits and climate resilience in three *Mesua* species from Sri Lanka. Flora 287: 152004. https://doi.org/10.1016/j.flora.2022.152004

Satori D, Tovar C, Faruk A, Hammond Hunt E, Muller G, Cockel C, Kühn N, Leitch IJ, Lulekal E, Pereira L, Ryan P, Willis KJ, Pironon S (2022) Prioritising crop wild relatives to enhance agricultural resilience in sub-Saharan Africa under climate change. Plants, People, Planet 4: 269–282. https://doi.org/10.1002/ppp3.10247

Septiana A, Analuddin (2019) Potential uses of Marine Bean (*Vigna marina* Burm.) as salt tolerant legume in coastal salty land, Southeast Sulawesi, Indonesia. IOP Conference Series: Earth and Environmental Science 260: 012142. https://doi.org/10.1088/1755-1315/260/1/012142

Shabala S (2013) Learning from halophytes: physiological basis and strategies to improve abiotic stress tolerance in crops. Annals of Botany 112: 1209–1221. https://doi.org/10.1093/aob/mct205

Shankar TU, Semwal DP, Gupta V, Archak S, Nair RM, Tripathi K (2023) Spatial distribution, diversity mapping, and gap analysis of wild *Vigna* species conserved in India's National Genebank. Diversity 15: 552. https://doi.org/10.3390/d15040552

Tomooka N, Vaughan DA, Moss H, Maxted N (2002) Genetic resources. In: Tomooka N, Vaughan DA, Moss H, Maxted N (Eds) The Asian *Vigna*. Springer, Dordrecht, 29–55. https://doi.org/10.1007/978-94-010-0314-8_3

Tomooka N, Isemura T, Naito K, Kaga A, Vaughan D (2014a) *Vigna* species. In: Singh M, Bisht I, Dutta M (Eds) Broadening the Genetic Base of Grain Legumes. Springer, New Delhi, 175–208. https://doi.org/10.1007/978-81-322-2023-7_9

Tomooka N, Naito K, Kaga A, Sakai H, Isemura T, Ogiso-Tanaka E, Iseki K, Takahashi Y (2014b) Evolution, domestication and neo-domestication of the genus *Vigna*. Plant Genetic Resources 12: S168–S171. https://doi.org/10.1017/S1479262114000483

USDA NRCS (2001) Soil quality test kit guide. Soil Quality Institute, United States Department of Agriculture, Natural Resources Conservation Service. https://www.nrcs.usda.gov/sites/default/files/2022-10/Soil%20Quality%20Test%20Kit%20Guide.pdf [accessed 21.07.2025]

Vincent H, Wiersema J, Kell S, Fielder H, Dobbie S, Castañeda-Álvarez NP, Guarino L, Eastwood R, León B, Maxted N (2013) A prioritized crop wild relative inventory to help underpin global food security. Biological Conservation 167: 265–275. https://doi.org/10.1016/j.biocon.2013.08.011

Wang F, Iki Y, Tanoi K, Naito K (2024) Phenotypic responses in the root of salt-tolerant accessions of *Vigna marina* and *Vigna luteola* under salt stress. Genetic Resources and Crop Evolution 71: 2631–2640. https://doi.org/10.1007/s10722-023-01794-3

Wang F, Tanoi K, Yamauchi T, Naito K (2025) Multi-layered apoplastic barrier underlying the ability of Na^+ exclusion in *Vigna marina*. Plant and Cell Physiology 66: 554–565. https://doi.org/10.1093/pcp/pcaf005

Warschefsky E, Varma Penmetsa R, Cook DR, von Wettberg EJB (2014) Back to the wilds: tapping evolutionary adaptations for resilient crops through systematic hybridization with crop wild relatives. American Journal of Botany 101: 1791–1800. https://doi.org/10.3732/ajb.1400116

Yoshida J, Tomooka N, Yee Khaing T, Shantha PGS, Naito H, Matsuda Y, Ehara H (2020) Unique responses of three highly salt-tolerant wild *Vigna* species against salt stress. Plant Production Science 23: 114–128. https://doi.org/10.1080/1343943X.2019.1698968

SUPPLEMENTARY MATERIALS

Supplementary material 1

Locations of seed collected from four populations of *Vigna marina*.
https://doi.org/10.5091/plecevo.161947.suppl1

Supplementary material 2

Results of ANOVA on population, salt concentration, and their interactions for the final height, growth rate, and root:shoot ratio of plants of *Vigna marina* from four populations and two *V. radiata* varieties (salt-tolerant and salt-sensitive) grown in five different salt concentrations.
https://doi.org/10.5091/plecevo.161947.suppl2

Supplementary material 3

Results of ANOVA between population, salt concentration, and their interactions for the dry mass of leaf, stem, and roots, and the chloride ion content in these tissues for four *Vigna marina* and two *V. radiata* populations.
https://doi.org/10.5091/plecevo.161947.suppl3

Supplementary material 4

Leaf injury score of seedlings at different saline conditions with time in four populations of *Vigna marina*.
https://doi.org/10.5091/plecevo.161947.suppl4