



Neo-domestication of Crop Plants for Managing Unproductive Salt-affected Lands

Avni Dahiya¹, Arvind Kumar¹, Shruti Kaushik¹, Sunita Devi¹,
Adhisha², Anita Mann¹, Ashwani Kumar^{1*} and Satish Kumar Sanwal¹

¹ICAR – Central Soil Salinity Research Institute, Karnal - 132001, Haryana, India

²Department of Biotechnology, GJUS&T, Hisar-125001, Haryana, India

*Corresponding author's E-mail: ashwanisharma107@gmail.com

Abstract

Global food security is increasingly threatened by a growing population, adverse climate changes and the expansion of degraded lands including salt-affected lands. As conventional crop domestication is a lengthy and continuous process and it struggles to keep pace with emerging human needs and the demand for diverse crops. With the escalating demand for food and the necessity for a variety of crops including nutrient-dense varieties, biofuels, phytoremediation plants, and crops for bio-farming the neo-domestication has emerged as a critical strategy. This approach focuses on developing novel crop plants and enhancing the resilience and productivity of existing crops in challenging environments, particularly on unproductive, salt-affected soils. Neo-domestication leverages the genetic variability existing among the crop wild relatives (CWRs) and underutilized species to develop resilient crop varieties exhibiting improved tolerance to salinity. Understanding the mechanisms of salinity stress in crop plants and their wild relatives is vital for the physiological adaptation of existing crops to salt stress and for formulating effective management strategies. Salinity stress disrupts water uptake, ion balance, and nutrient acquisition, ultimately leading to reduced growth and yield. To address these challenges, it is imperative to incorporate salinity tolerance traits such as ion homeostasis, osmotic regulation, and stress-responsive gene expression into domesticated crops. However, wild relatives of salt-tolerant crops harboring linkage drags are sometimes difficult to be used via traditional breeding approaches. Neo-domestication offers a novel solution by combining advanced genome editing tools, such as CRISPR-Cas9, with other modern approaches like genome-wide association studies (GWAS), pan-genomics, thereby harnessing the genetic potential of crop wild relatives (CWRs). This approach enables the precise modification of specific genes associated with undesired traits in crop wild relatives, including shattering, anti-nutritional factors, and crossing barriers, rendering them suitable for development as new crops or as germplasm in breeding programs. Several wild relatives exhibit salt-stress tolerance, which can be used to accelerate the development of crops capable of thriving in saline environments. Additionally, exploring alternative crops that inherently tolerate high salinity opens new avenues for cultivation in saline conditions with diverse applications.

Key words: Genome editing tools, Neo-domestication, Salt-affected lands, Salinity tolerance, Stress-resilient crops

Introduction

The increasing global population, coupled with the pressing challenges of climate change, has intensified the need for innovative strategies to ensure food security (Myers *et al.*, 2017). One of the most significant challenges in agricultural production is the degradation of arable land, particularly due to salinity. The presence of salt-affected soils, a term that broadly encompasses saline, sodic, and saline-sodic types, has been shown to severely hinder the agricultural productivity and environmental sustainability (Lee, 2023). As per the latest FAO report, titled

Global Status of Salt-Affected Soils (2024), approximately 1.381 billion hectares, representing 10.7% of the land globally, are affected by salinity, including both saline and sodic soils. Currently, around 10% of world's rainfed and irrigated croplands are impacted, with projections indicating this could rise to 24-32% due to climate change (FAO, 2024). This phenomenon is particularly prevalent in arid and semi-arid regions, where improper irrigation practices, poor drainage, and rising groundwater levels exacerbate the accumulation of salts in the soil. The consequences of soil salinity are severe, leading to reduced agricultural productivity, loss of arable

land, and ultimately, the displacement of farming communities (Ismail and Horie, 2017). Addressing these complex challenges necessitates a fundamental transformation of agricultural production systems. Improving crop productivity per unit area through responsible resource management and efficient use of water and fertilizers, can significantly contribute to sustainable crop production (Razzaq *et al.*, 2021). To address climate change and ensure food security, the development of climate-smart crop varieties capable of withstanding diverse environmental conditions is essential (Dawson *et al.*, 2019).

Neo-domestication refers to the process of bringing wild or semi-wild plant species into cultivation, with the aim of developing new crop varieties that can thrive under specific environmental conditions, such as high soil salinity (Gasparini *et al.*, 2021). Unlike traditional crop domestication, which occurred over thousands of years, neo-domestication leverages modern breeding techniques and biotechnological advancements to rapidly develop crop species that are better suited to the challenges posed by contemporary agriculture. The primary objective of neo-domestication is to enhance agronomic traits and improve acclimatization by rigorously screening and selecting the best-performing cultivars, including crop wild relatives (CWRs) and traditional landraces (Razzaq *et al.*, 2021). This strategy aims to create novel or improved crop varieties that can withstand diverse environmental conditions and deliver higher productivity, ensuring greater resilience to climate challenges (Purugganan, 2019; Fernie and Yan, 2019). Salinity imposes multiple stresses on plants, including osmotic stress, ion toxicity, and disrupted nutrient uptake, all of which severely limit plant growth and yield. Traditional crops, which have been bred for high yield under optimal conditions, often lack the resilience needed to cope with the harsh conditions of saline soils (Hossain and Shah, 2019). Consequently, there is a need to explore alternative crops that possess inherent tolerance to salinity and can be cultivated on marginal lands that are currently unproductive (Wani *et al.*, 2020). Neo-domestication provides a pathway to achieving this by harnessing the genetic diversity of wild plant species that have naturally adapted to saline environments.

Several wild and underutilized plant species have shown remarkable tolerance to salinity, making them prime candidates for neo-domestication (Purugganan, 2019). Since the introduction of first genetically modified crop, the “Flavr Savr tomato”, back in 1994, over 500 events belonging to 33 crop species have been approved by the regulatory authorities and commercialized across various countries (Paul *et al.*, 2018). By bringing these species into cultivation and improving their agronomic traits through breeding and genetic engineering, it is possible to develop new crop varieties that can be grown on salt-affected lands, thereby turning these unproductive areas into productive agricultural landscapes (Marsh *et al.*, 2021). In light of the outlined challenges, there is a pressing need to develop and adopt alternative and rapid molecular breeding strategies aimed at enhancing genetic gains and improving salinity resilience in domesticated crops.

Through this review, we examine the effects of soil salinity on crop productivity, with a focus on gaining insights into the underlying mechanisms that enable plants to tolerate saline conditions. We also discuss advanced techniques, such as genome editing and multi-omics approaches to better understand and enhance these salt tolerance mechanisms. Pan-genomics, which involves the study of the entire gene pool of a species, provides insights into genetic diversity and potential targets for neo-domestication. By integrating pan-genomic insights with genome editing tools, we can enhance our understanding of salt tolerance mechanisms and advance their effectiveness. We argue that neo-domestication, combined with these advanced tools, offers a promising strategy for developing salt-tolerant crop varieties. Additionally, we address current limitations and challenges in this field and propose future directions for research and application to improve crop resilience and productivity in saline-affected areas using accelerated crop domestication.

Salinity Stress in Crops-Response Mechanisms and Tolerance Strategies

In order to design effective agricultural practices that enhance salt tolerance capacity in plants and enable them to flourish under conditions of salt

stress, it is imperative to understand the implications of salinity on agricultural crops. Salinity causes a range of biochemical disruptions in plants, which in turn impairs their overall growth and development. However, some plants have a natural ability to tolerate higher concentrations of salt, whereas others may have difficulty coping with even low levels of salinity (Yadav *et al.*, 2019). The major physiological processes impacted during conditions of salt stress are impaired seed germination, reduced photosynthesis, nutritional imbalances, osmotic stress, ionic disturbances, specifically an altered Na^+/K^+ ratio, and accumulation of reactive oxygen species (ROS). Additionally, salt stress can alter morphological attributes such as stunted growth, delayed flowering, and root deterioration (Fig. 1; Kumar *et al.*, 2020). All these factors collectively contribute to the reduction in physiological functions, growth, and yield of agriculturally imperative crops. The notable impacts of soil salinity on plant survival, along with the various strategies plants employ to withstand salt stress, are discussed below.

Impaired photosynthesis under salinity

Salinity exerts a direct and detrimental impact on the process of photosynthesis in plants (Singh *et al.*, 2016; Zahra *et al.*, 2022). The generation of

ROS under salt stress inhibits enzyme activities and disrupts the biochemical reactions essential for energy conversion during photosynthesis (Jiang *et al.*, 2017). Additionally, salinity leads to a reduction in photosynthetic pigment content and interferes with the biosynthetic machinery necessary for pigment production (Singh *et al.*, 2022). Salinity has also been shown to disrupt the efficiency of photosystem II (PSII), affect the electron transport chain, and impair oxygen evolution (Singh *et al.*, 2022). Significant alterations in chlorophyll fluorescence have been observed in various plants species exposed to salt stress. For instance, in *Solanum melongna*, overall reduction in net photosynthetic rate has been reported which was attributed to reduced chlorophyll contents, excessive production of ROS, and inhibition of enzyme activities (Hannachi *et al.*, 2022). In case of Bermuda grass (*Cynodon dactylon*), photo-synthesis was reduced under saline conditions due to reduction in chlorophyll contents (Liu *et al.*, 2023). Salinity also impacts stomatal movements, transpiration rates, and levels of CO_2 (Tru'că *et al.*, 2023). Additionally, salt stress is known to impact chloroplast function, which in turn affects the process of photosynthesis (Hameed *et al.*, 2021). The deleterious impact of salt on overall photosynthetic efficiency leads to reduced energy production, growth, and yield potential.

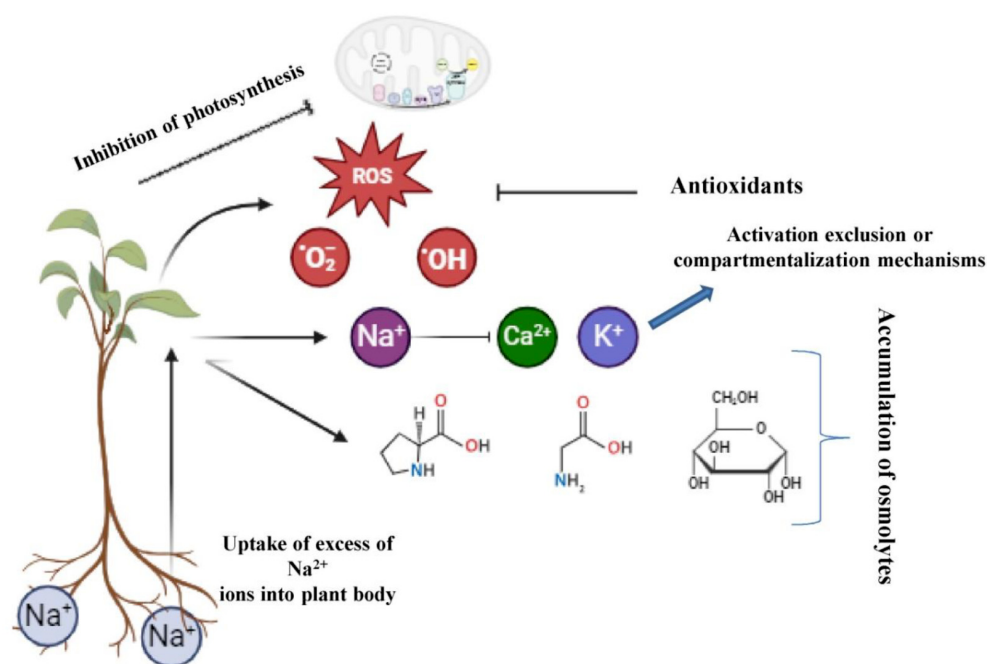


Fig. 1 Impact of excess salt on plants and some of the adaptive strategies they employ to manage saline stress

Salinity induced osmotic stress

Disturbed cellular metabolism and altered nutrient uptake leads to osmotic stress in plants that are exposed to salinity (Negrão *et al.*, 2017). Also, the negative osmotic potential due to high Na^+ ions creates an osmotic gradient and the water moves out of the cells and reduces turgor pressure. Furthermore, salinity leads to reduction in water use efficiency, relative water content and rate of transpiration (Sheldon *et al.*, 2017; Zhang *et al.*, 2016). Salinity directly leads to ionic imbalances and osmotic stress which further leads to ROS production and overall disruption in plant's growth and metabolism. Excess concentrations of salt leads to elevated levels of Na^+ ions and disturbs the overall Na^+/K^+ ratio thereby altering the osmotic potential and disrupting the normal physiological water uptake (Hualpa-Ramirez *et al.*, 2024). However, in order to overcome this osmotic stress generated due to ionic imbalances, plants deploy certain mechanisms of protection. One major strategy that plants incorporate in overcoming osmotic stress is production of compatible solutes or osmolytes like proline, glycine betaine, free amino acids, and sugars which help in maintaining optimum osmotic potential (Mehta and Vyas, 2023; Shehu *et al.*, 2023). Glycine betaine is an essential quaternary ammonium compound whereas proline is an amino acid and sugars like glucose, sucrose, mannitol, and other alcoholic sugars accumulate readily under conditions of salt stress (Datir *et al.*, 2020).

Disrupted mineral nutrition and ionic imbalances

Excessive Na^+ ions resulting from salinity induce disturbances in ionic balances, particularly affecting K^+ and Ca^{2+} concentrations, which consequently lead to deficiency symptoms (Hussain *et al.*, 2021). Reduced uptake of essential ions disturbs the overall ionic ratio, which hinders physiological processes and leads to growth retardation (Hualpa-Ramirez *et al.*, 2024). Research in spinach has shown a clear link between disrupted mineral nutrition and ionic imbalances under saline conditions, where increased salt levels led to lower concentrations of essential ions (Jan *et al.*, 2021). Furthermore, increased Na^+ concentrations in plants enhance

the uptake of chloride (Cl^-) ions while disrupting the absorption of sulfur and phosphate ions, thereby exacerbating growth-related impairments (Gupta and Huang, 2014). To mitigate ionic stress induced by salinity, plants must implement strategies to manage excess ions within their body. Major strategies include the compartmentalization of ions into organelles such as vacuoles, restricting ion influx into the plant, and enhancing the efflux of ions (Zhao *et al.*, 2020). Furthermore, the Salt Overly Sensitive (SOS) signaling pathway plays a major role in exporting Na^+ ions, with several studies reporting that the upregulation of *SOS1* contributes to the development of tolerance against saline conditions (Shahzad *et al.*, 2022). Also, High-Affinity Potassium Transporters (HKTs) facilitate the exclusion of Na^+ ions and promote the uptake of other divalent cations, thereby contributing to the maintenance of ionic balance (Xu *et al.*, 2020). The strategies of ion efflux, activation of transporters and compartmentalization are essential for maintaining optimum levels of different ions into the plant body and develop salt tolerance.

Generation of ROS under salinity

One of the most significant adverse effects of exposure to stress is the excessive production of ROS (Jiang *et al.*, 2017). Salt-induced oxidative stress disrupts various biochemical functions, starting with the inhibition of enzymatic activities and progressing to the degradation of biomolecules, loss of membrane integrity, and causing irreversible damage to plant cells (Ahanger *et al.*, 2017; Ahmad *et al.*, 2019). To mitigate deleterious impacts of ROS, it is imperative to uplift plant's antioxidant defense system. This system scavenges excess ROS and maintains a balance between ROS generation and detoxification, thereby ensuring the optimum functioning of biomolecules and enzymes. Indeed, several studies indicate that plants exposed to saline conditions often increase their antioxidant levels as a response to stress (Mushtaq *et al.*, 2020). Under salt stress, plants generate a variety of reactive oxygen species or ROS, including hydrogen peroxide (H_2O_2), hydroxyl radicals ($\text{OH}^\cdot$), singlet oxygen, and superoxide anions (O_2^-). To counter the damaging effects of these

reactive molecules, plants rely on a complex antioxidant defense system comprising of enzymatic antioxidants, such as superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), and ascorbate peroxidase (APX), together with non-enzymatic antioxidants like glutathione, carotenoids, and vitamins (Nahar *et al.*, 2015). In fact, salt-tolerant plants are known to upregulate their antioxidant activities to effectively scavenge the excess ROS produced under stress conditions. However, extended exposure to severe salinity can overwhelm and compromise these defense mechanisms, thereby impairing the plant's capacity to deal with oxidative damage.

Neo-domestication- Concept and Importance

Neo-domestication has emerged as a valuable approach in contemporary agriculture, particularly in addressing the challenges posed by unproductive, salt-affected lands. This innovative approach involves the intentional selection and incorporation of wild or semi-wild plant species, which are naturally adapted to stressful conditions, into the gene pool of cultivated crops (Ferne and Yan, 2019). By leveraging advanced genomic and

breeding technologies, neo-domestication aims to develop new crop varieties with improved salt-tolerant, specifically adapted for cultivation on marginal lands, ultimately boosting crop productivity and promoting sustainable agriculture and food security (Fig. 2) (Hoyos *et al.*, 2020). Neo-domestication diverges from traditional crop improvement methods by focusing on the potential of crop wild relatives (CWRs) and underutilized species that possess inherent traits for salt tolerance and resilience (Gasparini *et al.*, 2021; Razzaq, *et al.*, 2021).

These traits, which often get lost during the domestication of conventional crops, are reintroduced through targeted or precision breeding and genetic modification techniques, facilitating the rapid development of crops that are resilient to challenging environmental conditions. Unlike conventional breeding, which often dilutes these beneficial traits, neo-domestication preserves and enhances the genetic diversity essential for resilience against salinity and other abiotic stresses (Wang *et al.*, 2018). The process of neo-domestication involves several critical steps, beginning with the identification of

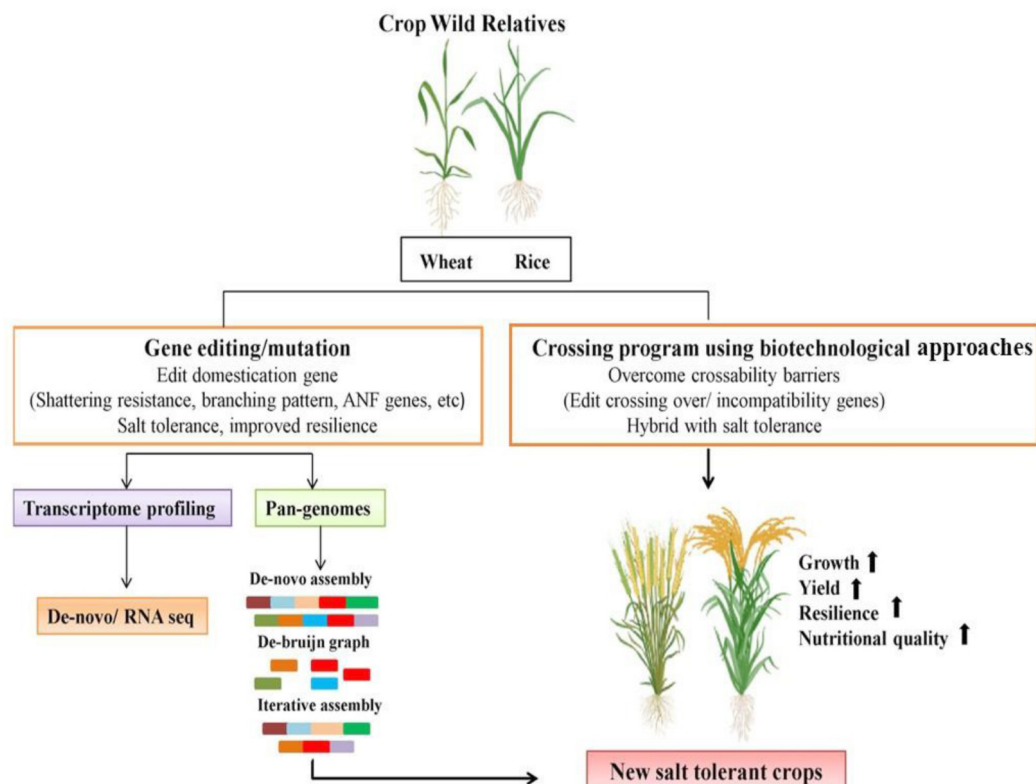


Fig. 2 Key progress in Neo-domestication strategies for increasing crop yield

stress-responsive candidate genes in the crop wild relatives (CWRs) through high-throughput sequencing and transcriptomic profiling (Shelef *et al.*, 2017). Advances in next-generation sequencing (NGS) technologies have made it possible to efficiently map and sequence the genomes of these wild species, uncovering key genes responsible for salinity tolerance. Once identified, these genes can then be incorporated into the genomes of domesticated crops through precision breeding techniques such as CRISPR-Cas9 based genome editing, that facilitates the incorporation of desirable traits without disrupting other agronomically important characteristics (Kang *et al.*, 2016). In the context of managing salt-affected lands, neo-domestication focuses on traits such as efficient ion regulation, osmotic balance, and salt exclusion mechanisms at the cellular level. These traits, which are typically polygenic and complex, can be challenging to harness. However, by targeting specific monogenic pathways using genome editing tools, researchers can create crop varieties that exhibit enhanced salt tolerance while maintaining high yield potential and nutritional value (Khan *et al.*, 2019).

The ultimate goal of neo-domestication is to develop crop varieties that not only survive but also thrive in salt-affected soils, transforming these unproductive lands into viable agricultural zones. This approach not only increases the genetic diversity of agricultural systems but also enhances the resilience of crops to future climate challenges. As more genomes of CWRs and halophytes are sequenced, the potential for neo-domestication to revolutionize agriculture on salt-affected lands increases, offering a sustainable solution to one of the most pressing challenges in global food production (Usadel *et al.*, 2018).

Accelerated Neo-domestication for Salt-tolerance in Crops Using Genome Editing

The entire history of crop improvement can be categorized into four generations. The first-generation (1G) breeding relied on traditional phenotypic selections by local farmers. This was followed by the generation of Hybrid breeding (2G) which employed mating designs and

statistical analyses, leading to the first “Green revolution” in the 1950s. The third generation (3G), also referred to as the second Green Revolution, introduced biotechnology-based breeding. The fourth generation (4G) is presently underway, integrating genome editing, high-throughput sequencing and data-driven precision breeding to adapt crops to specific regional climates. This approach aims to develop a more sustainable and climate-friendly agricultural system (Fernie and Yan, 2019).

Recent advances in genomics have significantly expanded our understanding of complex trait inheritance. With advent of next-generation sequencing and multi-omics technologies, it has now become possible for researchers to identify genes/alleles driving desirable traits in both domesticated crops and their wild ancestors. Such an understanding is critical for employing precise genome-editing strategies using tools like CRISPR/Cas9, which allows for the targeted and accurate alteration of the specific genes without introducing any foreign DNA (Pattnaik *et al.*, 2023). The CRISPR/Cas9 system, which is based on a prokaryotic immune system, uses the Cas9 nuclease to induce double-stranded DNA breaks at specific genome regions that match with pre-programmed guide RNAs. The cell’s repair mechanisms then modify the DNA, enabling gene knockouts, insertions, or base edits (Altpeter *et al.*, 2016).

In this context, genome editing can be used as a viable tool to target genes associated with key domestication traits in wild relatives or orphan crops, transforming them into viable agricultural options, a process often referred to as *de novo* domestication. This emerging approach enables the development of elite lines with enhanced performance, bypassing many of the limitations of conventional breeding (Krug *et al.*, 2023). In fact, some of the earliest attempts to manipulate domestication-related genes in crop wild relatives (CWRs) have already shown encouraging results. These proof-of concept studies serve as models for applying *de novo* domestication to a broader range of crops paving way to develop resilient, high-performing cultivars that are better adapted to environmental or other stress factors (Fernie

and Yan 2019). A pioneering study by *Li et al.* (2018) demonstrated the feasibility of *de novo* domestication in *Solanum pimpinellifolium*, a wild tomato species known for its inherent stress tolerance but limited agronomic performance. Using CRISPR/Cas9-based multiplex editing, the researchers simultaneously targeted multiple genes associated with key domestication traits such as plant architecture, flowering, and fruit development to accelerate the acquisition of agronomically suitable traits. The edited lines exhibited improved domestication characteristics, including a more compact plant architecture, increased fruit size and number, all the while retaining the plant's innate stress resilience. *Oryza alta*, an allotetraploid wild rice species, exhibits superior tolerance to both biotic and abiotic stresses and produces higher biomass compared to cultivated diploid rice (*Oryza sativa*). Despite these advantages, its utility as a crop is limited by undesirable agronomic traits, including excessive seed shattering, long awns, low grain yield, poor grain quality, tall stature, sparse panicles, and strong photoperiod sensitivity (Xie and Liu, 2021). In an effort to overcome these limitations, Yu *et al.* (2021) used CRISPR/Cas9 genome editing as a *de novo* domestication strategy targeting key traits in *O. alta*. A total of six agronomically important genes, namely *OaqSH1* (for seed shattering), *OaAN-1* (for awn length), *OaSD1* (for plant height), *OaGhd7* and *OaDTH7* (for heading date), and *OaGS3* (for seed size) were subjected to editing. The resulting lines showed reduced seed shattering and shorter awns, along with noticeable improvements in other agronomic traits. This work underscores the potential of targeted genome editing in accelerating the domestication of complex polyploid species into novel, resilient cereal crops within a few generations. Recent research has extended genome editing efforts to *Hordeum marinum* (sea barley grass), a wild Triticeae species naturally adapted to saline and waterlogged environments. With the assembly of a high-quality reference genome and the establishment of CRISPR/Cas9-based protocols, this work opens up new possibilities for tapping into its stress-resilience traits—paving the way for future crop improvement efforts in cereals (Kuang *et al.*, 2022).

Developing salinity tolerance in crops remains a complex challenge, as it involves multiple genes and intricate regulatory networks. Targeting a single gene is rarely sufficient, making genome editing approaches that can simultaneously modify several loci particularly valuable. In this context, *de novo* domestication emerges as a promising strategy to reprogram wild or underutilized species for stress resilience, including salt tolerance (Razzaq *et al.*, 2021). However, practical challenges, such as the need for efficient transformation systems, genotype-specific tissue culture protocols, and regulatory constraints, still limit its widespread application (Pattnaik *et al.*, 2023). Even so, genome editing stands out as a powerful tool in the breeder's toolkit—one that can work hand in hand with traditional approaches to build the next generation of resilient crops.

Resilient crops and their potential in saline environment

The increasing reliance on saline or low-quality water for irrigation has severely degraded arable land in many areas, making it necessary to explore alternative farming strategies. In areas facing increasing soil salinity, introducing salt-tolerant alternative crops is a key solution for sustaining agricultural productivity and supporting local economic growth. These crops provide farmers with diverse cultivation options, particularly when traditional crops become unprofitable due to high salinity in soil and water (Ismail *et al.*, 2019). Recently, the cultivation of alternative crops has been acknowledged as a viable strategy for ensuring nutritional adequacy and food sufficiency, particularly in ecologically vulnerable and evolving environments (Dagar *et al.*, 2016). This paper highlights several alternative crops and species that are essential for promoting food, nutrition, and income security, particularly for small-scale farmers operating in salt-affected regions. These crops range from moderately sensitive to highly tolerant varieties and include certain underutilized species such as halophytes. Below is an overview of alternative crops that have demonstrated the ability to maintain agricultural productivity under saline soil conditions.

Several fast growing, salt-resilient crops with dual use potential (as both forage and grain), particularly barley, sorghum, pearl millet, and brassica, have been successfully cultivated under saline field conditions, tolerating salinity levels as high as 15 dS m⁻¹. Likewise, oilseed crops such as canola and safflower have demonstrated resilience to saline conditions, with yield reductions limited to 12–15% under moderate salinity levels (10 dS m⁻¹) and reaching up to 30% under severe salinity stress (15 dS m⁻¹) (Dakheel *et al.*, 2015) (Table 1). Moreover, certain underutilized and orphan crops have also shown good productivity in harsh environments. For instance, salt-tolerant mustard varieties developed by the Central Soil Salinity Research Institute (CSSRI) in India have demonstrated the ability to yield between 1.18 to 1.73 tons of seeds per hectare when irrigated with water having salinity levels of up to 10 dS m⁻¹ (Dagar *et al.*, 2014). Barley has also been identified as a highly suitable crop for saline irrigation in

arid regions, yielding 2.46 tons of grain and 2.95 tons of straw per hectare with saline irrigation water (EC_{iw} 10 dS m⁻¹) (Rao *et al.*, 2017). Additionally, pearl millet has produced grain yields of 1.72–2.18 tons and fodder yields of 10.0–11.25 tons per hectare when cultivated with saline irrigation in agroforestry systems (Dagar, 2014). In contrast, staple crops like maize, rice, and wheat typically exhibit higher sensitivity to saline conditions, underscoring the value of neglected and underutilized crop species (NUCS) as viable alternatives for marginal environments. These crops tend to be more resilient and better suited to challenging growing conditions, such as poor soil fertility and water scarcity. NUCS not only play a vital role in food production, but also offer opportunities for local income generation through product diversification (Dagar, 2018). The strategic selection of crop species based on their potential to enhance food availability, alleviate poverty and strengthen ecological resilience is of

Table 1. Salt-tolerant crops suitable for saline environments

Crop/Species	Yield Performance	Reference
Barley (<i>Hordeum vulgare</i>)	Grain yield: 2.46 Mg ha ⁻¹ ; Straw yield: 2.95 Mg ha ⁻¹ at EC _{iw} 10 dS m ⁻¹	Dagar <i>et al.</i> (2014); Abdelrady <i>et al.</i> (2024)
Sorghum (<i>Sorghum bicolor</i>)	Dry matter yield: 11.1–31.9 Mg ha ⁻¹ (single-cut); 5.4–7.9 Mg ha ⁻¹ (multi-cut)	Dakheel <i>et al.</i> (2015); Calone <i>et al.</i> (2020)
Pearl millet (<i>Pennisetum glaucum</i>)	Grain yield: 1.72–2.18 Mg ha ⁻¹ ; Fodder yield: 10.0–11.25 Mg ha ⁻¹ under saline irrigation in agroforestry systems	Dagar (2014); Dhawi (2023)
Brassica spp.	Forage yield: 16.8–29.8 Mg ha ⁻¹	Dakheel <i>et al.</i> (2015); Ilyas <i>et al.</i> (2024)
Canola (<i>Brassica napus</i>)	Yield reduction: 12–15% at 10 dS m ⁻¹ ; up to 30% at 15 dS m ⁻¹	Dakheel <i>et al.</i> (2015); Ilyas <i>et al.</i> (2024)
Safflower (<i>Carthamus tinctorius</i>)	Grain yield: up to 2 Mg ha ⁻¹ ; Biological yield: up to 7 Mg ha ⁻¹	Fraj <i>et al.</i> (2013); Fatahiyan <i>et al.</i> (2025)
Mustard (<i>Brassica juncea</i>)	Seed yield: 1.18–1.73 Mg ha ⁻¹ under saline irrigation	Dagar <i>et al.</i> (2014); Sharaya <i>et al.</i> (2023)
Cluster bean (<i>Cyamopsis tetragonoloba</i>)	Seed yield reduction: 15% at 5 dS m ⁻¹ ; 24% at 10 dS m ⁻¹	Alinia <i>et al.</i> (2024)
Asparagus (<i>Asparagus officinalis</i>)	Spear yield: 36.3–159.2 g per plant at 15 dS m ⁻¹	Gao <i>et al.</i> (2021)
<i>Distichlis spicata</i>	Dry biomass: 10–15 Mg ha ⁻¹ under saline conditions	Rao <i>et al.</i> (2017)
<i>Paspalum vaginatum</i>	Dry biomass: 10–20 Mg ha ⁻¹ under saline conditions	Rao <i>et al.</i> (2017)
<i>Sporobolus virginicus</i>	Adapted to saline soils; specific yield data not available	Tada <i>et al.</i> (2019); Rao <i>et al.</i> (2017)
<i>Sporobolus arabicus</i>	Dry biomass: 10–15 Mg ha ⁻¹ under saline conditions	Tada <i>et al.</i> (2019); Rao <i>et al.</i> (2017)
Cotton (<i>Gossypium hirsutum</i>)	Yield decreases by 15% at 8–10 dS m ⁻¹ ; 55% at 18 dS m ⁻¹	An <i>et al.</i> (2025); Ren <i>et al.</i> (2021)
Wheat (<i>Triticum aestivum</i>)	Selection of salt-tolerant genotypes for better yield under saline conditions	Akram <i>et al.</i> (2025)
Rice (<i>Oryza sativa</i>)	Development of salt-tolerant varieties to sustain yield under saline conditions	Riaz <i>et al.</i> (2019)

paramount importance. However, many NUCS remain under-researched, necessitating further investigations to improve their yields and optimize cultivation techniques. By prioritizing high-potential crop species capable of meeting food and nutritional needs in marginal environments, the benefits of NUCS can be effectively realized.

Additionally, wild grasses, shrubs, and trees that are naturally adapted to extreme conditions such as drought and salinity have been explored for their potential use as forage and fuel sources (Shannon *et al.*, 2000). Halophytic perennial forage grasses, including species like *Distichlis spicata*, *Paspalum vaginatum*, *Sporobolus virginicus*, and *Sporobolus arabicus*, have been successfully cultivated on salt-affected lands. Research has shown that these grasses can accumulate significant amounts of salt in their leaves and stems while effectively excluding it at the root level, making them safe for livestock consumption. These grasses offer a sustainable solution for utilizing limited water resources to produce forage and help restore salt-degraded farms that are unsuitable for conventional crops (Rao *et al.*, 2017).

Pan-genomic analysis: advancing crop adaptation to stressful environments

Neo-domestication of crop plants, aided by advancements in pan-genomic techniques, offers a promising avenue to develop varieties with improved adaptability to salinity and other abiotic stresses, potentially transforming unproductive lands into cultivable areas. Historically, traditional breeding methods have been employed to select crop varieties exhibiting traits like enhanced yield, disease resistance, and resilience to environmental stresses. However, these methods rely on the genetic diversity present in domesticated crop species, which can be limited due to selective breeding practices. To overcome this limitation, pan genomics has emerged as a powerful tool, allowing the exploration of genetic diversity across entire species by assembling multiple genomes, including those of cultivated lines, landraces, and wild relatives of crop species (Della Coletta *et al.*, 2021). Unlike traditional reference genomes, which provide a single genome sequence for a

species, pan-genomes capture the complete genetic diversity within a species (Bayer *et al.*, 2020). By including structural variations (SVs), such as copy number variants (CNVs) and presence/absence variants (PAVs), pan-genomes provide a comprehensive view of the genetic repertoire, allowing researchers to investigate genotype-phenotype relationships in unprecedented detail. This approach has already been applied to several key crop species, including rice, wheat, soybean, and tomato, uncovering valuable information about the genetic foundations of traits like stress tolerance, disease resistance, and yield enhancement (Zhao *et al.*, 2020).

One of the main advantages of pan-genomics is its ability to detect structural variations that may not be captured by single reference genomes. SVs, including CNVs and PAVs, can significantly impact gene content, leading to variations in traits such as salinity tolerance (Hirsch *et al.*, 2014). CNVs refer to variations in the number of copies of a gene or genomic region, while PAVs are more extreme, where specific genes may be completely absent in some individuals (Danilevich *et al.*, 2020). These variations are particularly important in stress tolerance, influencing the expression of genes responsive to abiotic stresses like salinity, drought, and temperature extremes (Hirsch *et al.*, 2014). For instance, analysis of soybean pan-genome showed that approximately 20% of its genome is variable, consisting of genes linked to environmental adaptation, which could provide insights into stress tolerance mechanisms (Li *et al.*, 2018). Wild relatives of crop plants (CWRs) are an untapped reservoir of genetic diversity, harboring traits that have been lost or underutilized during domestication. CWRs often possess superior traits for stress tolerance, having evolved in diverse environments (Golicz *et al.*, 2016). Pan-genomics provides a platform to explore the genetic potential of CWRs by comparing their genomes with domesticated crop varieties (Tao *et al.*, 2019). For example, the *Brassica oleracea* pan-genome, which includes both cultivated varieties and wild relatives, revealed that close to 20% of its genes display CNVs and PAVs. These variable genes are functionally related to responses against cold, drought, salinity, and pathogens (Golicz *et al.*, 2016). Similarly, the

wheat pan-genome has uncovered genes involved in defense mechanisms and adaptation to environmental stresses, offering valuable information for improving stress tolerance in domesticated crops (Montenegro *et al.*, 2017). By incorporating the genetic diversity of CWRs into breeding programs, it becomes possible to reintroduce lost or underutilized traits, such as salinity tolerance, into modern crop varieties. This approach, known as neo-domestication, holds great promise for developing crops that can successfully grow in saline soils, thereby enhancing agricultural productivity in regions where traditional crops often underperform or fail (Bayer *et al.*, 2020).

Salt-affected lands pose a critical threat to global food production, as high salinity levels disrupt plant growth and reduce crop yields. Traditional methods for managing salt-affected lands, such as soil reclamation and salt-tolerant crops, have limited success. Pan genomics offers a new approach by identifying genetic variations related to salinity tolerance. For example, the rice pan-genome identified the *Sub1A* gene, which confers submergence tolerance (Schatz *et al.*, 2014). Pan-genomic studies have also identified loci linked to improved yield (*LTK*), and phosphorus stress (*Pup1*), highlighting their potential for managing salt-affected soils (Schatz *et al.*, 2014). Furthermore, pan-genomic analysis can offer a deeper understanding of genomic structures associated with stress tolerance. For example, the maize pan-genome revealed that 15-40% of the genome exhibits variability, with genes displaying PAVs linked to abiotic stress tolerance (Hirsch *et al.*, 2014).

The insights gained from pan-genomic research can be used to accelerate precision breeding for developing salt-tolerant crop varieties. Marker-assisted selection (MAS) enables breeders to identify and select individuals with desirable traits for breeding programs (Zhao *et al.*, 2020). Further, genome editing technologies, such as CRISPR-Cas9, can also be employed to neo-domesticate crops for salt-affected lands by introducing or enhancing specific traits. For instance, editing the *Sub1A* gene in rice can improve submergence tolerance, making crops more resilient to flooding. By integrating pan-

genomics with genome editing, it is possible to develop elite crop varieties specifically adapted to salt-affected soils, contributing to more sustainable agricultural practices (Khan *et al.*, 2020). Although the potential of pan-genomics to address challenges associated with salt-affected lands is evident, several issues persist. These include the need for comprehensive pan-genome assemblies for key crop species, particularly those cultivated in salt-affected regions. Furthermore, precise functional characterization of the variable genomic regions is critical for effective identification and utilization of candidate genes in crop improvement and breeding efforts. Interdisciplinary collaboration between geneticists, agronomists, and soil scientists is crucial to fully realize the benefits of pan genomics for managing salt-affected lands (Hübner *et al.*, 2019).

Conclusion

The continuous expansion of salt-affected soils worldwide is posing a serious threat to global food security and our ability to sustain a growing population. This calls for adoption of innovative and sustainable agricultural strategies that can develop stress-resilient crops in a directed and expedited manner. One promising solution gaining traction is neo-domestication, an approach that focuses on targeted domestication of wild and underutilized plant species by introducing key domestication traits while retaining their inherent stress tolerance. By harnessing the rich genetic diversity of crop wild relatives (CWRs) and lesser-known orphan crops, neo-domestication aims to reintroduce diversity and environmental adaptability into modern agriculture. Unlike traditional domestication, which is a long-drawn, multi-generational process, neo-domestication when combined with advances in molecular breeding and genome editing has the potential to accelerate crop improvement through rapid and precise incorporation of target traits. Breakthroughs such as high resolution pangenome assemblies have uncovered valuable genetic variations and stress-responsive alleles in both popular and underutilized crops. These insights, along with genome editing tools like CRISPR-Cas9, facilitate targeted modification of genes

regulating salt stress responses. While certain practical barriers, like limited transformation protocols and regulatory hurdles, still need to be addressed, the long-term potential of neo-domestication is compelling. By combining genetic exploration and modern biotechnological tools, this approach offers a viable path toward developing stress-tolerant crops and restoring productivity on saline and marginal lands.

References

- Abdelrady WA, Ma Z, Elshawy EE, Wang L, Askri SM, Ibrahim Z, Dennis E, Kanwal F, Zeng F and Shamsi IH (2024) Physiological and biochemical mechanisms of salt tolerance in barley under salinity stress. *Plant Stress* **11**: 100403
- Ahanger MA, Tomar NS, Tittal M, Argal S and Agarwal RM (2017) Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. *Physiology and Molecular Biology of Plants* **23**: 731-744.
- Ahmad R, Hussain S, Anjum MA, Khalid MF, Saqib M, Zakir I, Hassan A, Fahad S and Ahmad S (2019) Oxidative stress and antioxidant defense mechanisms in plants under salt stress. In: *Plant Abiotic Stress Tolerance: Agronomic, Molecular and Biotechnological Approaches* pp 191-205.
- Akram M, Ali Q, Ali S, El-Sheikh MA and Sarker PK (2025) Selection of salt-tolerant wheat genotypes for better yield considering physio-biochemical attributes and antioxidative defence potential: agronomic traits and stress tolerance indices. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science* **75(1)**: 2466433.
- Alinia M, Kazemeini SA, Meftahizadeh H and Mastinu A (2024) Alleviating salinity stress in *Cyamopsis tetragonoloba* L. seedlings through foliar application of silicon or melatonin in arid and semi-desert environments. *South African Journal of Botany* **174**: 347–359.
- Altpeter F, Springer NM and Bartley LE (2016) Advancing crop transformation in the era of genome editing. *Plant Cell* **28**: 1510–1520.
- An M, Huang X, Long Y, Wang Y, Tan Y, Qin Z, Ai X and Wang Y (2025) Salt tolerance evaluation and key salt-tolerant traits at germination stage of upland cotton. *Frontiers in Plant Science* **15**: 1489380.
- Bayer PE, Golicz AA, Scheben A, Batley J and Edwards D (2020) Plant pan-genomes are the new reference. *Nat. Plants* **6**: 914–920.
- Calone R, Sanoubar R, Lambertini C, Speranza M, Vittori Antisari L, Vianello G and Barbanti L (2020) Salt tolerance and Na allocation in *Sorghum bicolor* under variable soil and water salinity. *Plants* **9(5)**: 561.
- Dagar JC (2014) Greening salty and waterlogged lands through agroforestry systems. In: Dagar, JC, Singh AK and Arunachalam A (eds) *Agroforestry Systems in India: Livelihood Security & Environmental Services-Advances in Agroforestry* Vol 10, Springer Publishers, pp 333-344.
- Dagar J (2018) Utilization of Degraded Saline Habitats and Poor-quality Waters for Livelihood Security. *Sch. J. Food Nutr.* **1 (3)**-2018.” *SJFN. MS. ID* 115 (2018).
- Dagar JC, Lal K, Ram J, Kumar M, Chaudhari SK, Yadav RK, Ahamad S, Singh G and Kaur A (2016) Eucalyptus geometry in agroforestry on waterlogged saline soils influences plant and soil traits in North-West India. *Agriculture, Ecosystems & Environment* **233**: 33-42.
- Dagar JC, Pathak PS, Kaushal R and Chaturvedi OP (2014) Agroforestry systems in india: livelihood security & ecosystem services. *Indian Journal of Agroforestry* **18(2)**: 1-32.
- Dakheel A, Hussain I and Shabbir G (2015) Developing cropping sequence options for salt-affected rice-based production systems in the Nile. *Austin Journal of Plant Biology* **1(2)**: 1009.
- Datir S, Singh N and Joshi I (2020) Effect of NaCl-induced salinity stress on growth, osmolytes and enzyme activities in wheat genotypes. *Bulletin of Environmental Contamination and Toxicology* **104**: 351-357.
- Dawson IK, Powell W, Hendre P, Banèrè J, Hickey JM, Kindt R, Hoad S, Hale I and Jamnadass R (2019) The role of genetics in mainstreaming the production of new and orphan crops to diversify food systems and support human nutrition. *New Phytologist* **224(1)**: 37-54.
- Della Coletta R, Qiu Y, Ou S, Hufford MB and Hirsch CN (2021) How the pan-genome is changing crop genomics and improvement. *Genome Biol* **22**: 1–19.
- Dhawi F (2023) Molecular insights into the salt stress response of pearl millet (*Pennisetum glaucum*): pathways, differentially expressed genes and transcription factors. *Journal of Sustainable Agriculture and Environment* **2(4)**: 444–455.
- FAO. 2024. *Global Status of Salt-affected Soils – Main Report*. FAO Rome.
- Fatahiyan F, Najafi F and Shirkhani Z (2025) Enhancing salt stress tolerance in *Carthamus tinctorius* L. through selenium soil treatment: anatomical, biochemical, and physiological insights. *BMC Plant Biology* **25(1)**:100.
- Fernie AR and Yan J (2019) De novo domestication: an alternative route toward new crops for the future. *Molecular Plant* **12(5)**: 615-631.
- Gao H, Zhang X, Liang Y, Dong L, Han C and Cao Y (2021) Comprehensive evaluation of salt tolerance in asparagus germplasm accessions (*Asparagus officinalis* L.) at different growth stages. *Journal of Food Quality* **2021(1)**: 6626112.

- Golicz AA, Bayer PE and Barker GC (2016) The pangenome of an agronomically important crop plant Brassica oleracea. *Nat. Commun* **7**: 1-8.
- Gupta B and Huang B (2014) Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. *International Journal of Genomics* **2014**(1): 701596.
- Hameed A, Ahmed MZ, Hussain T, Aziz I, Ahmad N, Gul B and Nielsen BL (2021) Effects of salinity stress on chloroplast structure and function. *Cells* **10**(8): 2023.
- Hannachi S, Steppe K, Eloudi M, Mechi L, Bahrini I and Van Labeke MC (2022) Salt stress induced changes in photosynthesis and metabolic profiles of one tolerant ('Bonica') and one sensitive ('Black Beauty') eggplant cultivars (*Solanum melongena* L.). *Plants* **11**(5): 590.
- Hirsch CN, Foerster JM and Johnson JM (2014) Insights into the maize pan-genome and pan-transcriptome. *Plant Cell* **26**: 121–135.
- Hossain MS and Shah JSA (2019) Present scenario of global salt affected soils, its management and Importance of salinity research. *International Research Journal of Biological Sciences* **1**(1): 1-3.
- Hoyos V, Plaza G, Li X and Caicedo AL (2020) Something old, something new: Evolution of Colombian weedy rice (*Oryza* spp.) through de novo de-domestication, exotic gene flow, and hybridization. *Evolutionary Applications* **13**(8): 1968-1983.
- Hualpa-Ramirez E, Carrasco-Lozano EC, Madrid-Espinoza J, Tejos R, Ruiz-Lara S and Stange C, Norambuena L (2024) Stress salinity in plants: New strategies to cope with in the foreseeable scenario. *Plant Physiology and Biochemistry* 108507.
- Hübner S, Bercovich N and Todesco M (2019) Sunflower pan-genome analysis shows that hybridization altered gene content and disease resistance. *Nature Plants* **5**: 54–62.
- Hussain S, Hussain S, Ali B, Ren X, Chen X, Li Q, Saqib M and Ahmad N (2021) Recent progress in understanding salinity tolerance in plants: Story of Na⁺/K⁺ balance and beyond. *Plant Physiology and Biochemistry* **160**: 239-256.
- ismail am and horie t (2017) genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annual review of plant biology* **68**(1): 405-434.
- Ismail S, Rao NK and Dagar JC (2019) Identification, evaluation, and domestication of alternative crops for saline environments. *In: Research Developments in Saline Agriculture* pp 505-536.
- James C (1998) Global status and distribution of commercial transgenic crops in 1997. *Biotechnology and Development Monitor*.
- Jan R, Kim N, Lee SH, Khan MA, Asaf S, Lubna, Park JR, Asif S, Lee IJ and Kim KM (2021) Enhanced flavonoid accumulation reduces combined salt and heat stress through regulation of transcriptional and hormonal mechanisms. *Frontiers in Plant Science* **12**: 796956.
- Jiang C, Zu C, Lu D, Zheng Q, Shen J, Wang H and Li D (2017) Effect of exogenous selenium supply on photosynthesis, Na⁺ accumulation and antioxidative capacity of maize (*Zea mays* L.) under salinity stress. *Scientific reports* **7**(1): 42039.
- Kang YJ, Lee T, Lee J, Shim S, Jeong H, Satyawan D, Kim MY and Lee SH (2016) Translational genomics for plant breeding with the genome sequence explosion. *Plant biotechnology journal* **14**(4):1057-1069.
- Khan MZ, Zaidi SS e. A, Amin I and Mansoor S (2019) A CRISPR way for fast-forward crop domestication. *Trends in Plant Science* **24**(4): 293-296.
- Krug AS, Drummond EBM, Tassel DLV and Warschefsky EJ (2023) The next era of crop domestication starts now. *PNAS* **120** (14) e2205769120 <https://doi.org/10.1073/pnas.2205769120>.
- Kumar A, Singh S, Gaurav AK, Srivastava S and Verma JP (2020) Plant growth-promoting bacteria: biological tools for the mitigation of salinity stress in plants. *Frontiers in microbiology* **11**:1216.
- Lee C (2023) Climate change impacts on global food security. *In: Proceedings of the 7th International Conference of Recent Trends in Environmental Science and Engineering (RTESE 2023)*.
- Li C, Zong Y, Wang Y, Jin S, Zhang D, Song Q, Zhang R and Gao C (2018) Expanded base editing in rice and wheat using a Cas9-adenosine deaminase fusion. *Genome Biology* **19**: 1-9.
- Liu X, Xu X, Ji M, Amombo E and Fu J (2023) Growth, Photosynthesis, and gene expression of bermudagrass in response to salinity and shade stress. *Journal of the American Society for Horticultural Science* **148**(1): 1-8.
- Marsh JI, Hu H, Gill M, Batley J and Edwards D (2021) Crop breeding for a changing climate: integrating phenomics and genomics with bioinformatics. *Theoretical and Applied Genetics* **134**: 1677-1690.
- Mehta D and Vyas S (2023) Comparative bio-accumulation of osmoprotectants in saline stress tolerating plants: A review. *Plant Stress* **9**: 100177.
- Montenegro JD, Golicz AA and Bayer PE (2017) The pangenome of hexaploid bread wheat. *Plant Journal* **90**: 1007–1013.
- Mushtaq Z, Faizan S and Gulzar B (2020) Salt stress, its impacts on plants and the strategies plants are employing against it: A review. *Journal of Applied Biology and Biotechnology* **8**: 81-91.
- Myers SS, Smith MR, Guth S, Golden CD, Vaitla B, Mueller ND, Dangour AD and Huybers P (2017) Climate change and global food systems: potential impacts on food security and undernutrition. *Annual review of public health* **38**(1): 259-277.

- Nahar K, Hasanuzzaman M and Fujita M (2015) Roles of osmolytes in plant adaptation to drought and salinity. *In: Osmolytes and Plants Acclimation to Changing Environment: Emerging Omics Technologies* 37-68.
- Negrão S, Schmöckel SM and Tester M (2017) Evaluating physiological responses of plants to salinity stress. *Annals of Botany* **119**(1): 1-11.
- Pattnaik D, Avinash SP, Panda S. *et al.* (2023) Accelerating crop domestication through genome editing for sustainable agriculture. *J. Plant Biochem. Biotechnol* **32**: 688–704.
- Paul MJ, Nuccio ML and Basu SS (2018) Are GM crops for yield and resilience possible? *Trends in Plant Science* **23**(1): 10-16.
- Purugganan MD (2019) Evolutionary Insights into the nature of plant domestication. *Current Biology* **29**(14): R705-R714.
- Rao NK, McCann I, Shahid SA, Butt KUR, Araj B Al and Ismail S (2017) Sustainable use of salt-degraded and abandoned farms for forage production using halophytic grasses. *Crop and Pasture Science* **68**(5): 483-492.
- Razzaq A, Kaur P, Akhter N, Wani SH and Saleem F (2021) Next-generation breeding strategies for climate-ready crops. *Frontiers in Plant Science* **12**: 620420.
- Razzaq A, Saleem F, Wani SH, Abdelmohsen SAM, Alyousef HA, Abdelbacki AMM, Alkallas FH, Tamam N and Elansary HO (2021) De-novo domestication for improving salt tolerance in crops. *Frontiers in Plant Science* **12**: 681367.
- Razzaq A, Wani SH, Saleem F, Yu M, Zhou M and Shabala S (2021) Rewilding crops for climate resilience: Economic analysis and de novo domestication strategies. *Journal of Experimental Botany* **72**(18): 6123-6139.
- Ren F, Yang G, Li W, He X, Gao Y, Tian L, Li F, Wang Z and Liu S (2021) Yield-compatible salinity level for growing cotton (*Gossypium hirsutum* L.) under mulched drip irrigation using saline water. *Agricultural Water Management* **250**:106859.
- Schatz MC, Maron LG and Stein JC (2014) Whole genome de novo assemblies of three divergent strains of rice, *Oryza sativa*, document novel gene space of aus and indica. *Genome Biology* **15**: 506.
- Shahzad B, Shabala L, Zhou M, Venkataraman G, Solis CA, Page D, Chen ZH and Shabala S (2022) Comparing essentiality of SOS1-mediated Na⁺ exclusion in salinity tolerance between cultivated and wild rice species. *International Journal of Molecular Sciences* **23**(17): 9900.
- Shannon MC, Grieve CM, Lesch SM and Draper JH (2000) Analysis of salt tolerance in nine leafy vegetables irrigated with saline drainage water. *Journal-American Society for Horticultural Science* **125**(5) :658-664.
- Sharaya R, Gill R, Naeem M, Tuteja N and Gill SS (2023) Exploring salt tolerance in Indian mustard [*Brassica juncea* (L.) Czern. & Coss.] genotypes: a physiological and biochemical perspective. *South African Journal of Botany* **160**: 446–455.
- Shehu Z, Ayuba SA, Bello ZH, Abubakar M and Shehu A (2023) Comparative studies on the effect of salinity and drought stress on enzymatic antioxidant defense system of two maize (*Zea mays* L.) varieties. *Caliphate Journal of Science and Technology* **5**(2): 140-147
- Sheldon AR, Dalal RC, Kirchhof G, Kopittke PM and Menzies NW (2017) The effect of salinity on plant-available water. *Plant and Soil* **418**: 477-491.
- Shelef O, Weisberg PJ and Provenza FD (2017) The value of native plants and local production in an era of global agriculture. *Frontiers in Plant Science* **8**: 2069.
- Singh P, Choudhary KK, Chaudhary N, Gupta S, Sahu M, Tejaswini B and Sarkar S (2022) Salt stress resilience in plants mediated through osmolyte accumulation and its crosstalk mechanism with phytohormones. *Frontiers in Plant Science* **13**: 1006617.
- Singh P, Kumar V, Sharma J, Saini S, Sharma P, Kumar S, Sinhmar Y, Kumar D and Sharma A (2022) Silicon supplementation alleviates the salinity stress in wheat plants by enhancing the plant water status, photosynthetic pigments, proline content and antioxidant enzyme activities. *Plants* **11**(19): 2525.
- Singh M, Singh VP and Prasad SM (2016) Responses of photosynthesis, nitrogen and proline metabolism to salinity stress in *Solanum lycopersicum* under different levels of nitrogen supplementation. *Plant Physiology and Biochemistry* **109**: 72-83.
- Tada Y, Kawano R, Komatsubara S, Nishimura H, Katsuhara M, Ozaki S, Terashima S, Yano K, Endo C, Sato M and Okamoto M (2019) Functional screening of salt tolerance genes from a halophyte *Sporobolus virginicus* and transcriptomic and metabolomic analysis of salt tolerant plants expressing glycine-rich RNA-binding protein. *Plant Science* **278**: 54–63.
- Tao Y, Zhao X, Mace E, Henry R and Jordan D (2019) Exploring and exploiting pan-genomics for crop improvement. *Molecular Plant* **12**: 156–169.
- Tru'că M, Gâdea 'tefania, Vidican R, Stoian V, Vâtcă A, Balint C, Stoian VA, Horvat M and Vâtcă S (2023) Exploring the research challenges and perspectives in ecophysiology of plants affected by salinity stress. *Agriculture* **13**(3): 734.
- Usadel B, Tohge T and Scossa F (2018) The genome and metabolome of the tobacco tree, *Nicotiana glauca*: a potential renewable feedstock for the bioeconomy. *BioRxiv* 351-429.
- Wang M, Li W and Fang C (2018) Parallel selection on a dormancy gene during domestication of crops from multiple families. *Nature Genetics* **50**(10): 1435-1441.

- Wani SH, Kumar V, Khare T, Guddimalli R, Parveda M, Solymosi K, Suprasanna P and Kavi Kishor PB (2020) Engineering salinity tolerance in plants: progress and prospects. *Planta* **251**: 1-29.
- Xu B, Hrmova M and Gilliam M (2020) High affinity Na⁺ transport by wheat HKT1;5 is blocked by K⁺. *Plant Direct* **4**(10): e00275.
- Yadav SP, Bharadwaj R, Nayak H, Mahto R, Singh RK and Prasad SK (2019) Impact of salt stress on growth, productivity and physicochemical properties of plants: A review. *International Journal Of Chemical Studies* **7**(2): 1793-1798.
- Zahra N, Al Hinai MS, Hafeez MB, Rehman A, Wahid A, Siddique KHM and Farooq M (2022) Regulation of photosynthesis under salt stress and associated tolerance mechanisms. *Plant Physiology and Biochemistry* **178**: 55-69.
- Zhang P, Senge M and Dai Y (2016) Effects of salinity stress on growth, yield, fruit quality and water use efficiency of tomato under hydroponics system. *Reviews in Agricultural Science* **4**: 46-55.
- Zhao J, Bayer PE, Ruperao P, Saxena RK, Khan AW, Golicz AA, Nguyen HT, Batley J, Edwards D and Varshney RK (2020) Trait associations in the pangenome of pigeon pea (*Cajanus cajan*). *Plant Biotechnology Journal* **18**: 1946–1954.
- Zhao C, Zhang H, Song C, Zhu JK and Shabala S (2020) Mechanisms of plant responses and adaptation to soil salinity. *Innovation* **1**(1).

Received: January 9, 2025; Accepted: June 27, 2025