



***Prosopis juliflora* and *Vachellia nilotica*: Boon for Salt-affected Land and Livelihood Security-A Review**

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Abstract

Tree species *Prosopis juliflora* and *Vachellia nilotica* are nitrogen fixers besides important source of biomass production on degraded salt-affected lands. These are remarkably well adapted to the saline areas through natural selection and traditional breeding. These trees are playing a vital role as a source of fuel, small timber, wood and fodder (dry season) for sustaining the livelihoods of the arid and semi-arid area. Thus, genetic improvement of these trees can be potential alternative for restoring soil health for salt-affected soils for further yield improvement by using conventional and modern approaches.

Key words: Agroforestry, *Prosopis juliflora*, *Vachellia nilotica*, Rehabilitation of soil, Salt-affected soils

Introduction

Prosopis juliflora and *Vachellia nilotica* (syn. *Acacia nilotica*) have prominent effects on soil health in arid and semi-arid regions. Being leguminous species, these trees are capable of nitrogen fixation along with biomass production (Matinkhah *et al.*, 2015). The deterioration of global climate has increased the frequency of abiotic stresses like drought, heat wave, and salinization (Easterling *et al.*, 2000); hence, agricultural productivity and soil health are facing a greater challenge due to these environmental stresses. Both experts and research scholars worldwide are of the opinion that breeding of stress-tolerant crops with higher yields, improved qualities and agroforestry management can be an effective strategy to face greatest challenges by modern agriculture (Takeda and Matsuoka, 2008).

Soil salinity is a major factor which vitiates agricultural productivity globally (Epstein *et al.*, 1980). Efforts to improve crop performance under salinity have been pernicious owing to its multigenic and quantitative nature (Vinocur and Altman, 2005). The trees from salinity-prone areas have evolved in a selective environment that

privileged salt-adaptive trait. Furthermore, the resulting salt-adaptive traits have evolved in locations where none of model crop/plant is found naturally. It can, therefore, be assumed that these wild species possess many as yet unknown salinity tolerance genes and processes. Understanding salinity tolerance mechanisms in wild tree/plant species of extreme climate, and harnessing this knowledge to develop crops with enhanced salt stress tolerance carry greater importance of “Learning from nature’s approach”. There are several tree species found in extreme saline areas. *Prosopis juliflora* and *Vachellia nilotica* are most important trees which can be grown in degraded salty or established using saline waters that are generally not advisable for agriculture, help to purify these waters, and their roots fix heavy metals with a bacterial filter. Many of them are highly resistant to biotic and abiotic stresses prevalent globally and greater ecological value. They are excellent source of fodder for livestock, fuel, provide shelter for fauna, cheap construction material and basketry. The genera *Prosopis* and *Vachellia* contain some of the most widespread and important tree species in the arid and semi-arid zones of the world and

sometimes back it was estimated that different species of these two genera occupy almost 3.1 million square kilometers (Griffith, 1961).

Prosopis juliflora is one of the most economically and ecologically important tree species in arid and semi-arid zones of the world because of its high nitrogen fixing potential in very dry areas and in drought seasons and also because of it provides shelter and food to many species of animals on its nectar, pollen, leaves and fruits. The plants of *Prosopis juliflora* are highly valued for windbreaks, soil-sand stabilizers, living fences, fuel wood and animal feed. These uses, together with fast growth, drought resistance and salt tolerance have led to its introduction in many arid zones.

This review focuses on the potential of *P. juliflora* and *V. nilotica* as sources for genetic improvement. These are often remarkably well adapted to their environment through natural selection and traditional breeding. Their relatives provide a resource for mining novel traits for the genetic improvement of cultivated crops that are vulnerable to environmental stress and providing sustainable alternatives for improving crop production in saline soils.

Potential of *Prosopis* and *Vachellia* in Rehabilitating Salt-affected Soils

P. juliflora and *V. nilotica* on salt-affected land have given the chance to produce timber, fuel and biomass for energy on land that is of little economic value for food production. Thus, one of the major drawbacks of the current production of biomass for energy: the competition with food production is avoided. With growing populations, increasing demand for basic resources (food, fiber and shelter) is growing hence these challenges are providing new opportunities for the salt-affected lands which occur in many arid, semiarid and even sub-humid areas.

The world's salt-affected soils are mostly degraded and decertified, deficient in soil nutrients, vegetation cover and biodiversity. Productivity enhancement of salt-affected soils and water resources through crop-based management has the potential to transform them from stress prone into productive. *P. juliflora* and *V. nilotica* has agricultural significance in terms of

their local utilization on the farm. Therefore, crop diversification systems based on these salt-tolerant plant species are likely to be the key to future agricultural and economic growth in regions where salt-affected soils exist and saline water is used for irrigation (Qadir *et al.*, 2008). Research has shown the usefulness of different *Prosopis* and *Vachellia* species in rehabilitating and protecting various soil types in various parts of the tropical arid and semi-arid zones and agricultural practices can be successfully re-introduced.

Prosopis is potentially useful for rehabilitating degraded saline soils due to high temperatures and irregular precipitation in dryland ecosystems. *Prosopis* planted on degraded sodic soils increases soil fertility through adding to and increasing the soil organic C, available nitrogen, phosphorus, exchangeable K, Ca and Mg levels. In addition, decreases in the exchangeable Na level, pH and EC as well as improvement in water infiltration and biomass accumulation have a positive effect on the rehabilitation of sodic soils through the improvement of nutrient cycling and detoxifying sodicity. *Prosopis juliflora* also improved, germination, survival, plant growth, grain yield and crop productivity of wheat (Bhojvaid *et al.*, 1996; Bhojvaid and Timmer, 1998; Garg, 1998; Maliwal, 1999).

Similarly, *Vachellia nilotica* (syn. *Acacia nilotica*) is an important multipurpose, leguminous tree species, grown widely under agroforestry systems. It is a valuable source of, timber, gum and medicines, fodder, fuel. It also contributes to nutrient recycling enhanced soil water infiltration, reduced evaporation and enhanced plant productivity for further-enhanced soil quality of salt-affected areas. *Vachellia* plantation plot showed more advanced rehabilitation in the soil microbial functions represented by soil dehydrogenase activity when compared with natural forest which was found progressing towards a full restoration of the degraded land to its original conditions (Doi and Ranamukhaarachchi, 2013; Gupta *et al.*, 2019). Consecutive plantings of *Vachellia* hybrid on degraded and abandoned salt-affected land can lead to changes in some soil properties. Total soil carbon, total nitrogen, exchangeable calcium,

magnesium and sodium were significantly higher compared with abandoned land. Electrical conductivity was significantly higher while bulk density, $\text{pH}_{\text{CaCl}_2}$ and $\text{pH}_{\text{H}_2\text{O}}$ were significantly lower in plantations than abandoned land (Dong *et al.*, 2014). A summary of morpho-physiological traits and mechanisms of salt tolerance in some *Prosopis* and *Vachellia* spp. is given in Table 1.

Global Perspective of Conventional and Molecular Research in *Prosopis* and *Vachellia*

In the figure 1, it has been summarized the established conventional and molecular breeding techniques for salt tolerance in *P. juliflora* and *V. nilotica* and reviewed some of the case study. Trees of the genus *Prosopis* followed by *Vachellia* are to

Table 1. The traits and mechanisms of salt tolerance in some *Prosopis* and *Vachellia* species

Sr. no.	Traits/mechanism	Reference
1	Physiological and biochemical mechanisms of salt tolerance	
a.	Retrieving Na^+ from the xylem, compartmenting Na^+ in vacuoles of cortical cells, and effluxing of Na^+ back to the soil	Roy <i>et al.</i> , 2014; Arce <i>et al.</i> , 1990; Ahmed, 1991;
b.	Accumulating osmoprotective compounds (proline, amino acids and sugars) (<i>Vachellia auriculiformis</i>)	Ahmad <i>et al.</i> , 1994; Ala <i>et al.</i> , 1995
2	Antioxidant enzyme and ion homoeostasis for salt tolerance	
a.	Higher rates of <i>catalase</i> and <i>glutathione reductase</i> activities	Morais <i>et al.</i> , 2012;
b.	Higher K^+/Na^+ ratio (<i>Vachellia longifolia</i> and <i>Prosopis cineraria</i>)	Ramoliya <i>et al.</i> , 2006; Cushman and Bohnert, 2000; Jithesh <i>et al.</i> , 2006
3	Ion homoeostasis for salt tolerance	
a.	Na^+ exclusion	Marcar <i>et al.</i> , 1991;
b.	Low shoot Na^+ and Cl^- concentrations (dry weight basis) and high phyllode succulence (<i>Vachellia ampliceps</i> and <i>Prosopis</i> spp.)	Virginia and Jarrell, 1983
4	Change in physico-chemical and biological properties of soil (Hardy vigorous root system that breaks the barrier of clay and loosens the subsoil, thus increases the permeability, water holding capacity, infiltration rate and hydraulic conductivity of soil, downward translocation of sodium increases cation exchange capacity and decrease SAR) (<i>Prosopis glandulosa</i> , <i>Prosopis juliflora</i> and <i>Vachellia nilotica</i>)	Virginia and Jarrell, 1983; Basavaraja <i>et al.</i> , 2007; Behera, <i>et al.</i> , 2015
5	Osmotic and ionic balancing for salt tolerance	
a.	Balance among Na accumulation and compartmentation in vacuoles	Reginato <i>et al.</i> , 2012;
b.	Maintaining a high degree of K/Na discrimination~ normal Ca levels in leaves	Llanes <i>et al.</i> , 2013;
c.	Osmotic balance and protection by compatible solutes such as proline, polyols and polycations such as polyamines under salt stress (<i>Prosopis strombulifera</i>)	Reginato <i>et al.</i> , 2014
6	Root system architecture	
a.	The smaller Root diameter with fewer cortex layers and a reduction of the vascular system	Serrato Valenti <i>et al.</i> , 1991; Schreiber <i>et al.</i> , 1999;
b.	Precocious suberization and (or) lignification of endodermal cells resulted in a discernible endodermis, with Casparian strips much closer to the root tip	Shannon <i>et al.</i> , 1994;
c.	Increase in the size of phloem parenchyma cells as well as the parenchyma originating from the pericycle to regulate the internal concentration of solutes and protect the cytoplasm from toxic levels of ions by storing them in the vacuole	Reinoso <i>et al.</i> , 2004
d.	Phellem development by the roots of tolerant plants (<i>Prosopis tamarugo</i> and <i>Prosopis strombulifera</i>)	
7	Salt responsive genes expression	
a.	Presence of salt tolerant gene NHX1, Catalase (CAT), Glutathione reductase (GR), Ascorbate peroxidase (APX) and Peroxidase (POX) and their overexpression in saline conditions	Morais <i>et al.</i> , 2012 Shinozaki <i>et al.</i> , 2003 Fall <i>et al.</i> , 2016
b.	Tonoplast associated Na^+/H^+ antiporter makes able to sequester the Na^+ in the vacuole enhance adaptation to salinity (<i>Senegalia senegal</i> , <i>Vachellia seyal</i> , <i>Prosopis juliflora</i> , <i>Vachellia longifolia</i> , <i>Prosopis alba</i>)	Beritognolo <i>et al.</i> , 2007

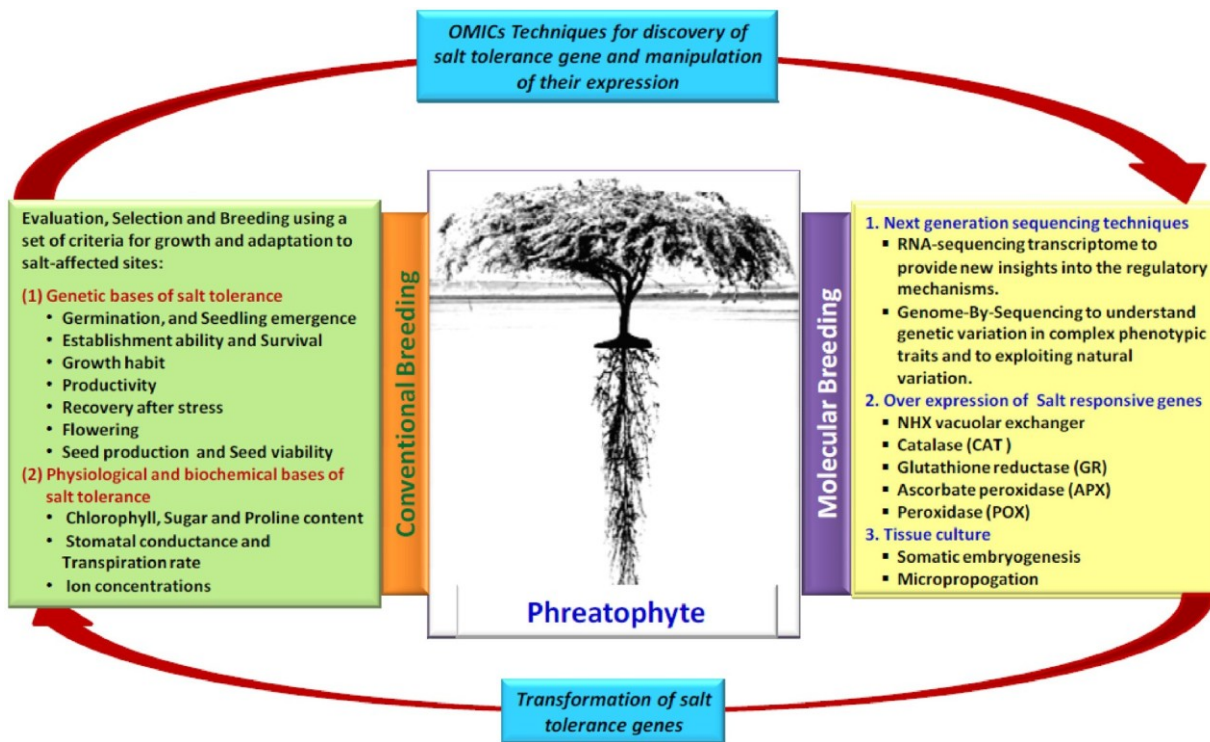


Fig. 1 A schematic diagram summarizing the conventional breeding and molecular breeding techniques for salt tolerance in *Prosopis juliflora* and *Vachellia nilotica*

be highly promising for the rehabilitation of salt lands. The trace nutrient composition like Fe, Mn, Zn and Cu of the shoots, make *Prosopis* species a highly important for the development of alkali soils. Mesquite (*Prosopis*) plantation with Kallar grass (*Leptochloa fusca*) for two years, reduced soil pH and EC significantly. Average pH of surface soil came down from 10.4 to 9.6 and electrical conductivity decreased from 2.4 to 0.5 dS m⁻¹ and also improved organic carbon and available N contents. The grass improved water infiltration rates and moisture storage in the lower layers of the profile (Singh *et al.*, 1988). This mixed plantation improved permeability of deflocculated alkali soils and helped in their amelioration, downward movement of water and the addition of organic matter (Singh, 1995).

A greenhouse experiment was carried out on the survival and growth of *P. juliflora* and *V. nilotica* to determine the effect of water salinity with four water salinity levels EC_{iw} 2.5, 6.45, 12.80, and 19.30 dS m⁻¹. *P. juliflora* tolerated soil salinity up to EC_e 39.5 dS m⁻¹ and *V. nilotica* up to 44.9 dS m⁻¹ when irrigated with water salinity of 12.80 dS m⁻¹. Strong correlations (r²) were observed between

soil salinity and plant biomass which indicated a significant decrease in biomass with an increasing soil salinity resulting from saline irrigation (Sharma *et al.*, 2010). Another studied conducted to measure the salt tolerance of *P. juliflora* using germination, growth and physiological responses to salinity stress with seven concentrations of NaCl (0, 86, 171, 257, 342, 428, and 514 mM) on Petri dishes containing water agar (0.9%, w/v) in greenhouse conditions. Results showed that germination rate was higher than 85% at 257 mM. However, it decreased at 342 mM with a 20% reduction.

Further, to assess plants growth and physiological responses, seedlings were cultivated individually in plastic bags containing non-sterile soil and irrigated with saline water having 0, 86, 171 and 257 mM NaCl. Four months after, the results showed that for all species, the salinity reduced significantly the height, the collar diameter, the shoot and root dry biomass as well as the total chlorophyll, K⁺ and K⁺/Na⁺ ratio whereas proline content, Cl⁻ and Na⁺ accumulation in leaves were increased (Fall *et al.*, 2016). *Prosopis juliflora* plantation over ten years

significantly decreased pHs, ECe, saturated extract cations like Ca, Mg and K content and anions like CO₃, HCO₃, SO₄ and Cl. The sodium adsorption ratio (SAR) and exchangeable sodium percentage (ESP) reduced whereas, organic carbon, cation exchange capacity (CEC), available N, P₂O₅ and K₂O increased as compared to barren land (Basavaraja *et al.*, 2007; Dave *et al.*, 2013). Genetic diversity of six *Prosopis* populations based on random amplified polymorphic DNA markers showed that molecular variation was larger within populations than between population which is attributed to their geographical separation and multiple introductions while the low variation within populations is due to gene flow between individuals within a population (Muturi *et al.*, 2012).

Characterization of genes that contribute to combating abiotic stress, construction and analysis of a cDNA library of *P. juliflora* genes is reported that random expressed sequence tag (EST) sequencing of 1750 clones produced 1467 high-quality reads. These clones were classified into functional categories, and BLAST comparisons revealed that 114 clones were homologous to genes implicated in stress responses and included heat shock proteins, metallothionein, lipid transfer proteins, and late embryogenesis abundant proteins (George *et al.*, 2007). It was also found that salt tolerance genes (NHX1), which allow *P. juliflora* to be considered as salt tolerant and seemed to be potential species for the restoration of salt-affected land. Studies using morphological characters, isoenzymes, seed protein electrophoresis and molecular markers have shown the occurrence of intra- as well as inter-series hybrids (Pasicznik *et al.*, 2001).

Single nucleotide polymorphisms (SNPs) at candidate genes involved in abiotic stress in *Prosopis* species and their hybrids was identified by Pomponio *et al.*, (2014). Partial sequences of 6 candidate genes were amplified (2107bp) on *P. chilensis*, *P. flexuosa* and hybrids, consisting 1234bp of coding and 873bp of non-coding regions. The average SNP frequency was one per 84bp in *P. chilensis*, one per 51bp in *P. flexuosa* and one per 41bp in hybrids. In comparison with *Prosopis juliflora*, the SNP frequency from ESTs library 1.60

SNPs/100bp result intermediate between *P. flexuosa* and hybrids. SNP frequency found in *Prosopis* species was lower in coding regions than in non-coding regions and are mostly synonymous. The relative rates of development of the high throughput computational methods for the detection of SNPs (Single Nucleotide Polymorphism) and small *indels* (insertion/deletion) has gained wide applications in the field of the molecular markers (Sablok and Shekhawat, 2008). These SNP markers identified in candidate genes can be use to estimate genetic diversity related to adaptive variation of natural populations, as complement to other neutral molecular markers or association mapping for identification of genomic regions that controlled traits like drought stress response (Mottura, 2006).

Molecular techniques are very useful in characterization and estimation of genetic relationship among different species of *Vachellia* which is lacking in India. Cross transferability of SSRs from *Vachellia tortilis*, *V. senegal* and *V. koa* were highly transferable in *V. nilotica*. Primers showed amplification with an average of 1.36 alleles per locus. Jaccard's similarity coefficient showed a high level of diversity (Yadav *et al.*, 2016). Based on molecular phylogenetic analysis, *V. pendula*, *V. salicina*, *V. victoriae* and *V. stenophylla*, had been identified as salt tolerant for saline land reclamation using nuclear ribosomal DNA markers ITS and ETS (Joseph *et al.*, 2013; Bui *et al.*, 2014). Highest genetic diversity was reported between and within *V. aulacocarpa* based on information derived from the RAPD analysis of nuclear DNA and SSCP (single strand conformation polymorphism) analysis of chloroplast DNA (Widyatmoko *et al.*, 2010). Reconstruction of phylogeny for evaluation of genetic relationship among *Vachellia* using Internal transcribed spacer sequence of nrDNA (nrDNA-ITS) found this gene locus helpful in evaluating the genetic relationship (Alkalabi, 2015). The genetic diversity assessment using Inter Simple Sequence Repeats (ISSR) in *V. auriculiformis* revealed that mean polymorphism was 85.5% and exhibited higher gene diversity (Shanthi and Priya, 2015). However, genetic variability analysis of nine *V. nilotica* subspecies of various origins using 166 RAPD polymorphic markers revealed large

differences between subspecies but geographic distances and genetic distances were not correlated (Ndoye-Ndir *et al.*, 2008). Microsatellite primers developed from an enriched library of clones sequenced were initially tested on the individual on nine *V. nilotica* ssp. *indica* individuals. Five microsatellite loci were found important to determine the genetic origin and extent of genetic diversity of *V. nilotica* (Wardill *et al.*, 2004).

Rajput *et al.* (2014) studied in 15 provenances of India for salt tolerance of *Vachellia*. The solutions of different compound like sodium chloride, sodium bi-carbonate, calcium chloride, magnesium sulphate and calcium sulphate was prepared with five level of salinity concentration, which have electrical conductivity of 3, 6, 9, 12 and 15 dS m⁻¹, respectively. EC 15 dS m⁻¹ was found most deleterious to the seed germination of *Vachellia* in all the provenances.

Greater efforts have been devoted to breeding crop genotypes with salt tolerant traits in the past few decades. Mainly two approaches have been employed to this process. One is classical breeding methods such as wide-cross hybridization and mutation breeding, which often brings about unpredictable results. Another is to identify the genetic loci that are related to osmotic stress physiology viz.; ion homeostasis, metabolic adjustment including hormone regulation, growth control and injury control (Zhu, 2002) and introducing these novel exogenous genes in to crops to alter the expression levels of endogenous genes for improving salt tolerance.

Since conventional breeding approaches have marginal success due to the complexity of salt tolerance traits (Yamaguchi and Blumwald, 2005), therefore, deciphering the molecular mechanisms by which plants perceive and transduce salt stress signals to cellular machinery to initiate adaptive responses is a prerequisite for identification of the candidate genes and pathways to engineer salt tolerant genotypes (Ray *et al.*, 2009; Heidary and Amiri, 2010; Sanchez *et al.*, 2011).

Significant progress has been made to unravel the molecular mechanisms of abiotic stress responses in plants through high throughput sequencing and functional genomics tools like genome by sequencing and transcriptome analysis.

A number of key genes involved in salt tolerance have been identified and validated till date, which can be classified into two categories: functional genes and regulatory genes (Shinozaki *et al.*, 2003). Functional genes encode important enzymes and metabolic proteins like detoxification enzyme, water channel, ion transporter and late embryogenesis abundant (LEA) protein, which directly protect cells from salt stresses. Regulatory genes encode various regulatory proteins including transcription factors, protein kinases and protein phosphatases, which regulate signal transduction and gene expression in the salt stress responses.

P. juliflora and *V. nilotica* have developed sophisticated systems for responding to salt stress during their long life-spans. Physiological and molecular analyses enabled us to better understand their responses, and to determine the potential and effective genes under field conditions. Genome sequences have provided access to essential information on gene products and their function, transcript levels, putative *cis*-acting regulatory elements and alternative splicing patterns. Here we are elucidating our perspective on research directions for development of salt tolerant crop genotypes using precious and unexploited gene reservoir *i.e.* *P. juliflora* and *V. nilotica* in near future as:

Genetic analysis and physiology of salt stress responses

In order to fully assess salt stress responses at the whole-plant level, better gain insight into tree stress physiology, water and ion transport, growth cycles and ability to recover from salt stress environment are needed. Complete understanding of genes that can be used for *P. juliflora* and *V. nilotica* improvement has been hampered by their recalcitrance to genetic analyses. An approach involving genetics, genomics and phenomics is necessary to understand unexplored mechanisms of salt stress tolerance in these plants and manipulation take place to overcome salt stress (Harfouche *et al.*, 2014).

Systems-biology approaches

Recent advances in the areas of genomics, digital imaging and computational biology, equanimous to use systems-biology approaches for elucidating

the molecular mechanisms of salt stress in *P. juliflora* and *V. nilotica* at whole-plant level. In the context of the whole tree, integrating data collected at different levels into networks may uncover complex molecular mechanisms and pathways that underpin the abiotic stress response. Ultimately, this holistic approach will enhance our understanding of salt stress responses (Harfouche *et al.*, 2014).

Next-generation sequencing: functional genomics

Next-generation sequencing techniques can provide ready access to transcriptome profiling and replaced microarrays as the tool of choice for genome-wide transcriptome studies. RNA-sequencing will also provide new insights into the regulatory mechanisms. Nevertheless, improvements are still needed to overcome problems related to multireads and splice variants. Next-generation genomics *e.g.* Genome-By-Sequencing will also facilitate to understand genetic variation in complex phenotypic traits (Harfouche *et al.*, 2014). This opens the door to exploiting natural variation of *P. juliflora* and *V. nilotica*.

Phenomics

Heterogeneous conditions of soil salinity and unpredicted climate change will make it challenging to conduct field tests for salt stress tolerance in *P. juliflora* and *V. nilotica*. An amalgam of approaches included careful attention to variation in field conditions, and extensive testing in both the greenhouse and the field, likely to be needed to precise phenotyping. Relating sequence information to the phenotype of plants is critical for the identification and characterization of genes conditioning salt tolerance traits. However, next-generation phenomics platforms will be contributed most significantly to abiotic stress tolerance are being quantified with increasing ease of conducting experiments (Harfouche *et al.*, 2014).

Conclusion

Keeping in view the importance of bio-reclamation, *P. juliflora* and *V. nilotica* are appropriate trees for rehabilitation and reclamation of salt-affected lands. These have the potential for fuel, fodder and timber production

from most degraded lands. The agroforestry practice and management involving these trees appears to be promising for exploiting those salt lands which cannot be readily reclaimed through conventional techniques. This may help in reducing the hunger of billions and revolutionize the economies of developing tropical and subtropical countries.

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