

Salt stress in pulses: A learning from global research on salinity in crop plants

Rekha Joshi¹, Naleeni Ramawat¹, Jyoti Jha², Kumar Durgesh*, Madanpal Singh², Akshay Talukdar, S. M. S. Tomar and Dharmendra Singh*

Division of Genetics, ²Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi 110 012; ¹Amity Institute of Organic Agriculture, Amity University, Uttar Pradesh, Sector 125, Noida 201 313, Uttar Pradesh

(Received: August 2020; Revised: March 2021; Accepted: April 2021)

Abstract

Pulse crops are overly sensitive to salinity stress as compared to cereals and other crops. The growth, development and yield of the pulses are severely affected by high concentration of salts accumulated in the soil due to inadequate drainage or other reasons. However, some of the pulse species have developed adaptive mechanism to overcome the salinity stress and hence, thorough screening of the germplasm through hydroponics or field testing is essential to identify the potential genotypes. Several cost-effective techniques of mitigating the salt stress including the physical, chemical and biological approaches have been analyzed and discussed. The mechanism of salinity stress and plant's response towards changes in morphological, physiological, biochemical and molecular features have been delineated in detail. Effective breeding approaches and progress in development of salt tolerant pulse crops have been highlighted. However, current leads in understanding the mechanism of salt stress and the genotypes developed may not be sufficient to enhance the productivity and availability of the pulse crops. The kind of efforts needed to improve pulse crops are rare and hence, require special attention. Therefore, integration of the traditional and modern breeding approaches including 'omics' technologies and biological agents are needed to address the issue of salt stress effectively. The development of stress tolerant pulse crops through genetic engineering has also shown promise. High-quality genotypic and phenotypic data including high throughput imaging approaches might lead to proper understanding of the mechanism of salt tolerance which in turn would help designing effective breeding programme for the development of pulse crops tolerant to salinity stress.

Key words: Pulse crops, salinity stress, tolerance, mechanism, genetics

Introduction

Most of the intrinsic chemical, physical and biological stress conditions are the result of climate change and soil-forming factors such as weathering over very long term in which prolonged leaching, impeded drainage and possible accumulation of organic, inorganic and soluble salts have led to infertile soil conditions. Various environmental stresses such as high winds, extreme temperatures, acidity, aluminium toxicity, soil salinity and alkalinity (sodicity), drought and flood have affected the production and cultivation of agricultural crops. Among these, soil salinity is one of the most devastating environmental stresses, which causes major reduction in cultivated land area, crop productivity and quality (Eswaran et al.2003; Yamaguchi and Blumwald 2005; Shahbaz and Ashraf 2013; Singh et al. 2011a, b; 2014). The salts that accumulates in the soil includes chlorides and sulfates of sodium, calcium and magnesium. More than half of the saline soils throughout the globe contain sodic alkaline salts (FAO; http://www.fao.org/ag/agl/agll/spush/intro.htm). Therefore, salt-induced land degradation is a global issue.

A saline soil is generally defined as one in which the electrical conductivity of the saturation extract (EC_e) in the root zone exceeds 4 dS m⁻¹ (approximately 40 mM NaCl) at 25°C and has an exchangeable sodium of 15%. The yield of most crop plants is reduced at this EC_e, though many crops exhibit yield reduction at lower EC_es (Munns 2005; Jamil et al. 2011). It has been reported that globally 20% of the total cultivated

^{*}Corresponding author's e-mail: durgeshgenetix@gmail.com; dharmendrapbg@rediffmail.com

Published by the Indian Society of Genetics & Plant Breeding, A-Block, F2, First Floor, NASC Complex, IARI P.O., Pusa Campus, New Delhi 110 012; Online management by www.isgpb.org; indianjournals.com

and 33% of the irrigated agricultural lands are afflicted by high salinity. The salinity affected areas are increasing day by day at alarming rate due to several reasons such as low precipitation, high surface evaporation, irrigation with saline water including faulty cultured practices. It has been a threat to the agriculture for over 3000 years in some parts of the world (Flowers 2006). Salinization is a natural process of increasing salts due to lack of water for adequate leaching and poor drainage leading to degradation in the quality of soil. The surface irrigation has aggravated the condition in arid and semi-arid environments (Rao et al. 2016). The salinity stress is caused by the accumulation of soluble salts like Cl⁻, SO₄, HCO₃⁻, Na⁺, Ca²⁺, and Mg²⁺ and several others. These ions chiefly come from the irrigation and poor soil drainage (Acosta-Motos et al. 2017). Similarly, alkalinity stress is caused by the presence of carbonate (CO_3^2) , bicarbonate (HCO3)and hydroxyl (OH⁻) anions. The excess of borates, phosphates, silicates, and other bases increase concentration of these salts leading to alkalinity which drastically reduces plant growth and development. Ironically, the salinized areas are increasing at a rate of 10% annually, which is expected to cover more than 50% of the arable land by the year 2050 (Jamil et al. 2011). In India, about 6.73 million ha (mha) area is alkalinity affected soils (2.1% of the country) of which salinity occupies 1.71 mha, alkaline soils is 3.79 mha and coastal saline, sodic and alkaline soils is about 1.25 mha (Mandal et al. 2009; ICAR and NAAS. 2010; Mandal et al. 2018). The characterization of salinity affected soil is given in Table 1. The most affected states due to salinity includes Gujarat, Uttar Pradesh, Rajasthan, West Bengal, Telangana and Andhra Pradesh. Annually, 3000-4000 ha new areas are being affected by salinity due to surface irrigation and poor drainage (Minhas and Reddy 2017). The situation is alarming and needs immediate attention.

Pulse crops are a wonderful gift of nature to the menkind. Several pulse crops such as chickpea (*Cicer arietinum*), pigeonpea (*Cajanus cajanifolius*), lentil (*Lens culinaris*), urad bean (*Vigna mungo*), mung bean (*Vigna radiata*), field pea (*Pisum sativum*), cowpea (*Vigna unguiculata*) moth bean (*Vigna aconitifolia*), French bean (*Phaseolus vulgaris*), lablab bean (*Lablab purpureus*), faba bean (*Vicia faba*), horse gram (*Dolichos uniflorus*) and grasspea or khesari (*Lathyrus sativus*), etc. are being grown world over including India. They play a significant role in mitigating protein

Type of soil	Saline soils	Alkaline soils	Sodic soils
Definition	 The definition derives from the EC that wouldreduce yield of most crops. Higher concentration of soluble salts are present 	 The definition derives from high pH caused by carbonate salts in parent material These are sodic soil with high pH 	 The definition derives from the high ESP that results in poor soil physical conditions Low concentration of soluble salts present but a high exchangeable Na+ percentage (ESP).
Electrical conductivity (EC)	\geq 4 dS/m	ECe< 4 dS/m	ECe< 4 dS/m
pH value	< 8.2	pH > 8.5–10	pH<8.5
Exchangeable Na+ percentage (ESP)	ESP <15	$ESP \ge 15$	$^{2}ESP \ge 15$
Dominant ions present	Na ⁺¹ ; appreciable quantities of Ca ⁺² and Mg ⁺² Gypsum also present in significant quantities	Na ⁺¹ , Ca ⁺² and Mg ⁺² precipitate due to high pH	Gypsum nearly always absent; Exchangeable sodium affecting uptake of P,Fe,Mn and Zn
Effect on plant growth	Osmotic and salt specific compo- nents inhibit root and shoot growth	High pH affectsnutrient uptake	Poor soil structure inhibits root growth

 Table 1.
 Characterization of soils affected by salinity stress

Note: 1.EC is the electrical conductivity of the saturated paste extract, and reflects the concentration of salts in the saturated soil. A conductivity of 4 dS m^{"1} is equivalent to 40 mM NaCl.

2. At high ESP, the clay particles separate. The soil drains poorly, becomes waterlogged when wet and gets very hard when dry. Source: Adopted and modified from Rana Munns, 2005 (USDA Salinity Laboratory, 2005)

malnutrition and providing nutritional security to millions of poor vegetarian people of the semi-arid tropics of the world. They also assume special significance because of efficient bio-productivity in marginal soils. Pulses constitute an important component in the cropping patterns of several developing countries in Asia, Africa, and Latin America. They occupy about 5.8% of the world's arable land area and are grown mainly in less fertile and marginal lands as sole or intercrops with cereals and oilseeds (Joshi and Rao 2017). However, the pulse crops are overly sensitive to salinity stress and therefore, the growth, development and yield are severely reduced. The excess concentration of Ca, Na, K and Mg ions causes degradation of the soil and leads to induction of leaf chlorosis and stunted growth due to high uptake of Na+ and low uptake of nutrients (Millar et al. 2007). The effect, however, varies from one genotype to another due to its adaptive mechanisms.

The Indo-Gangatic plain where the pulses are grown on large scale, has about 2.8 mha area affected by alkaline stress. Gradually, the area under the pulse crops in the traditional pulse growing areas is decreasing over the years partly due to increased soil salinity and enhanced use of brackish water for irrigation (Gowda et al. 2009). Salinity is thus a major constraint limiting plant growth and development, and severely affecting the reproductive processes resulting in lowered pulse productivity and thus threatening sustenance of global production of pulses. The imperative is therefore, to mitigate the salinity stress and sustaining pulses production by stress management approaches and breeding tolerant cultivars of the pulse crops. In this review we have elucidated a few strategic points to provide holistic view of recent advances in breeding for salinity tolerance in pulse crops.

Global scenario: Area, production, and per capita availability of pulses

The pulse crops grown in different parts of the world include the pulse family consists of a number of pulse crops and the FAO broadly classifies them into 10 pulse types in addition to a category including many minor pulses as a group whose data are not given separately in FAOSTAT (e.g., lablab, sword bean, gaur bean). As a combined group, pulses include dry beans, broad bean, cowpea, chickpea, pigeon pea, lentil, dry peas (field pea), bambara bean, lupin, vetches, and other minor pulses. As per the classification given by FAO, the dry bean category comprises common bean, mung bean, black gram, and adzuki bean. All of these beans belong to the genus *Phaseoulus*, but they are grown in different regions and environments. The farmers in Asian countries grow common bean/dry bean mainly green gram, black gram, and moth bean. Another category includes broad bean or faba bean, which further constitutes broad bean, horse bean, and field bean etc. Global share of the major pulses in terms of area and production is shown in Fig. 1. The



Fig. 1. Per cent area under cultivation and per cent production of different pulse crops

pulses accounts for 80.3 mha of global crop area with 72.3 million metric tons (mt) produce. The top 20 pulseproducing countries account for about 82% of pulse area and production in which top seven countries contribute for 60%. India is the world's largest producer of pulses, accounting for 29.28 mha (34% of area) and 22.40mt (24% of production) followed by Myanmar, Canada, China, Nigeria, Brazil, and Australia (Joshi and Rao 2017). Among the pulse growing countries of the world, the most significant expansion of pulses in terms of area and production is observed in Africa.

The yield variations among the pulse producing countries of the world is very high. Usually, the countries with higher yields found to have lesser area under pulses as compared to other countries (Fig. 2).



Fig. 2. Pie diagram showing per hectare production of pulse crops in different countries of the world

For example, countries such as Niger, Nigeria, Myanmar etc.have more area under pulses but total production and productivity is low.

In global scenario, India stands twelve in production despite having the largest share of area under pulses. Production of pulses in India found to increase by 1.3% during 1980-2013; however, import remains at around 15 per cent of the domestic production, and the per capita availability remained stagnant at around 6.5 kg/capita/year, which is far below the per capita requirement of 43g/day. To meet the local demand, India has now become the largest importer of pulses in the world. Akibode et al. (2011) reported that more than 75% of the pulse crop in developing countries is grown in rain-fed and low-input production systems. In India and other countries in Southern Asia, only 10-15% area of pulses is under irrigation. In India, Madhya Pradesh is the largest producer of pulses followed by Maharashtra, Rajasthan, Uttar Pradesh, Andhra Pradesh and Karnataka. Being the largest producer (18-20mt), India is also the largest consumer (20-24mt) and importer (4-6mt) of pulses resulting in a loss of \$ 2.3 billion foreign exchange each year (Business line, 2015). Estimates indicate that India needs an annual growth rate of 4.2% in pulse production to ensure projected demand of 30 mt by 2030 (Rana et al. 2016). These crops being grown as rainfed (87%) on marginal and sub-marginal lands are frequently prone to biotic and abiotic stresses (Rana et al. 2016) which are the major barriers in realizing the yield potential of the pulses.

The effects of salinity in pulse crops

Soil salinity, in general, creates a soil condition unfavorable for crop growth and development. Maas and Hoffman (1977) observed the relationship between response of the crop yield against salinity and quantified crop's relative growth or yield as a continuous function of gradually higher levels of soil saline condition, which follows a sigmoid curve. It indicated that at low salt concentration yield is either unaffected or decrease slowly, then decrease in yield at a greater but relatively constant rate at moderate concentrations and lastly the yield start to decline more slowly towards zero at high concentrations.

De Pascale and Barbieri (1994) studied the effects of soil salinity and removal of top soil in faba bean by using two different models viz., Maas and Hoffman (1977) model $Yr = 100 - S(EC_e) - T$) and the van Genuchten (1980) model Yr = 100/[1 + 100]

(ECeECe50)p] and concluded that shoot and leaf dry mass, leaf area, leaf number and shoot length declines with increase in salt stress level. The models depicted that in terms of relative yield per unit area, the threshold value was 1.7 dS m⁻ and yield was reduced at the rate of 15% compared to 4.7 dS m⁻ of the van Genuchten model. Broadbean was more sensitive two weeks after flowering i.e. at higher EC level, leaf area reduction was 60% at flowering and 73% after two weeks and leaf dry mass reduction was 50% and 55% respectively. Rameshwaran et al. (2015) studied the effect of salinity to the response of faba bean, chickpea and lentil by using the threshold-slope linear response function and modified discount function. Comparison was also done by SALTMED model predictions. It was concluded that the variation in response is dependent on the accession of these three crops and a wide range of response was found for each crop. The study showed similar range of variation in relative yield for faba bean and chickpea while lentil has small range of variation in yield compared to faba bean and chickpea.

Under condition of salt stress, the plants suffer from disruption of ion homeostasis; however, in the salt stress tolerant plant, the inherent mechanisms of exclusion and compartmentalization and self-inducible Na⁺/H⁺ antiporter enzyme overcome the damage (Apse et al. 1999). The disruption of normal homeostasis under salt stress also causes abnormal photosynthesis and increased photorespiration generating high level of reactive oxygen species such as super oxide radical, hydrogen peroxide and hydroxyl radical which disturb cells and damage normal pathways (Mayak et al. 2004). A fully developed leaf maintains high Na⁺ and Cl⁻ ion concentration in the reproductive organs during pod filling stage resulting in restricted ion accumulation in flowers and the developing ovules. The salinity effect in chickpea is minimized by compartmentalization of toxic ions in the leaf's vacuoles (Munns 2008; Mullan et al. 2007; Reginato et al. 2014). The high ion accumulation in leaves might result in decreased photosynthesis efficiency which ultimately affects the seed yield. A very few studies have been done relating salinity, seed germination and yield, however, Manchanda and Sharma (1990) found a good agreement between seedling stage evaluation and yield-based assessment in chickpea.

Ebbisa and Getachew (2015) evaluated the effects of different salinity levels on growth performance and number of nodulation in chickpea (*Cicer arietinum* L.) under green house condition at

five levels of NaCl concentrations (0, 3, 6, 12 and 18 g of NaCl) which were mixed in 200ml of water for each NaCl levels. The study showed that the number of germinated plants, root length, root number, number of nodulation and harvested fresh and dry seedling weights were significantly reduced as compared to control. Only plant height was not reduced at 3g NaCl and the number of nodules, number of root also showed positive response. This gradual reduction in growth parameters and nodulation as NaCl levels increases (highest at 18g) indicated that chickpea is extremely sensitivity to NaCl out of the legume crops.

Legumes are comparatively hardy crops generally known for tolerance against various abiotic stresses. Hence, they are often considered as crops for the stress affected regions of the world. However, the physiological effects of salt stress in many legume crops are less investigated. Genotype dependent responses in salt affected soils are mostly observed in chickpea, lentil and to some extent in pigeonpea cultivars in the form of accumulation of osmolytes like proline, glycine betaine, starch and soluble sugars during salt stress (Joshi 1984). However, a little is known about the salinity tolerance in pigeonpea. In an attempt to understand the effect of salinity in pigeonpea plants, Tayyab et al. (2016) found that the plants survived up to 3.5 ECe dS.m-1 in sea salt salinity. An increase of chlorophyll contents and carotenoids in leaf was recorded at 1.6 dS.m-1 but subsequently decreased in higher salinity. Low moisture content and succulence along with more accumulation of soluble sugars and proteins may be attributed to leaf osmotic adjustments at low salinity. Salinity adversely affects reproductive growth where production of flowers, pods, number of seeds and seed weight are significantly reduced.

Under salinity stress, phosphorus and potassium contents get reduced while those of calcium, magnesium, sodium, chloride, and sulphate get enhanced. As a result, regulation on the uptake of latter elements under saline conditions is highly affected and, the photosynthetic efficiency of the plant is decreased due to degradation of essential pigments like chlorophyll and carotenoids. Salinity reduces plant growth chiefly in three mechanism- osmotically induced water stress, specific ion toxicity due to high concentration of sodium and chloride ion and nutrient imbalances which hampers the uptake of water by plants (Greenway and Munns 1980; Manchanda and Sharma 1990). Salinity stress also limits physiological response and photosynthetic capacity. Gama et al (2007) studied the effect salt stress in common bean (*Phaseolus vulgaris* L.) and found that high concentration of NaCl is associated with a reduction in leaf chlorophyll fluorescence and photosynthesis (Fig. 3). It is envisaged that blocking of the electron



Fig. 3. Schematic representation of effect of salinity stress in crop plants

transport might reduce the chlorophyll content in the plants under salt stress.

Since pulses are more sensitive to saline soil as compared to cereals and oilseeds, the damage caused in yield is enormous. This might be due to the fact that, pulses accumulate excess salts that quickens the anthocyanin pigmention in leaves and stems which ultimately reduce germination and seedling establishment (Kumar et al. 2016). Thus, growth and development of the pulse crops are more prone to salinity-induced moisture stress. In mungbean, salt stress along with other pests (stemand pod-borer) and yellow mosaic disease caused 80-100% yield loss particularly during rainy season (Sehrawat et al. 2015).

Mitigation of salinity stress

Management of salt stress may be rewarding to the farmers who face the serious challenge by the type of soils they have. Several strategies are being followed to reclaim the sick soil and bring it back under cultivable condition. Sharma and Minhas (2005) suggested the modification of the saline environment to suit the plant or to modify plant to suit the environment for improving and sustaining the production under salinity. The gypsum-based technology has been quite successful for reclamation of the alkaline land. In India, approximately, >1.8 mha a of alkaline soils has been reclaimed and the same has been used to cultivate rice and wheat for uplifting socio-economic condition of the people (CSSRI 2015). Experiments on removal of top soil have been conducted to grow legume crops. In one such study, Pascale and Barbieri (1997) found the response of faba bean genotypes on top soil removal during irrigation free season with irrigation treatment ranging from 0% to 1% commercial NaCl and observed that soil salinity at low level affected higher early production indicating more efficient of assimilation to growing pods. At low soil salinity the only effect of top removal was higher early production, indicating a more efficient partition of assimilates to growing pods and, therefore, rapid pod enlargement and higher yield at the first harvest was recorded.

In arid or semi-arid regions with salt affected soils, farmers are forced to use saline water for irrigation in areas with poor water quality or less available water for irrigation. Legumes are very sensitive crops towards soil salinity, and secondary salinization mainly through irrigation water is the hardest challenge for survival of legume crops in arid regions (Mann et al. 2020).

For saline soils, the amendment is to lower the salt concentration through leaching with good quality water and disposal of drainage effluent through well laid out horizontal sub-surface drainage system (Minhas and Sharma 2002). The sub-surface drainage technology has successfully been used in Gujarat, Haryana and Rajasthan reclaiming waterlogged soils (Kamra 2015). However, the technology requires high initial investments and need continuous operational and maintenances. Cuevas et al. (2019) analysed a case specific optimization of irrigation and drainage management including the residue management and reported that these amendments can significantly reduce the soil salinity and help increase the productivity. Although, it is difficult to manage salt affected soils by chemical amendments, the only precautionary measure is to use quality water and salt tolerant pulse varieties. The other alternative may be the change in cropping pattern, green manuring, use of drainage and mulching technologies. The conservation agriculture can also achieve the higher yields required for upscaling and sustaining crop production (Yadav et al. 2017). It is suggested that the desi types of chickpea are more tolerant than kabuli types (Vadez et al. 2007). In view of the cost effectiveness, agro-forestry is now emerging as a potential tool in not only arresting salinity but to

mitigate climate change, sequestering carbon, and restoration of biodiversity (Minhas and Dagar 2016). Zhou and Li (2013) studied the effects of oasis ecosystem hydrological processes on soil salinization in the lower reaches of the Tarim River, China and found that the methodology is useful in reclaiming the saline soils.

Plant growth promoting bacteria are associated with several plant species and improve plant performance under stress environments (Ruiz-Lozano 1996). Kasotia et al. (2015) emphasized the role of plant growth promoting bacterium to characterize activities of stress-associated enzymes, proline ______*/K⁺ ratio

in soybean (Glycine max L.) under salt stress and showed that inoculation of plants with Psedomonas koreensis strain AK-1 grown under salt treatment induced growth promotion, reduced Na⁺ levels but increased K⁺ levels in leaves and roots in comparison to non-inoculated plants. To improve the growth of faba bean cultivars in saline soil, Metwali et al (2015) investigated the effect of bacterial isolates, Pseudomonas putida, P. fluorescens and Bacillus subtilis of plant growth promoting rhizobacteria under two levels of salinity stress (S1=4000 and S2=8000 ppm). They found high percentage of germination (96%) in the tested cultivars (Wadi 1 and Line 1) in presence of P. fluorescens. Futher, the plants treated with P. fluorescens showed significant increase in plant length (10.66%), plant shoot fresh weight (9.52%), and plant leaf area (61.86%). This positive effect was highest in P fluorescens followed by B. subtilis then P. putida. Bio-fertilization with soil yeast, Rhodotorula glutinis also reduces the deleterious effect of salinity stress. Increasing salinity level was accompanied by decreasing dry weight particularly at higher concentration (6000 ppm) of salt. Gaballah and Gomaa (2004) found a few faba bean varieties (Giza Blanka and Giza 674) performing better at the above level of salinity. Exploring genetic variation for salinity tolerance, Asif (2017) reported that most tolerant varieties of faba bean possessed better ability to maintain higher leaf K⁺/Na⁺ and Cl⁻ accumulation, lower root K⁺/Na⁺ and leaf chlorosis resulting in greater salt tolerance at 100 mM NaCl concentration. The potential role of nicotinamide in alleviating the deleterious effects of salinity on some physiological and biochemical traits of faba bean has also been envisaged by Abdelhamid et al. (2013). Common adaptation mechanisms of plants exposed to environmental stresses such as drought, temperature and salinity changes the root morphology (Potters 2007). Modulation of some plant hormones could also improve crop salt tolerance by reducing the toxic effects of salinity (Bianco and Defez 2009).

Genetic variations for salinity stress tolerance

Salt tolerance is genetically variable, and the degree of salt tolerance varies with plant species and varieties within a species. In case of cereals barley is more tolerant than rice and wheat. However, the degree of variation is more pronounced among dicotyledonous plants; Arabidopsis thaliana is highly sensitive to salinity than Mesembryanthemum crystallinum, Atriplex spp., Thellungiella salsuginea a close relative of Arabidopsis (Pang et al. 2010; Abraham et al. 2011). Some legumes are very sensitive e.g., threshold salinity level of beans (Phaseolus vulgaris) is 1 dS/m (Table3) as compared to rice (3 dS/m), wheat (6dS/m) and barley (7dS/m). Alfalfa or lucerne (Medicago sativa) is very tolerant, and halophytes such as salt bush (Atriplex spp.) continue to grow well at salinity level greater than that of seawater.

The knowledge of genetic variation in different pulse crops is essential to develop genotypes, which have the capacity to withstand the salinity stress. Most of the pulse crops are sensitive to salinity, which is reflected in poor rate of germination, vegetative growth, reproduction (Maliro et al. 2004), reduction in nodule formation and yield (Hailesilasse et al. 2012). In chickpea a large genotypic variation has been reported in landraces and core collection based on shoot mass under saline conditions at vegetative and maturity stage in glasshouse conditions (Turner et al. 2013). Differences in tissue-ion regulation in different parts of the plants of various pulse crops due to Na⁺/Cl⁻/K⁺ ion concentration has also been observed. Lo'pez (1999) studied the role and effect of Na⁺and Cl⁻ ions in salt-tolerance mechanism in plants and found that salt tolerance is associated with the ability to limit the uptake and/or transport of ions from root to aerial parts, while Singh et al. (2017) found that Na⁺ concentration in shoot was lower than the roots of Lens culinaris but it was reverse for CI. The tolerant genotypes develop inherent capacity in terms of regulation of Na⁺ and Cl⁻ to the aerial parts in order to avoid the deleterious effect of salt on plant metabolism in Vigna unguiculata (Fernandes de Mello et al. 1994). Samineni et al. (2011) observed salt sensitivity at vegetative and reproductive stages in chickpea (Cicer arietinum) podding in particular. Genetic variation in different morphological features under salinity stress was also recorded in Vicia faba L. (Tavakkoli et al. 2012).

Significant genetic variation for salinity tolerance also prevails among the genotypes of lentil (Singh et al. 2017a). They endorsed that seed germination and seedling growth are the major limiting factors for normal crop growth under salt stress may be due to water imbibition and toxic effects during seed germination. Salt injury and yellowing of leaves leading to necrosis at leaf margins resulting in wilting and poor survival of the plants occurs in lentil. Variation for seedling survivability in saline soils has been considered a useful parameter to evaluate salt tolerance. The contrasting differences in root and shoot anatomical features at 120mM NaCl treatment, such as vascular arrangement in stele region in tolerant accession (PDL-1) and susceptible/sensitive cultigens L-4076 were observed (Figs. 4a and 4b). Murillo-Amador et al. (1986) evaluated seedling emergence of cowpea and found that salt tolerant genotypes survived at 120 mM NaCl concentration. Kökten (2010) studied germination percentage, shoot and root length and shoot/root ratio, shoot and root weight and shoot/root ratio and salt tolerance index salt tolerance in lentil at 50 mg/l, 100 mg/l, 150 mg/l and 200 mg/l⁻ NaCl concentrations and reported significant differences in the salt tolerance of lentil genotypes and their different responses to increasing salt concentrations. Although genotypes responded similarly during the first 3 salt treatments, significant differences among the genotypes were obvious with the 150 and 200 mg l⁻¹ treatments, concerning the salt tolerance index of genotypes.

Dry matter production is also a potent indicator of plant's performance under salinity stress associated with yield (Maas 1986). As compared to the gathering of root and shoot mass by the plant, normal flowering and flower development in a plant is an indication of tolerance during salinity stress (Vadez et al. 2012a). The observations on number of flowers on plants under salt stress recorded by Vadez et al. (2012b) in chickpea were well supported by Kotula et al. (2015). Physiological studies have also shown delayed flowering, failure of fertilization even after the development of pollen tube resulting into poor pollen viability affecting pod filling and is also affected resulting in empty pods (Kotula et al. 2015). The leaf area, dry weight, and chemical analysis by atomic absorption spectrophotometer and chloride content by Mohr's volumetric method, relative water content (Subbarao et al. 1990), membrane stability index chlorophyll content, K⁺/Na⁺ estimation (Sherawat et al. 2013) and SCMR (Spad chlorophyll metre reading) and shoot sodium accumulation (Srivastava et al. 2007) can be used for screening and identifying tolerant and







Fig. 4b. Changes in stellar region and vascular bundles in cross-sections of stem in tolerant and sensitive *Lens* species raised *under* control (0 mM) and (120mMNaCl) saline stress condition grown in hydroponics

susceptible genotypes. Bulut and Akinci (2010) determined the influence of salinity tolerance in faba bean at 50 and 100 mM NaCl concentration and reported reduction in plant height, number of internodes and leaf dry weight in cultivars, Eresen 87 and Filiz 99 at higher level of salinity. According to the flame photometer, flame atomic absorption spectrophotometers (FAAS) and inductively coupled

plasma atomic emission spectrometry (ICP-AES) analyses of Filiz 99, Na⁺ was found in higher amounts in roots, stems and leaves of seedlings exposed to 100 mM NaCl. In leaves, the elements K⁺, Ca₂⁺ and Mg_2^+ were decreased significantly and, sodium and potassium content was 3- and 2.4- times higher than in cv. Eresen 87 indicating that Filiz 99 was slightly more resistant to salinity.

Sehrawat et al. (2015) reported salinity induced moisture stress and retarding of growth and development in mungbean. Similarly, nodulation, nodule size, nitrogen fixation are highly affected by sodium saline conditions and thus impact on yield and yield traits in kabuli chickpea (Swaraj and Bishnoi 1999; Flowers et al. 2010; Jha et al. 2014).

Genetics of salinity tolerance

Understanding the genetic basis of salt tolerance is vital to develop tolerant varieties. Genetics of salinity tolerance has been worked out in several crops namely, rice (Lee et al. 2007), wheat (Ma et al. 2007), pigeonpea (Subba Rao et al. 1990, 1994), tomato (Villalta et al. 2007); however, limited progress has been made in the pulse crops. In an inter-specific crosses in pigeonpea, dominant monogenic control was observed in (Subbarao et. al. 1990). Similar reports of genetic control for some attributes of salinity tolerance in soybean, and chickpea has been reported. Salt tolerance rating (STR) and ion accumulation found to determine the salinity stress tolerance in soybean (Abel 1969; Hamwieh and Xu 2008; Liu et al. 2016). However, Phang (2008) had reported that salt tolerance in soybean is a quantitative trait and controls by a few major loci. Hamwieh and Xu (2008) identified conserved salt tolerance quantitative trait locus (QTL) in wild and cultivated soybeans and later, Hamwieh et al. (2011) observed a major QTL with PVE ranging from 44.0-47.1 and 38.2-40.7 in salinity tolerance rating and chlorophyll content, respectively. Guan et al. (2014) mapped a salt tolerance gene on chromosome 3 using SSRs and INDELs markers in soybean, whereas Singh et al. (2020) identified a major QTL or salt tolerance in lentil explaining comparatively less phenotypic variance. Earlier, Singh et al. (2017b) reported that different traits such as seedling growth, biomass accumulation, seedling survival, antioxidant activities and fluorescent signals, and Na⁺, K⁺ and Cl⁻ contents could be used in lentil for salinity stress tolerance. All these parameters have been used to map the QTLs for salinity stress tolerance in other crops also (Dubcovsky et al. 1996; Farshdfar et al. 2008;

Shavrukov et al. 2010). In chickpea, dominant effects mostly controlled the seed yield in saline environment, with minor contributions from additive effects (Ashraf and Waheed 1998). Only additive gene effects have been reported to be important for seed yield in pigeonpea under saline environment (Ashraf 1998).

Attempts to study genetics of salt tolerance in other species suggested that it is highly unlikely that one gene alone determines plant salinity tolerance in the pulse crops, rather it is a complex trait (Flowers 2004). Diallel analysis for assessment of salt tolerance in terms of relative root length in different crops witnessed both additive and dominance effects of salt (Azhar and McNeilly 1988). Phang (2008) reported salt tolerance in soybean as quantitative trait dominated by a few major loci. Studies on biochemical, physiological and phenological genetic analysis in common bean (Phaseolus vulgaris L.) under salt stress conducted by Yacine et al (2018) also suggested both additive and dominant gene action in salt tolerance. Thus, salt tolerance is multi-genic features regulated by a number of biochemical, physiological and molecular processes and is involved in modulating accumulation of various solutes/osmolytes, polyamines, reactive oxygen species and proteins (Kumar et al. 2015). Therefore, for accuracy and certainty, analysis of salinity responses should be done not only at whole plant level but also at the level of traits contributing to salinity tolerance.

Singh et al. (2020a) investigated salinity stress tolerance at seedling stage in lentil to understand the genetics in a segregating population derived from sensitive (L-4147 and L-4046) and salt tolerant (PDL-1 and PSL-9) lentil genotypes. The parents, F₁, F₂, F₃ and backcross populations were evaluated in salt solution at 120 mM NaCl concentration on seedling survivability and a Fluorescein diacetate (FDA) signal. The study revealed a dominant monogenic control of salinity stress tolerance. The test of allelism confirmed that a single dominant gene governed salt tolerance in both PDL 1 and PSL 9 genotypes. They further identified seven markers to be closely associated with seedling survival under salinity stress. A QTL was mapped on linkage group 1 (LG_1) that explained about 65.6% of phenotypic variances.

Strategies to breed salinity tolerant genotypes

The development of saline tolerant cultivars can be an appropriate approach for minimizing yield losses under salinity stress conditions. The foremost understanding of genetic determinant is essential to breed a suitable genotype for salinity tolerance. Indepth understanding of mechanism of salt tolerance and the traits which can be manipulated genetically is also a pre-requisite.

Salinty stress in plants is observed right from the beginning of germination, initial growth and development and reproductive development by imposing ion toxicity, osmotic stress, nutrient deficiency (N, Ca, K, P, Fe and Zn) and oxidative stress on plants resulting in water uptake from the soil. Therefore, identification of morphological and physiological traits and determination of different genetical parameters are essential pre-requisite to manipulate the plant mechanism for developing salt tolerant genotypes through conventional and/or molecular techniques. Osmotic adjustment is the main mechanism to conserve plant cell hydration under salt and drought stresses. The osmo-protectants accumulation realizes the prime cell tolerance response providing adaptation, improve plant growth, osmotic and anti-oxidative defense of Cajanus cajan modulated by salt stress and therefore, the osmotic pressure in cytoplasm is to be maintained (Garg and Noor 2009; Hanafy et al. 2013).

The ion channel regulation mechanism improves salt tolerance in chickpea. Effects of sodium chloride and sodium sulphate on the content of some organic and inorganic constituents in the leaves of pigeonpea (*Cajanus cajan* L. Var. C-11) were studied. Increased water content under saline conditions made the leaves succulent. The concentration of reducing sugars appeared to be higher while that of total sugars and starch was lower. The plants also failed to accumulate proline at higher salinity levels. Phosphorus and potassium content were lowered while those of calcium, magnesium, sodium, chloride, and sulphate were increased under salinities. This indicates that there is no regulation on the uptake of latter elements under saline conditions.

Genetic improvement of pulses for tolerance to salinity stress

The response of plants to various abiotic stresses at the cellular level is often interconnected leading to morphological, physiological, biochemical and molecular changes that affect plant growth, development and productivity (Ahmad and Prasad 2012). The kind of efforts needed to improve pulse crops are limited and therefore, require special attention. The emphasis must be laid upon trait-based breeding to ensure yield stability across the locations as well as crop seasons. Appreciable improvement in salt tolerance of important crops (barley, rice, pearl millet, maize, sorghum, alfalfa, and many grass species) have been attained in the past, but not in legumes.

The need to produce salt-tolerant crops has been realized from the days of yore (Jacobsen and Adams 1958) and different approaches and strategies were extensively rehearsed to increase tolerance against salinity. Epstein (1977) reported that germplasm display a spectrum of salt tolerance capability from high to low. Existence of a wide range of germplasm from euhalophytes to extremely sensitive glycophytes within a species provides a good scope for intensive and precise screening and identification of tolerant lines for use in breeding programs to deliver agronomically superior cultivars tolerant to salt stress. Ndakidemi and Makoi (2009) established that there is a high genetic potential into salt tolerance among Phaseolus vulgaris cultivars. In fact, several national breeding programs in Africa have been established to find dry bean genotypes with better salt tolerance, plant growth, chlorophyll levels and high seed yield.

Mungbean [Vigna radiata (L.) R. Wilczek var. radiata] is an important food and cash legume crop in Asia. Mungbean productivity is constrained by several abiotic stresses including salinity. Salt stress mainly reduces seed germination, fresh and dry biomass, shoot and root length, and yield attributes of mungbean (Promila and Kumar 2000; Rabie 2005; Ahmed 2009). It affects root growth and elongation, thereby, hampering nutrient uptake and distribution. Root growth was significantly reduced with higher Sodium Chloride concentrations. In general, salinity tolerance breeding work is limited in pulses, in general and mungbean, in particular (Ambede et al. 2012). Breeding for salt tolerance in mungbean has been critical in developing varieties with resistance to salinity however, the lack of identification of resistance source(s) is major constraint. Nevertheless, BARI Mung4 showed better performances at higher NaCl concentration considering a yield-contributing character. Nodules/plant decreased with the increase of salinity although the nodule size increased (Naher and Alam, 2010). Being polygenic in nature, salinity tolerance is genotype-dependent and growth stage-specific phenomenon, therefore, tolerance at an initial (seedling) stage may not be corroborated with tolerance at later growth (maturity) stages (Sehrawat et al. 2013). It also involves multidimensional responses at several organ levels in plants (e.g., tissue, molecular, physiological and plant

Table 2. Susceptibilit	iy of	major	crops to	soil	salinity
------------------------	-------	-------	----------	------	----------

S. No.	Сгор	Threshold salinity (dS/m)
1. Bean (<i>Phaseolus vulgaris</i> L.)		1.0
2.	Eggplant (Solanum melongena L.)	1.1
3.	Onion (<i>Allium cepa</i> L.)	1.2
4.	Pepper (Capsicum annuum L.)	1.5
5.	Corn (<i>Zea may</i> s L.)	1.7
6.	Sugarcane (<i>Saccharum</i> officinarum L.)	1.7
7.	Potato (Solanum tuberosum L.)	1.7
8.	Cabbage (<i>Brassica oleracea</i> var. <i>capitata</i> L.)	1.8
9.	Tomato (<i>Lycopersicon esculentum</i> Mill.)	2.5
10.	Rice (Oryza sativa L.)	3.0
11.	Peanut (<i>Arachis hypogaea</i> L.)	3.2
12.	Soybean (Glycine max L. Merr.)	5.0
13.	Wheat (Triticum aestivum L.)	6.0
14.	Sugar beet (<i>Beta vulgaris</i> L.)	7.0
15.	Cotton (Gossypium hirsutum L.)	7.7
16.	Barley (Hordeum vulgare L.)	8.0
17.	Broad Bean (<i>Vicia faba</i> L.)	1.0
18.	Cowpea (<i>Vigna unguiculata</i> L. Walp)	2.5
19.	Pigeonpea (<i>Cajanus cajan</i> L. Millspaugh)	4.0
20.	Lentil (Lens culinaris)	1.2

Source: Maas 1993; Subbarao et al.1991; Singh et al. 2017

canopy levels) (Hanumantha Rao et al. 2016). Because of this complexity and lack of appropriate techniques for introgression, little progress has been achieved in developing salt-tolerant mungbean varieties over years (Ambede et al. 2012; HanumanthaRao et al. 2016).

In breeding for salinity tolerance, one should not select a genotype based on overall performance; rather one should look for the traits that contribute to salinity tolerance (such as shoot Na⁺ content or plant vigour) (Yeo et al. 1990) Wild relatives of pigeonpea from secondary and tertiary gene pools (*C. scarabaeoides, C. albicans* and *C. platycarpus*) confers resistance to salinity stress involving traits such as root retention of Na⁺ and Cl⁻ and their limited translocation to shoots, and maintenance of optimum rates of transpiration

Name of crop	Donor for salt tolerance
Chickpea	JG 62, ICC 5003, ICC 15610, and ICC 1431 (Vadez et al. 2007); ICC 10755 (Serraj et al. 2004); SG-11(SG-11); CSG 8962 and CSG 8927 (Dua and Sharma 1995)
Pigeonpea	ICPL 227 (Subbarao et al. 1991); <i>C. platycarpus, C. scarabaeoides, and C. sericeus</i> (Srivastava et al. 2006); <i>C. albicans</i> (Subbarao et al. 1990)
Adzuki bean	JP107879 of V. nakashimae (strain 'Ukushima'), JP205833 of V. riukiuensis (strain 'Tojinbaka') (Yoshida et al. 2016); V. trilobata, V. vexillate, V. marina subsp. Oblonga, V. luteola, V. marina (Iseki et al. 2016)
Lentil	PDL-1, PSL-9 and ILWL-09, ILWL-137, ILWL-96 and ILWL-428 (Dharmendra et al. 2017); Cagil and Altin Toprak (Kökten et al. 2010)
Soybean Lee, Le	ee 68, and S-100 (Do et al. 2016)

Table 3. List of donors for salt tolerances in different pulse crops

under salinity. Srivastava et al. (2006) reported that the cultivated and wild accessions of pigeonpea varies widely for salinity susceptibility index (SSI) and relative reduction per cent (RR%). Such genotypic differences for salinity provide opportunity for selecting tolerant genotypes. However, the concentration of salt in the screening experiments, need to be optimized as it varies from one species to another. The level of salt concentration optimal for discriminating sensitive and tolerant genotypes in different species is given in Table 3. Further, salinity tolerance of a species may vary between growth stages, therefore, screening needs to be performed at different growing times during the vegetative and reproductive stages. Ion exclusion (from root), tissue tolerance of toxic ions, and perhaps internal detoxification may be simultaneously operating to mitigate the effects of salinity stress. Screening of core and mini-core germplasm sets can lead to identification of genotypes with salt tolerance which can further be used in breeding programme for salt tolerance. There is a lack of direct correlation between the threshold salinity and yield decrease per unit increase in salinity which may be attributed to the differences in salt exclusion. uptake, compartmentation, and other mechanisms of salt tolerance among these crop species. Differential responses and genetic variations to salinity stress in plants have enabled researchers to identify physiological mechanisms, sets of genes, and gene products that are involved in increasing stress tolerance. Basic tolerance mechanisms involve the activation of different stress regulated genes through integrated cellular as well as molecular responses.Hence, the breeding of salt tolerant genotypes of different pulse crops need specific emphasis on the traits need to be improved so that these could contribute directly or indirectly to yield.

Plant type or ideotype of a plant need to be designed to help acclimatize it to the saline stress conditions with remarkable physiological and biochemical adjustments. Selection should be directed towards individual plant that has improved capacity of taking the nutrients from the soil. Further, emphasis should be given on both constitutive and adaptive traits while selecting the plants for salinity stress tolerance. The plants having higher number of flowers and higher number of seeds under salinity stress indicate its tolerance to salinity in chickpea (Vadez et al. 2012a). Genetic variation in different pulse genotypes has been studied by several workers (Saxena 1984; Flowers et al. 2010). Lauter and Munns (1986) evaluated a large number of chickpea genotypes using 50mM NaCl and/ or 25 mM Na₂SO₄ salts and identified tolerant cultivar L550 which showed normal growth under saline conditions. Turner et al. (2013) tested about 50 chickpea genotypes at various levels of salinity and concluded that that high pod and seed number bearing genotype which may accumulate low concentration of salt will provide better tolerance under salinity stress. Remarkable efforts have been made to identify donors for and decipher the inheritance and genetics of tolerance to salt stress in pulses. Details of donors are presented in Table 3.

Breeding approaches for salinity tolerance

Legume crops in general are highly sensitive to salinity stress (Mass and Hoffman 1977) and therefore, breeding for salinity tolerance has been a major challenge due to complexity of various factors including the inheritance pattern of genes governing tolerance/ susceptibility, genotype, and its interaction with environment and, the level of salinity. However, genomic resources and various molecular breeding (MB) approaches including marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS), etc., may act as a catalyzing agent facilitating breeding for salinity stress (Greenway and Munns 1980).

Salinity tolerance, a complex phenomenon, is controlled by traits involving intrinsic morphological, physiological and biochemical responses of multiple genes under stress. Before choosing any breeding approach to develop salt tolerant genotypes, a breeder has to identify genes associated with salt tolerance. Several attempts have been made to understand the molecular and physiological basis of salt tolerance in crop species. However, very limited work has been done in pulse crops as compared to cereals and other crops. Recent advances made in biotechnology such as high-throughput next-generation sequencing, generation of functional genomics resources, microarray analysis in order to identify differentially expressed genes under high salinity, salt related transcriptome analysis of root nodules, shoots tissues, root morphogenesis, cell wall modifications, electrolyte movements and ion (Na+/K+) dynamics in soil and plant organisms etc. have paved the way to identify differentially expressed genes and their regulatory mechanisms under salinity stress (Jain 2011, Jain and Chattopadhyay 2010; Kudappa et al. 2018; Mantri et al. 2007; Kaashyap et al. 2018).

The phenotypic responses to salinity stress are mainly due to the genetic constitution of plant(s) and genotype environmental variables. Availability of genetic variation within a gene pool of a crop would enable the identification of desirable salinity tolerance related traits. Since salinity tolerance is conferred by several physiological factors, the traits giving positive response to salinity stress may help in identification of sensitive and tolerant genotypes. Following molecular approaches, Mantri et al. (2007) identified salinity tolerant (CPI 060546) and sensitive (CPI 60527) chickpea genotypes both differing in temporal gene regulation. Kaur et al. (2014) delineated on the molecular mechanism underlying salt tolerance in well characterized tolerant, ICCV 10 and JG 11 and sensitive, DCP-92-3 and Pusa 256 genotypes and studied phenological and physiological attributes, viz., seedling growth, relative water content (RWC), EL, chlorophyll content, and ionic distribution of Na⁺ and K⁺. They found that sensitive genotypes had higher Na⁺/K⁺ ratios than the tolerant genotypes, whereas shoot Na⁺/K⁺ ratios in the tolerant genotypes (ICCV 10 and JG 11) was maintained under salt stress by accumulating less Na⁺ and more K⁺ than the sensitive

genotypes and the distribution of Na⁺ and K⁺ in plant tissue is critical for tolerance and supported the earlier reports (Shabala and Cuin, 2008). Understanding salinity tolerance at the molecular level can facilitate the development of salt-tolerant varieties through molecular breeding approaches in chickpea.

Using comparative transcriptome analysis of the same set of contrasting genotypes taken by Kaur et al.(2014), Kumar et al. (2021) studied salt tolerance mechanism. They identified a total of 530 million reads from root samples of four genotypes, generated 21,698 differentially expressed genes (DEGs) which were upand down-regulated. These DEGs were likely to be associated with crucial metabolic pathways such as hormone signaling, photosynthesis, lipid and carbohydrate metabolism, and cell wall biogenesis. Significant up-regulation of transcripts encoding potassium transporter family of different proteins occurred under salinity stress. The tolerant lines (ICCV 10 and JG 11) engaged highly efficient machinery in response to elevated salt stress, especially for signal transduction, transport and influx of K+ ions, and osmotic homeostasis. Earlier, Kasshyap et al. (2018) reported that NACs transcription factor genes impart salt tolerance in Cicer arietinum. These studies have emphasized the role of potential candidate gene(s) and the identification of these gene(s) responding to tolerance mechanisms will support the development of salt-tolerant high-yielding chickpea varieties.

Soren et al. (2020) also identified two genotypes of chickpea, ICCV 10 showing salt-tolerance whereas, DCP 92-3 exhibiting salt-sensitivity and developed RIL population to generate data for phenotyping and genotyping analysis. Salinity stress tolerance at seedling stage in lentil has been investigated to understand the genetics in a segregating population derived from sensitive (L-4147 and L-4046) and salt tolerant (PDL-1 and PSL-9) lentil genotypes (Singh et al. 2020). Combining field and hydrponic screening techniques two varieties of lentil, PDL- 1 and PSL-9 have been released for cultivation under saline conditions. Similarly, Manasa et al. (2017) selected five mungbean germplasm lines by canopy phenotyping assay based on seedling tolerance under 150 and 300 mM NaCl level of stress. These lines may serve as useful donor to breed salinity tolerant mungbean genotypes. The research findings clue available so far in different pulse and other crops can eventually pave the path for genetic improvement of salinity tolerance utilizing the candidate genes and their regulatory mechanisms to formulate effective

May, 2021]

genomic-assisted breeding approaches for chickpea breeding programs.

Screening for identification of salinity tolerant genotypes/donors

Differences in salt tolerance at the varietal or genotypic levels have been reported in several leguminous crops (Dua et al. 1989; Subbarao et al. 1991; Subbarao and Johansen 1994). Rapid screening methods and evaluation techniques are required to identify putative donor parents in a breeding program (Malhotra 1997; Saha et al. 2010). In a comprehensive study, Manasa et al. (2017) screened 40 mungbean lines sourced from World Vegetable Center for salinity tolerance using Salinity Induction Response (SIR) technique at the seedling as well as at whole plant levels by canopy phenotyping assay under 150 and 300 mM NaCl stress scenario. The results showed a marked reduction in growth and yield performances of both tolerant and susceptible lines, but a few lines displayed a relatively better biomass and pod yield on par with non-stressed control plants. The intrinsic ability of salt portioning to vacuole (more influx of Na+ ions) by tolerant lines during high salt concentration in the cytocol could be one of the reasons for their tolerance. Based on the extent of salt tolerance both at seedling and whole plant stages, a few salt tolerant lines viz., EC 693357, EC 693358, EC 693366, EC 693371, and ML1299 lines were identified (Manasa et al. 2017). A set of 105 pigeonpea genotypes/germplasm of different maturity groups ranging from super early to late maturing, popular varieties and wild accessions of Cajanus cajanifolius were screened in 2019 under lab conditions at different levels (0,40,80,100 and 120 mM) of sodium chloride (NaCl) concentrations for 30 days (Fig. 2) with regular maintenance of electric conductivity (Kumar Durgesh unpublished). A large variation in tolerance was recorded at 100 mM concentration.

It is well known that the degree of salt tolerance of different crops varies with their ontogeny. Salt tolerance in three varieties, Local arhar, ICPL 151 and ICPL 850014 of pigeon pea (*Cajanus cajan* (L.) Millsp.), was determined at three growth stages viz., germination, seedling, and adult plant by Ashraf (1994). It was also found that there is no positive correlation between tolerance at the early growth stages and at the adult stage since no clear difference in salt tolerance of the three accessions was observed at the germination and the seedling stages, whereas accessions differed considerably at the adult stage. Although increasing salt concentrations adversely



Fig. 5. Growth of tolerant genotype (BDN708) is higher as compared to sensitive genotypes (Hy3c) under saline conditions (80 mM). C = Control, T = Salt tolerant and S = Salt sensitive

affected the growth of all three accessions, ICPL 151 was however, superior to the other two accessions in fresh and dry biomass, yield and yield components when tested at the adult stage. It accumulated significantly lower Na⁺ and Cl⁻ in shoots but by contrast it was higher in shoot and root K^+ , K/Na ratios, K vs Na selectivity, soluble sugars, free amino acids and proline compared with the other two accessions. Sharma et al. (2001) screened a few genotypes of pigeonpea and its wild relatives, Atylosia platycarpa and A. albicans and found differences in tolerance to salinity and sodicity which was attributed to regulation of uptake and distribution of Na+ and K_ ions. Ashraf (1998) studied Some F1 hybrids derived from salt tolerant and salt sensitive parents of pigeonpea and observed that the high value of additive effect showed a



Fig. 5. The plates depicting significant genotypic variation for salinity stress in pigeonpea. A: Genotypes growing before salt stress and B: Differential behaviour of genotypes in salt stress conditions

significant improvement of salt tolerance is possible through mass selection and breeding.

Lentil like other pulse crops is also sensitive to salinity stress (Ashraf and Waheed 1990). Significant genetic variation for salinity tolerance prevails among the genotypes of lentil (Singh et al. 2017). An effective screening for salinity stress tolerance is required to develop salt tolerant genotypes. Screening under field conditions is generally difficult because of soil heterogeneity and other environmental factors. Therefore, laboratory-based techniques such as hydroponic may provide a suitable method for screening as it provides uniform salinity in the growing medium. However, a sensitive stage needs to be identified for accurate phenotyping.

Several reports have earlier suggested that selection of genotypes at the seedling stage is a more accurate and rapid criterion as compared to vegetative and reproductive stages for salinity stress tolerance (Gregorio 1997). Different physiological and biochemical traits such as seedling survivability salinity score, seedling growth and biomass, Na+ and Cl" accumulation, production of H2O2, antioxidant activities etc. can be used for characterization of salinity tolerance at the seedling stage in crop plants (Singh et al. 2017; Singh et al. 2018a; Singh et al. 2018b). The hydroponic system of screening is more reliable, less time consuming and can be used to diminish the environmental variation commonly encountered in the field trials (Chen et al. 2008). Seedling survival and FDA-based florescent signals have been considered the most important parameters for accurate

phenotyping of salinity tolerance in crops. Amador et al. (2000) distinguished salt-tolerant and sensitive lines of cowpea based on seedling survival trait as criterion using the hydroponic method of screening while Singh et al. (2017) using similar parameter to distinguish between salt-tolerant and salt-sensitive lines in lentil. Further, the FDA-based fluorescent signal (H_2O_2) production) in roots is reported as a more reliable parameter for the evaluation of genotypes of different plant species, based on the intensity of fluorescent signals. These traits have been found suitable and well correlated with salinity stress tolerance (Singh et al. 2017). Physiological parameters such as stomatal conductance, evapo-transpiration and leaf area, early maturity, higher predawn water potential, maintenance of high osmotic adjustment and retention of high number of stems per plant provide indications about tolerance to salinity in chickpea (Katerji et al. 2005).

Molecular approaches have recently been developed to identify trait associated molecular markers to facilitate the understanding of involved mechanism and genetics of salt tolerance. The bulk segregant analysis approach has been used for the identification of markers linked with specific genes or QTLs of interested traits (Michelmore et al. 1991). A few researchers have reported the QTLs associated with salt tolerance in various crop plants based on morpho-physiological traits (Mano and Takeda 1997; Rivandi et al. 2011; Shavrukov et al. 2010; Tiwari et al. 2016). However, the QTLs associated with different traits for salt tolerance have been studied only in few legume crops, such as chickpea (Pushpavalli et al. 2015), cowpea (Arraouadi et al. 2012) and soybean (Lee et al. 2004). Tuyen et al. (2010) studied two RIL populations (F_6 and F_2) developed by crossing salt tolerant (JWS156-1, *G soja*) and sensitive (Jackson, *G max*) genotypes of soybean and mapped a significant QTL for alkaline salt tolerance on chromosome 17, which accounted for 50.2 and 13.0% of total phenotypic variations in the F_6 and F_2 population, respectively. It was further resolved that the QTL for alkaline salt tolerance and NaCl tolerance are not the same.

Transcriptomic analysis provides detailed knowledge about the gene expression at mRNA level, which is widely used to screen candidate genes involved in stress responses. Genomic approaches which play a significant role in encoding, cloning, and characterization of important genes may lead to identification and utilization of genes/QTL for improvement of pulse crops towards salinity stress. Screening can also be done through traditional and image-based approaches to quantify growth under salt stress. Genotyping could be performed using two contrasting methods such as targeted (tGBS) and transcriptome (GBS-t) genotyping-by-sequencing. tGBS may help constructing number of single-base variants (SNPs) and markers which may evenly be distributed across the genome compared to GBS-t. A genome-wide association (GWAS) needs to be conducted to pin-point the marker-trait associations on specific chromosome. The methodology could facilitate the identification of candidate gene(s) from the reference genome to find a nutrient transporter which may be involved in salt tolerance (Dissanayake et al. 2021)

Mechanism of salinity tolerance

The physiological, biological, cellular and molecular mechanisms of salt tolerance have been studied in cereals (rice, barley and wheat), Arabidopsis and other crop plants. However, limited work on salinity tolerance has been carried out in pulse crops. Various physiological and metabolic processes are affected by salinity stress, depending on severity and duration of the stress (Munns 2005; Rozema and Flowers 2008). The soil salinity represses plant growth in the form of osmotic stress which is then followed by ion toxicity, reduces water absorption capacity by roots, decrease water loss from leaves due to osmotic stress of high salt accumulation in soil and plants (Gupta and Huang 2014). The salinity stress, which is also considered as hyperosmotic stress (Munns 2005), leads to several physiological changes in the plants such as interruption of membranes, nutrient imbalance, impairs the ability to detoxify reactive oxygen species (ROS), differences in the antioxidant enzymes and decreased photosynthetic activity, and decrease in stomatal aperture (Munns and Tester 2008).

Under salinity stress the ion uptake is affected and therefore, ion homeostasis plays a crucial role for normal plant growth and development. Singh et al. (2018) elucidated the role of osmotic, ionic and major salt responsive transcript components towards salinity tolerance in contrasting chickpea (Cicer arietinum L.) genotypes and found that under lower electrolyte leakage (EL) ratio in tolerant genotypes improves their ability to protect the membranous cellular network from uncontrolled EL under salt stress. Previous reports have shown plant tolerance to salt stress is closely related to the maintenance of high cytosolic K+/Na+ homeostasis under salinity stress. For example, coexpression of ZxNHX and ZxVP1-1 in transgenic alfalfa plants resulted in a higher accumulation of Na⁺, K^+ , and Ca²⁺ in both leaves and roots (Bao et al. 2016).

Both glycophytes and halophytes do not tolerate high concentration of salts in their cytoplasm due to salt stress, hence excess salt is either transported to vacuole or sequestered in older tissues to protect the plant (Hasegawa 2013; Jhu 2003; Dietz et al. 2001). In saline soils, a major form of salt present is NaCl. The Na⁺ ion is transported from the cytoplasm to the vacuole via Na⁺/H⁺ antiporter. Two types of H⁺ pumps are present in the vacuolar membrane: vacuolar type H⁺-ATPase (V-ATPase) and the vacuolar pyrophosphatase (V-PPase) (Dietz et al. 2001; OliveiraOtoch et al. 2001). Both Na⁺ and Cl⁻ are readily translocated in the phloem so that higher concentrations can be redistributed throughout the plant. They also accumulate salt and soluble carbohydrates in cell sap to maintain low osmotic potential. Many plants have inherent system to keep the ion concentration in the cytoplasm in a low level. The transport phenomenon is maintained by different carrier proteins and antiporters. Ma et al. (2012) have reported cellular Na⁺/K⁺ homeostasis in Arabidopsis NADPH oxidases AtrbohD and AtrbohF function in ROS- dependent regulation of Na⁺/K⁺ homeostasis under salt stress. Both ions, Na⁺ and K⁺ have similar transport mechanism and thereby decrease the uptake of K⁺. Salinity tolerance in cultivated pigeonpea is perhaps facilitated by low accumulation of Na in roots and translocation of high content of K to shoots (Subbarao et. al. 1991). Oliveira Otoch et al. (2001) observed in the hypocotyls of Vigna unguiculata seedlings that the activity of V-ATPase pump increased when exposed to salinity stress while that of V-PPase got inhibited. On the otherhand, in the case of halophyte *Suaeda salsa*, V-ATPase activity was upregulated and V-PPase played a minor role (Wang et al. 2001).

The role of Salt Overly Sensitive (SOS) stress signaling pathway has come in prominence recently in ion homeostasis in salt tolerance (Hasegawa et al. 2000; Shi et al. 2000a). Three major proteins namely, SOS1, SOS2 and SOS3 play a major role in encoding a plasma membrane bound Na⁺/H⁺ antiporter, which is essential in regulating Na⁺ efflux at cellular level facilitating transport of Na⁺ from root to shoot. The second protein, SOS2 encodes a serine/threonine kinase and that is activated by salt stress elicited Ca⁺ signals. Viswanathan et al. (2005) advocated that Na_ efflux and vacuolar compartmentation. putative osmosensory histidine kinase (AtHK1)-MAPK cascade probably regulates osmotic homeostasis and ROS scavenging. Os- motic stress and ABA (abscisic acid)mediated regulation of LEA (late-embryogenesisabundant)-type proteins also play important roles in plant salt tolerance. Over expression of this protein confers salt tolerance in plants (Shi et al. 2000b; Liu et al. 2000). The third type of protein SOS3 is also involved in the stress signaling pathway which is a myristoylated Ca⁺ binding protein and contains a myristoylation site at its N-terminus (Hasegawa et al. 2000; Shi vet al. 2000; Shi et al. 2000; Liu et al. 2000).

Compatible solutes or compatible osmolytes, include proline (Nounjan et al. 2012), glycine betaine (Wang and Nii 2000), sugar (Kerepesi and Galiba 2000; Kerepesi and Galiba 2000) and polyols (Ashraf and Foolad 2007; Ford 1985). The accumulation of proline and antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and Glutathione peroxidase (GPX) are efficiently involved in scavenging of ROS (reactive oxygen spices) produced during salt stress conditions, and act as an important tolerance mechanism against oxidative stresses in plants. It is reported that soybean salt tolerance 1, named GmST1, exhibited strong tolerance to salt stress in the Arabidopsis transgenic lines. The GmST1-overexpressed Arabidopsis also increased sensitivity to ABA and decreased production of reactive oxygen species under salt stress (Ren 2016). Organic osmolytes are synthesised and accumulated in varying amounts amongst different plant species. And their major functions are to protect the structure and to maintain osmotic balance within

the cell via continuous water influx (Hasegawa et al. 2000). Glycine betaine, a non-toxic cellular osmolyte, plays an important role in stress mitigation by raising the osmolarity of cell during stress period. It also also protects the cell by osmotic adjustment (Gadallah 1999), stabilizes proteins (Makela et al. 2000), and protects the photosynthetic apparatus from stress damages (Cha-Um and Kirdmanee 2010) and reduction of reactive oxygen species (ROS) (Saxena et al. 2013).When glycine betaine is applied as a foliar spray in a plant subjected to stress, it led to pigment stabilization and increase in photosynthetic rate and growth (Cha-Um and 2010; Ahmad et al. 2013). In higher plants glycine betaine is synthesized by the enzyme choline monooxygenase (CMO), and catalysed by betaine aldehyde dehydrogenase (BADH).

A few amino acids such as cysteine, arginine, and methionine are decreased when exposed to salinity stress, whereas proline concentration rises in response to salinity stress (EI-Shintinawy and EI-Shourbagy 2001). Proline accumulation is a well-known measure adopted for alleviation of salinity stress (Saxena et al. 2013; Matysik et al. 2001). Intracellular proline which is accumulated during salinity stress not only provides tolerance towards stress but also serves as an organic nitrogen reserve during stress recovery. To maintain the concentration of compatible solutes and osmolarity in the cells different genes and biochemical pathways are involved are to protect the structure and to maintain osmotic balance within the cell via continuous water influx (Hasegawa et al. 2000). Similarly, polyamines also play a significant role in abiotic stress tolerance including salinity stress. They are small, low molecular weight, ubiquitous, polycationic aliphatic molecules widely distributed throughout the plant kingdom. The most common polyamines that are found within the plant system are diamine putrescine, triamine spermidine and tetra-amine spermine (Kuznetsov and Shevyakova; Hussain et val. 2011; Shu et al. 2012). Polyamine biosynthesis pathway in Arabidopsis involves six major enzymes. The exposure of plants to salinity stress increases the level of polyamines, which is regulated by polyamine catabolism. They are oxidatively catabolised by amine oxidases which include copper binding diamine oxidases and FAD binding polyamine oxidases. These enzymes play a significant role in stress tolerance (Takahashi and Kakehi 2010; Cona et al. 2006). Further, salt stress regulates polyamine biosynthesis and catabolism by acting as a cellular signal in hormonal pathways and

May, 2021]

thereby regulating abscisic acid (ABA) in response to stress (Shevyakova et al. 2013).

War et al. (2011) studied different sensory mechanisms in chickpea to cope up with salt stress. They found that signaling mechanism is regulated at three different levels, first at the plant hormonal level, second by activation of transcription factors for gene expression and third by activation of metabolic pathways. Deinlein et al. (2014) found that plasma membrane is the first line of defense which perceives the stress through trans-membrane protein sensors. Initially, phospholipids receive the signal when high extracellular NaCl concentration occurs at ionic receptors of the root cell. The phospholipids have specific roles in regulating activation of calciumdependent protein kinase CaCDPK1 genes, which are involved in the release of signaling messengers such as calcium ions (Ca²⁺) (Zepeda-Jazo et al.2011; Syam Prakash and Jayabaskaran 2006; Geiger et al. 2011) through the control of transcription factors during the saline stress responses in chickpea (Dixit and Jayabaskaran 2012).

Transcription factors bind to the promoter regions of the genes to facilitate the RNA polymerase to start the transcription and subsequent translation of the gene products (Franco-Zorrillaa et al. 2014). They are important regulators of stress response and have been widely found to show differential expressions in saltchallenged tissues in *Cicer arietinum* (Hiremath et al. 2011; Jain et al. 2013). A number of transcription factors in *Arabidopsis* have been identified to be associated in the activation of genes responsible for osmotic adjustments (Peng et al. 2009). Transcription factors such as *CAP2/AP2*, *CarNAC1*, *CaZF* and *CarF* that are known to up-regulate the *Ca*CDPK1 genes have been identified in chickpea (Jain et al. 2013; Jia et al. 2012).

The application a phytohormone ABA to plant ameliorates the effect of stress condition(s). This phytohormone is upregulated due to soil water deficit around the root. Salinity stress causes osmotic stress and water deficit, increasing the production of ABA in shoots and roots (Cabot et al. 2009). The accumulation of ABA can mitigate the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates (Jeschke et al. 1997) probably due to the accumulation of compatible solutes and assimilates. The accumulation of K⁺, Ca²⁺ and compatible solutes, such as proline and sugars, in vacuoles of roots, which counteract with the uptake of Na⁺ and Cl⁻ and thus modulates the expression of several salt and water deficit-responsive genes. Certain compounds such as salicylic acid (SA) and brassinosteroids (BR) produce plant abiotic stress responses in plants (Fragnire et al. 2011; Clause and Sasse 1998). Jayakannan et al. (2013) have shown that SA improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-induced K⁺ loss via a guard cell outward rectifying K(+) (GORK) channel and also upregulate H⁺-ATPase activity, thereby improving K⁺ retention during salt stress. Nazar et al. (2011) found that SA alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in mung bean cultivars. The negative effects of salinity may also be mitigated by BR (EI-Mashad and Mohamed 2012; Krishna 2003). Application of BR enhanced the activity of antioxidant enzymes (SOD, POX, APX, and GPX) and the accumulation of nonenzymatic antioxidant compounds (tocopherol, ascorbate, and reduced glutathione) (El-Mashad and Mohamed 2012). Both BRs and SA are ubiquitous in the plant kingdom, affecting plant growth and development in many ways, and are known to improve plant stress tolerance. The possible applications of BRs and SA to mitigate the harmful effects of salt stress in plants has been reviewed (Ashraf et al. 2010) and discussed the roles of exogenous applications of BRs and SA in the regulation of various biochemical and physiological processes leading to improved salt tolerance in plants.

A huge number of salt-responsive transcription factors and genes which are either upregulated or downregulated in response to salinity stress have been identified and characterized using transcriptomic and genomic approaches. To screen candidate genes involved in gene expression of stress response, transcriptomic analysis at mRNA level is essential. Transcription factors such as bZIP, WRKY, AP2, NAC, C2H2 zinc finger gene, and DREB families comprise many stress-responsive members which can control the expression of a broad range of target genes by binding to the specific cis-acting element in the promoters of these genes. Vincente and Plasencia(2011) found that transcriptomic factors and gene transcription are highly activated on up-regulated plant hormones such as ABA, Indole Acetic Acid (IAA), gibberellic acid (GA) and methyl jasmonate (MeJA), which induce expression of CarLEA genes. Accordingly, these genes viz., CarLEA genes (CarLEA1, CarLEA2 and CarLEA4) isolated from chickpea cDNA libraries, were found to impart desiccation tolerance during seed development, thereby protecting plants against a variety of stresses, including drought, salinity and freezing (Gu et al. 2012; Romo et al. 2001).

Transcriptions factors such as OsNAC5 and ZFP179 show an upregulation under salinity stress, which may regulate the synthesis and accumulation of proline, sugar, and LEA proteins that in turn play an integral role in stress tolerance (Hu et al. 2013). A transcription factor gene, *SALT-RESPONSIVE ERF1* (*SERF1*) has shown root-specific induction upon salt and H_2O_2 treatment and the loss of *SERF1* impairs the salt-inducible expression of genes (Schmidt et al 2013). It has been observed that the plants deficient for SERF1 are more sensitive to salt stress compared with the wild type, while constitutive overexpression of SERF1 improves salinity tolerance in crops.

Transcription factors are considered as most important regulators that control gene expressions. They are important regulators of stress response and have been widely found to show differential expressions in salt-challenged tissues (Hiremath et al. 2011: Jain et al. 2013). Several transcription factors have been identified to be associated in the activation of genes responsible for osmotic adjustments (Peng et al. 2009). Transcription factors such as *CAP2/AP2*, *CarNAC1*, *CaZF* and *CarF* that are known to up-regulate the *Ca*CDPK1 genes have been identified in chickpea (Jia et al. 2012).

Singh et al. (2021) conducted an extensive transcriptomic skimming to determine the molecular, morphological, physiological, and biochemical responses in salt-tolerant variety, PDL-1 and saltsensitive cultivar, L-4076 under control (0mMNaCl) and salinity stress (120mMNaCl) conditions at seedling stage. The investigation revealed that PDL-1 had no salt injury and showed higher K+/Na+ ratio, relative water content, chlorophyll, glycine betaine, and soluble sugars in leaves while lower H₂O₂ induced fluorescence signals in roots as compared to L-4076. The study further indicated that putative molecular mechanism of salinity tolerance in lentil together with identification of 5643 simple sequence repeats (SSRs) and 176,433 single nucleotide polymorphisms (SNPs) would facilitate the construction of dense linkage maps along with detection of quantitative trait loci (QTLs) associated with traits of interests. They further argued that stress-related pathways can be targeted to improve salinity stress tolerance in crop species.

Potential strategies to develop salt stress tolerant genotypes of pulse crops

Identification of morphological and physiological traits and determination of other genetical parameters are essential prerequisite to manipulate the plant mechanism for developing salt tolerant genotypes by conventional or molecular techniques. Viswanathan et al. (2005) suggested that genetic engineering of ion transporters and their regulators, and of the CBF (Crepeat-binding factorholds promise for future development of salt-tolerant crops.

Mielewczik et al. (2013) demonstrated a novel method of analyzing two-dimensional leaf expansion in high temporal solution based on marker tracking approach in soybean. Similarly, ion channel regulation has been found to be effective in enhancing salinity tolerance in chickpea.

Screening of the germplasm and identification of tolerant genotypes would remain to be to the most effective and guick approach of developing genotype tolerant to salinity stress. A set of specific physiological indicators may be selected while assessing the crop for salt tolerance. Vadez et al. (2012b) screened chickpea genotypes based on sensitivity at reproductive stage and reported large variation for salt tolerance. The identified genotypes could be used as potential resource for salt tolerance related traits to facilitate genet transfer of useful alleles. Molecular breeding approaches would facilitate effective translation of the genomic knowledge towards the development of salinity tolerant genotypes. With the advent of next generation phenomics platforms such as robotic field sensors, high resolution multi-spectral mapping using UAVs and laser light back scattering technology, it has become easier to study developmental stages of plant more precisely and analyses the multi-dimensional large volume of bioimaging data (Mielewczik et al. 2013; Cai et al. 2016).

Biotechnological approaches for improvement of pulses against salinity stress

The attempts in the development of salt-tolerant pulse crops through genetic engineering approach are limited. One of the possible ways is to increase the plant's ability to limit the uptake of salt ions from the soil, increasing the active extrusion rate of salt ions and improving the compartmentalization of salt ions in the cell vacuole may the best strategy.

Kaashyap et al. (2018) investigated physiological

and transcriptional responses in salt tolerant and salt sensitive chickpea genotypes and created RNA-Seq reads from root tissues and identified differentially expressed genes responding to salt stress. They also reported major transcriptional reorganization in response to salt stressand significant upregulation of various genes encoding important enzymes including DREB1E and ERF in the tolerant genotype. Further, the study identified important genes involved in cell wall modification and root morphogenesis. The integration of phenotypic and genomic data may provide a better understanding of salt tolerance mechanism. The availability of genome of several pulses could offer an important opportunity in finding the candidate genes involved in salt tolerance mechanisms in the pulse crops. Soren et al. (2020) carried out an extensive analysis of the phenotypic and genotypic data generated from the RILS derived from a cross, ICCV 10 (salt-tolerant) x DCP 92-3 (saltsensitive) chickpea genotypes. The RIL population was evaluated under salt stress conditions in field and phenotypic data was assembled. Axiom®CicerSNP analysis identified 28 quantitative trait loci (QTLs) explaining up to 28.40% of the phenotypic variance in the population. Deployment of such QTL may help development of chickpea genotype with salt tolerance.

A wide range of genes encoding different structural and regulatory proteins have been reported and/or have been employed over the past decades to develop abiotic stress-tolerant transgenic plants (Bhatnagar et al. 2008). Pathogenesis-related (PR) proteins accumulate in plants upon pathogen infestations and, in many cases, in response to abiotic stresses for survival (Stratilová et al. 2020). The protein PR10 iswell known as osmotically inducible protein and elicitor and plays an important role in plant defense mechanisms of salinity stress (Abreu et al. 2013; Agarwal et al. 2016). Studies on proteomic investigation of pea under salt stress revealed significant increase in the level of several classes of PR10 proteins.

The constitutive expression of a pea PR10 gene in *Brassica napus* enhanced germination and growth rates under salinity (Srivastava et al. 2004). Accumulation of PR10 proteins was also observed in grass pea in response to salt stress (Chattopadhyay et al. 2011). Overexpression of the *PR10a* gene in faba bean (*Vicia faba*) plants promotes sustained growth and development under salt stress (Desouky et al. 2021).

Future perspectives

Breeding pulse crops for stressful environments is especially important for enhancing the production and productivity of the pulses. Genomic approaches and available molecular marker technology will help in the evaluation and identification of salt tolerant genotypes and donors for developing new lines and reduce dependency on the phenotypic data alone. Genome Wide Association Studies would help in better understanding the genetic basis of the phenotypes. The traits related to salinity stress needs to be quantified for strategic application of phenomics tools. As evident from the published literature, some of the traits such as high photosynthesis or quantum yields have been associated with tolerance to drought, salinity, or high temperature. Generally, it is attributed to the capacity of plants to maintain nutrient and water balance in the tissue reflected by relative water content and stress avoidance mechanism. Therefore, an efficient integration of genomics, proteomics, metabolomics, ionomics and phenomics will enrich biological understanding of salinity stress tolerance. Of late, converging various ultra-modern technologies like, infra-red thermography, automated robotics, camera images, and computational algorithms, which all make components of high throughput phenotyping facilities (phenomics and phenospex) can facilitate high throughput phenotyping for stress tolerance. Genetic engineering has been proved to be an efficient approach to the development of salinity-tolerant plants, and this approach will become more powerful as more candidate genes associated with salinity tolerance are identified and widely utilized.

Declaration

The authors declare no conflict of interest.

Acknoweldgements

The authors acknowledge the National Phytotron Facility, IARI, New Delhi for providing facility for conducting experiments.

References

- Asif A. 2017. Exploring genetic variation to improve salinity tolerance in faba bean. The University of Adelaid, Australia (Presentation), adelaid.edu.au.
- Ábrahám E., Salamó I. P., KonczC. and Szabados L. 2011. Identification of *Arabidopsis* and *Thellungiella* genes involved in salt tolerance by novel genetic system," Acta Biologica Szegediensis, **55**(1): 53-57.
- Abreu I.A., Farinha A.P., Negrão S., Gonçalves N.M.,

Fonseca C., Rodrigues M.A.A., Batista R., Saibo N.J. and Oliveira M.M. 2013. Coping with abiotic stress: Proteome changes for crop improvement. J. **93**: 145-168.

- Acosta-Motos J.R., Ortuño M.F., Bernal-Vicente A., Diaz-Vivancos P., Sanchez-Blanco M.J. and Hernandez J.A. 2017. Plant Responses to Salt Stress: Adaptive Mechanisms. Agron., **7**: 18.
- Agarwal P., Dabi M., More P., Patel K., Jana K. and Agarwal P.K. 2016. Improved shoot regeneration, salinity tolerance and reduced fungal susceptibility in transgenic tobacco constitutively expressing PR-10a gene. Front. Plant Sci., **7**: 217.
- Ahmad P. and Prasad M. N. V. 2012. Abiotic stress responses in plants: Metabolism, productivity and sustainability. New York, NY: Springer. doi: 10.1007/ 978-1-4614-0634-1.
- Ahmad P. and Prasad M. N. V. 2012. Abiotic stress responses in plants: Metabolism, productivity and sustainability. New York, NY: Springer. doi: 10.1007/ 978-1-4614-0634-1.
- Ahmad R., Lim C. J. and Kwon S.Y. 2013. Glycine betaine: a versatile compound with great potential for gene pyramiding to improve crop plant performance against environmental stresses," Plant Biotechnol. Rep., **7**: 49-57.
- Ahmed, S. (2009). Effect of soil salinity on the yield and yield components of mungbean. Pak. J. Bot., **41**(1): 263-268.
- Ahmed, S. (2009). Effect of soil salinity on the yield and yield components of mungbean. Pak. J. Bot., **41**(1): 263-268.
- Amador B. M., Troyo-Diéguez E., Jones H. G., Ayala-Chairez F., Tinoco-Ojanguren C. and López-Cortés A. 2000. Screening and classification of cowpea genotypes for salt tolerance during germination.PYTON Inter. J. Exp. Bot., 67: 71-84.
- Ambede J. G., Netondo G. W., Mwai G. N., and Musyimi D. M. 2012. NaCl salinity affects germination, growth, physiology, and biochemistry of bambara groundnut. Braz. J. Plant Physiol., 24: 151-160. doi: 10.1590/ S1677-04202012000300002.
- Ambede J. G., Netondo G. W., Mwai G. N., and Musyimi D. M. 2012. NaCl salinity affects germination, growth, physiology, and biochemistry of bambara groundnut. Braz. J. Plant Physiol., 24: 151-160. doi: 10.1590/ S1677-04202012000300002.
- Ashraf M, Wu L (2011) Breeding for salinity tolerance in plants. Crit. Rev. Plant Sci., **13**: 17-42.
- Ashraf M. 1994. Salt tolerance of pigeonpea (*Cajanus cajan* L. Millsp) at three growth stages. Annals Appl. Biol., http://doi.org/10.1111/j.1744-7348.1994. tb04123.x.
- Ashraf M. 2004. Some important physiological selection

criteria for salt tolerance in plants. Flora Morphol. Distrib. Funct. Ecol. Plants, **199**: 361-376.

- Ashraf M. and Foolad M. R. 2007. Roles of glycine betaine and proline in improving plant abiotic stress resistance. Env. Exp. Bot., **59**(2): 206-216.
- Ashraf M., Akram N. A., Arteca R. N., and Foolad M. R. 2010. The physiological, biochemical and molecular roles of brassinosteroids and salicylic acid in plant processes and salt tolerance.Critical Rev. Plant Sci., 29(3): 162-190.
- Ashraf M. 1998. Components of genetic variation of salt tolerance in pigeon pea (*Cajanus cajan* (L.) Millsp.). Arch.Agro. Soil Sci., **43**: 409-416. http://doi.org/ 10.1080/03650349809366056.
- Ashraf M. and Waheed A. 1990. Screening of local/exotic accessions of lentil (*Lens culinaris*) for salt tolerance at two growth stages. Plant and Soil, **128**: 167-176.
- Ashraf M. and Waheed A. 1998. Components of genetic variation of salt tolerance in chickpea (*Cicer arietinum* L.). Arch. Agron. Soil Sci., **42**: 415-424.
- Bao A.K., Du B.Q., Touil L., Kang P., Wang Q.L. and Wang S.M. 2016. Co-expression of tonoplast Cation/H+ antiporter and H₊⁻ pyrophosphatase from xerophyte *Zygophyllumxanthoxylum* improves alfalfa plant growth under salinity, drought and field conditions. Plant Biotechnol. J., **14**: 964-975.
- Benerjee A., Ghosh P. and Roychoudhury. 2018. Salt stress responses in pigeonpea (*Cajanus cajan* L.): In: Pulse Improvent Physiological, molecular and genetic perspectives (Eds. S.H. Wani and Mukesh Jain). Springer Nature, Switzerland. Pp 99-108.
- Bhatnagar-Mathur P., VadezV. and Sharma K.K. 2008.Transgenic approaches for abiotic stress tolerance in plants: Retrospect and prospects. Plant Cell Rep., 27: 411-424.
- Bianco and Defez. 2009. *Medicago truncatula* improves salt tolerance when nodulated by an indole-3-acetic acid-overproducing *Sinorhizobiummeliloti* strain. J. Expl. Bot., **60**: 3097-3107.
- Cabot C., Sibole J. V., Barceló J. and Poschenrieder C. 2009. Abscisic acid decreases leaf Na⁺ exclusion in salt-treated *Phaseolus vulgaris* L.J. Plant Growth Reg., **28**(2): 187-192.
- Bulut F. and Akinci S. 2010. The effect of salinity on growth and nutrient composition in broad bean (*Vicia faba* L.) seedlings. Fresenius Env. Bull., **19**(12): 2901-2910.
- Cai J., Okamoto M., Atieno J., Sutton T., Li Y. and Miklavcic S.J. 2016. Quantifying the onset and progression of plant senescence by color image analysis for high throughput applications. PLoS One, **11**(6):e0157102.
- Chattopadhyay A., Subba P., Pandey A., Bhushan D., Kumar R., Datta A., Chakraborty S. and Chakraborty N. 2011. Analysis of the grasspea proteome and

- Cha-Um S. and Kirdmanee C. 2010. Effect of glycinebetaine on proline, water use, and photosynthetic efficiencies, and growth of rice seedlings under salt stress. Turkish J. Agric. Forestry, 34(6): 517-527.
- Chen H., Cui S., Fu S., GaiJ. and Yu D. 2008. Identification of quantitative trait loci associated with salt tolerance during seedlinggrowth in soybean (*Glycine max* L.). Aust. J. Agric. Res., **59**: 1086-1091.
- Clause S. D. and Sasse J. M. 1998. Brassinosteroids: essential regulators of plant growth and development. Annual Rev. Plant Biol., **49**: 427-451.
- Cona A., Rea G., Angelini R., Federico R. and Tavladoraki P. 2006. Functions of amine oxidases in plant development and defence. Trends Plant Sci., **11**(2): 80-88.
- CSSRI. 2015. Vision-2050. Central Soil Salinity Research Institute, Karnal, India. p31.
- Deinlein U., Stephan A.B., Horie T., Luo W., Xu G., Schroeder J.I. Plant salt-tolerance mechanisms. Trends Plant Sci., **19**(6): 371-379.
- DesoukyAbeer F., Hanafy Ahmed A. H., Stutzel H., Jacobsen Hans-Jorg, Pao Yi-Chen and Hanafy Moemen S. 2021. Enhanced Abiotic Stress Tolerance of *Vicia faba* L. Plants Heterologously Expressing the PR10a Gene from Potato. Plants (Basel)., **10**(1): 173. doi: 10.3390/ plants10010173.
- Dietz K. J., Tavakoli N., Kluge C. et al. 2001. Significance of the V-type ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level.J. Exp. Bot., **52**(363): 1969-1980.
- Dissanayake R., Cogan N.O.I., Smith K.F. and Kaur S. 2021. Application of genomics to understand salt tolerance in lentil. Genes, **12**(3): 332. https://doi.org/ 10.3390/genes 12030332.
- Dixit A.K. and Jayabaskaran C. 2012. Phospholipid mediated activation of calcium dependent protein kinase 1 (CaCDPK1) from chickpea: a new paradigm of regulation. PLoS One. **7**(12): e51591.
- Dua R.P., Sharma S.K. and Mishra B. 1989. Response of broad bean (Vicia faba) and pea (Pisum sativum) varieties to salinity. Indian J. agric. Sci., 59: 729-731.
- DubcovskyJ., Maria G. S., Epstein E., Luo M. C. and Dvorak J. 1996. Mapping of the K⁺/Na⁺ discrimination locus *Kna1* in wheat. Theor. Appl. Genet., **92**: 448-454.
- Ebbisa A. and Essubalew G. 2015. Influence of different salinity concentration on growth and nodulations of chickpea (*Cicer arietinum* L.) at jimma, southwest

ethiopia. Int. J. Inno. Appl. Res., 3(8): 1-9.

- El-Mashad A. A. A. and Mohamed H. I. 2012. Brassinolide alleviates salt stress and increases antioxidant activity of cowpea plants (*Vigna sinensis*). Protoplasma, **249**(3): 625-635.
- EI-Shintinawy F. and EI-Shourbagy M. N. 2001. Alleviation of changes in protein metabolism in NaCI-stressed wheat seedlings by thiamine. Biologia Plantarum, 44(4): 541-545.
- Eswaran H., Beinroth F.H. and Reich P.F. 2003. A global assessment of land quality. In: Land quality, agricultyral productivity, and food security: biophysical process and economic choice at local, regional and global levels (Ed. K. Wiebe). Pub. Edward Elgar, Northampton, pp 11-132.
- Farshadfar E., Safavi S. A. and Aghaee-Sarbarzeh M. 2008. Locating QTLs controlling salt tolerance in barley using wheat-barley disomic addition lines. Asian J. Plant Sci., **7**: 149-155.
- Flowers T. J., Gaur P. M., Gowda C. L. L., Krishnamurthy L., Srinivasan S., Siddique K. H. M., Turner N. C., Vadez V., Varshney R. K., and Colmer T. D. 2010. Salt sensitivity in chickpea. Plant, Cell Environ., 33: 490-509.
- Ford C. W. 1985. Accumulation of low molecular weight solutes in water-stressed tropical legumes. Phytochemistry, **23**(5): 1007-1015.
- Fragnire C., Serrano M., Abou-Mansour E., MétrauxJ.P. and L'Haridon F. 2011 Salicylic acid and its location in response to biotic and abiotic stress. FEBS Letters, **585**(12): 1847-1852.
- Franco-Zorrillaa J.M., Lopez V.I., Carrasco J.L., Godoy M., Vera P. and Solano R. 2014. DNA-binding specificities of plant transcription factors and their potential to define target genes. Proc. Natl. Acad. Sci. USA., 111(6): 2367-2372.
- Gaballah M.S. and Gomaa A.M. 2004. Performance of faba bean varieties grown under salinity stress and biofertilized with yeast. J. App. Sc., 4: 93-99. Doi: 10.3923/jas.2004.93.99.
- Gadallah M. A. A. 1999. Effects of proline and glycinebetaine on Vicia faba responses to salt stress," Biologia Plantarum, 42(2): 249-257.
- Gama P.B.S., Inanaga S., Tanaka K. and Nakazawa R. 2007. Physiological response of common bean (*Phaseolus vulgaris* L.) seedlings to salinity stress. Afr. J. Biotechnol., **6**: 79-88.
- Garg N. and Noor Z. 2009. Genotypic differences in plant growth, osmotic and antioxidative defence of *Cajanus cajan* (L.) Millsp. modulated by salt stress. Arch. Agron. Soil Sci., **55**: 3-33.
- Geiger D., Scherzer S., Mumm P., Marten I., Ache P., Matschi S., Liese A., Wellmann C., Al-Rasheid K.A., Grill E., Romeis T. and Hedrich R. 2010. Guard cell

anion channel SLAC1 is regulated by CDPK protein kinases with distinct Ca^{2+} affinities. Proc. Natl. Acad. Sci. USA. **107**(17): 8023-8028.

- Gowda C.L.L., Rao P.P., Tripathy S., Gaur P.M., Deshmukh R.B. 2009. Regional shift in chickpea production in India. In: Milestone in Food Legumes Research. (Eds. Masood Ali and,S. Kumar), Indian Institute of Pulses Research, Kanpur, 208.024, India, pp.21-35.
- Greenway H. and Munns R. 1980. Mechanisms of salt tolerance in non halophytes. Ann. Review Plant Physiol., **31**: 149-190.
- Gu H., Jia Y., Wang X., Chen Q., Shi S., Ma L., Zhang J., Zhang H., Ma H. 2012. Identification and characterization of a LEA family gene CarLEA4 from chickpea (*Cicer arietinum* L.). Mol. Biol. Rep., **39**(4): 3565-3572.
- Guan R., Chen J., Jiang J., Liu G.,LiuY., Lei, Tetal. 2014. Mapping and validation of a dominant salt tolerance gene in the cultivated soybean (*Glycine max*) variety Tiefeng 8. The Crop J., **4**: 358-365.
- Gupta B. and Huang B. 2014. Mechanism of Salinity Tolerance in Plants: Physiological, Biochemical, and Molecular Characterization. Inter. J. Genomics,Vol. 2014, Article ID 701596. https://doi.org/10.1155/ 2014/701596.
- Hamwieh A. and Xu D. 2008. Conserved salt tolerance quantitative trait locus (QTL) in wild and cultivated soybeans. Breed. Sci., **58**(4): 355-359.
- Hamwieh, A., Tuyen, D. D., Cong, H., Benitez, E. R., Takahashi, R., & Xu, D. H. (2011). Identification and validation of a major QTL for salt tolerance in soybean. Euphytica, **179**(3): 451-459.
- Hanafy M., El-Banna A., Schumacher H.M., Jacobsen H.-J. and Hassan F. 2013. Enhanced tolerance to drought and salt stresses in transgenic faba bean (*Vicia faba* L.) plants by heterologous expression of the PR10a gene from potato. Plant Cell Rep., **32**: 663-674.
- Hanumantha Rao B., Nair R. M. and Nayyar H. 2016. Salinity and high temperature tolerance in mungbean [*Vigna radiata* (L.) Wilczwk] from a physiological perspective. Front. Plant Sci., **7**: 1-20. doi: 10.3389/ fpls.2016.00957
- HanumanthaRao B., Nair R. M. and Nayyar H.2016. Salinity and high temperature tolerance in mungbean [*Vigna radiata* (L.) Wilczwk] from a physiological perspective. Front. Plant Sci., 7: 1-20. doi: 10.3389/ fpls.2016.00957.
- Hasanuzzaman M., Nathan K. and Fujita M. 2013. Plant response to salt stress and role of exogenous protectants to mitigate salt induced damages. In: Ecophysiology and Responses of Plant under Salt Stress (Eds. P. Ahmad, M.M. Azooz and M.N.V. Prasad), Springer, New York, pp. 25-87.

Hasegawa P. M., Bressan R. A., Zhu J.K. and Bohnert H.

J. 2000, Plant cellular and molecular responses to high salinity. Annual Rev. Plant Biol., **51**: 463-499.

- Hasegawa P. M. 2013. Sodium (Na⁺) homeostasis and salt tolerance of plants. Env. Exp. Bot., **92**: 19-31.
- Hashimoto M., Kisseleva L., Sawa S., Furukawa T. Komatsu S. and Koshiba T. 2004. A Novel Rice PR10 Protein, RSOsPR10, Specifically Induced in Roots by Biotic and Abiotic Stresses, Possibly via the Jasmonic Acid Signaling Pathway. Plant Cell Physiol., 45: 550-559.
- Hiremath P.J., Farmer A., Cannon S.B., Woodward J., Kudapa H., Tuteja R., Kumar A., Bhanuprakash A., Mulaosmanovic B., Gujaria N., Krishnamurthy L., Gaur P.M., Kavikishor P.B., Shah T., Srinivasan R., Lohse M., Xiao Y., Town C.D., Cook D.R., May G.D. and Varshney R.K. 2011. Large-scale transcriptome analysis in chickpea (*Cicer arietinum* L.), an orphan legume crop of the semi-arid tropics of Asia and Africa. Plant Biotechnol. J., **9**(8): 922-931.
- Hu Y., Chen L., Wang H., Zhang L., Wang F. and Yu D. 2013. *Arabidopsis* transcription factor WRKY8 functions antagonistically with its interacting partner VQ9 to modulate salinity stress tolerance. The Plant J., 74: 730-745.
- Hussain S. S., Ali M., Ahmad M. and Siddique K. H. M. 2011.Polyamines: natural and engineered abiotic and biotic stress tolerance in plants. Biotechnol. Adv., 29(3): 300-311.
- ICAR and NAAS. 2010. Degraded and Wastelands of India: Status and spatial distribution. Indian Council of Agricultural Research and National Academy of Agricultural Science, New Delhi, p 158.
- Jain M., Misra G., Patel R.K., Priya P., Jhanwar S., Khan A.W., Shah N., Singh V.K., Garg R., Jeena G., Yadav M., Kant C., Sharma P., Yadav G., Bhatia S., Tyagi A.K. and Chattopadhyay D. 2013. A draft genome sequence of the pulse crop chickpea (*Cicer arietinum* L.). Plant J., **74**(5): 715-729.
- Jain M. 2011. Next-generation sequencing technologies for gene expression profiling in plants. Brief. Funct. Genomics, 11(1): 63-70. https://doi.org/10.1093/bfgp/ elr038.
- Jain D. and Chattopadhyay D. 2010. Analysis of gene expression in response to water deficit of chickpea (*Cicer arietinum* L.) varieties differing in drought tolerance. BMC Plant Biol., **10**(1): 24. https://doi.org/ 10.1186/1471-2229-10-24.
- Jayakannan M., Bose J., Babourina O. et al. 2013. Salicylic acid improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing saltinduced K⁺ loss via a GORK channel," J. Exp. Bot., 64(8): 2255-2268.
- Jeschke W. D., Peuke A. D., Pate J. S. and Hartung W. 1997. Transport, synthesis and catabolism of abscisic acid (ABA) in intact plants of castor bean (*Ricinus*

communis L.) under phosphate deficiency and moderate salinity. J. Exp. Bot., **48**(314): 1737-1747.

- Jha Uday C., Caturvedi Sushil K., Bohra Abhishek , BasuPartha S. , Khan M. and BarhDebmalya A.. 2014. Abiotic stresses, constraints and improvement strategies in chickpea. Plant Breed., **133**: 163–178 doi:10.1111/pbr.12150
- Jia Y., Gu H., Wang X., Chen Q., Shi S., Zhang J., Ma L., Zhang H., Ma H. 2012. Molecular cloning and characterization of an F-box family gene CarF-box1 from chickpea (*Cicer arietinum* L.). Mol. Biol. Rep., **39**(3): 2337-2345.
- Johnson R. R., Wagner R. L., Verhey S. D. and Walker-Simmons M. K. 2002. The abscisic acid-responsive kinase PKABA1 interacts with a seed-specific abscisic acid response element-binding factor, TaABF, and phosphorylates TaABF peptide sequences. Plant Physiol., **130**(2): 837-846.
- Joshi P.K. and Rao Parthasarathy. 2017. Global pulses scenario: status and outlook. Ann. N.Y. Acad. Sci., **1392**: 6-17.
- Joshi Snehal S. 1984. Effect of salinity stress on organic and mineral constituents in the leaves of pigeonpea (*Cajanus cajan* L. Var. C-11). Plant Soil,**82**: 69-76.
- Kaashyap, M., Ford, R., Kudapa, H., Jain, M., Edwards, D., Varshney, R., Mantri, N., 2018. Differential regulation of genes involved in root morphogenesis and cell wall modification is associated with salinity tolerance in chickpea. Sci. Rep., 8(1) https:// doi.org/10.1038/ s41598-018-23116-9.
- Kamra S.K. 2015. An overview of subsurface drainage for management of saline and waterlogged soils in India. Water Energy Int., **6**(9): 46-53.
- Kasotia A., Varma A. and Choudhary. 2015. *Psedomonas* -mediated mitigation of salt stress and growth promotion in *Glycine max* L. Agric. Res., **4**(1): 31-41.
- Kaur, P., Kaur, J., Kaur, S., Singh, S., Singh, I., 2014.
 Salinity induced physiological and biochemical changes in chickpea (*Cicer arietinum* L.) genotypes.
 J. Appl. Nat. Sci., 6(2): 578-588. https://doi.org/ 10.31018/jans.v6i2.500.
- Kav N.N., Srivastava S., Goonewardene L. and Blade S.F. 2004. Proteome-level changes in the roots of *Pisum* sativum in response to salinity. Ann. Appl. Biol., **145**: 217-230.
- Kerepesi I. and Galiba G. 2000. Osmotic and salt stressinduced alteration in soluble carbohydrate content in wheat seedlings. Crop Sci., **40**(2): 482-487.
- Kökten K., Karaköy T., Bakoðlu A. and Akçura M. 2010. Determination of salinity tolerance of some lentil (*Lens culinaris* M.) varieties J. Food, Agri. Env., 8(1): 140-143.
- Kotula L., Khan H.A., Quealy J., Turner N.C., Vadez V., Siddique K.H., Clode P.L., Colmer T.D. 2015. Salt

sensitivity in chickpea (*Cicer arietinum* L.): lons in reproductive tissues and yield components in contrasting genotypes. Plant Cell Environ., **38**(8): 1565-1577.

- Kudapa H., Garg V., Chitikineni A. and Varshney R.K. 2018. The RNA-Seq-based high resolution gene expression atlas of chickpea (*Cicer arietinum* L.) reveals dynamic spatio-temporal changes associated with growth and development. Plant Cell Environ., **41**(9): 2209-2225. https://doi.org/10.1111/ pce.13210.
- Kumar K., Solanki S., Singh S.N. and Khan M.A. 2016. Abiotic constraints of pulse production in India. In: Biswas SK, Kumar S, Chand G (Eds.), Disease of pulse crops and their sustainable management pp. 23–39, Biotech Books, New Delhi, India. (Eds. Shiv Kumar), Indian Institute of Pulses Research, Kanpur, Uttar Pradesh, India, pp. 21-35.
- Kuznetsov V. V. and Shevyakova N. I. 2007. Polyamines and stress tolerance of plants. Plant Stress, 1: 50-71.
- Kumar N., Soren K.R., Bharadwaj C., P.R. Sneha Priya, Shrivastava A. K., Pal M., Roorkiwal M., Kumar K., Patil B.S., Soni A., M.S. Nimmy, K.H.M. Siddique and Varshney Rajeev K. 2021. Genome-wide transcriptome analysis and physiological variation modulates gene regulatory networks acclimating salinity tolerance in chickpea. Exptl. Env. Bot., **187**: 104478, https://doi.org/10.1016/j.envexpbot.
- Lee D. J., Shannon J. G., Vuong T. D. and Nguyen H. T. 2009. Inheritance of salt tolerance in wild soybean (*Glycine soja* Sieb. and Zucc.) accession PI483463. J. Heredity, **100**: 798-801.
- Lee G. J., Boerma H. R., Villagarcia M. R., Zhou X., Carter T. E. Jr., Li Z. and Gibbs M. O.2004. A major QTL conditioning salt tolerance in S-100 soybean and descendent cultivars. Theor. Appl. Genet., **109**: 1610-1619.
- Lee D. J., Shannon J. G., Vuong T. D. and Nguyen H. T. 2009. Inheritance of salt tolerance in wild soybean (*Glycine soja* Sieb. and Zucc) accession PI483463. J. Heredity, **100**: 798-801.
- Lee O.R., Pulla R.K., Kim Y.-J., Balusamy S.R.D., Yang D.C. Expression and stress tolerance of PR10 genes from Panax ginseng CA Meyer. Mol. Biol. Rep., **39**: 2365-2374.
- Liu J., Ishitani M., Halfter U., Kim C.S. and Zhu J.K. 2000. The *Arabidopsis thaliana* SOS2 gene encodes a protein kinase that is required for salt tolerance. Proc. National Acad. Sci., U. S. A., **97**(7): 3730-3734.
- Liu Y., Yu L., Qu Y., Chen J., Liu X., Hong H et al. 2016. GmSALT3, which confers improved soybean salt tolerance in the field, increases leaf Cl⁻ exclusion prior to Na+ exclusion but does not improve early vigor under salinity. Front. Plant Sci., **7**: 1485.
- Ma L., Zhang H., Sun L. et al. 2012. NADPH oxidase

- Makela P., Karkkainen J. and Somersalo S. 2000. Effect of glycinebetaine on chloroplast ultrastructure, chlorophyll and protein content, and RuBPCO activities in tomato grown under drought or salinity," Biologia Plantarum, **43**(3): 471-475.
- Maliro M.F., McNeil D., Kollmorgen J., Pittock C., Redden B. 2004. Proc. 4th Inter. Crop Sci. Cong., New directions for a diverse planet; Brisbane. September 26, 2004; Brisbane, Australia.
- Manasa R., Rameshreddy K., Bindumadhava H., Nair R. M., Prasad T. G. and Shankar A. G. 2017. Screening mungbean (*Vigna radiata* L.) lines for salinity tolerance using salinity induction response technique at seedling and physiological growth assay at whole plant level. Intl. J. Plant Anim. Environ. Sci., 7: 1-12. doi: 10.21276/ljpae.
- Mann A., Kumar A., Sanwal S.K. and Sharma P.C. 2020. Sustainable production of pulses under saline lands in India. DOI: 10.5772/intchopen.91870.
- Mantri N.L., Ford R., Coram T.E., Pang E.C. 2007. Transcriptional profiling of chickpea genes differentially regulated in response to high-salinity, cold and drought. BMC Genomics, 8:303.
- Malhotra R. S. 1997. Evaluation techniques for abiotic stresses in cool Season food legumes. In: Recent Advances in Pulses Research (Eds: A. N. Asttranu and A. Masood). Indian Society of Pulses Research and Development, IIPR, Kanpur, India, pp. 459-473.
- Manchanda H.R. and Sharma S.K. 1990. Influence of different chloride sulfate ratios on yield of chickpea (*Cicer arietinum*) at comparable salinity levels. Indian J. agric. Sci., **60**: 553-555.
- Mass E.V. and Hoffman G.1. 1977. Crop salt tolerance-Current assessment. 1. Irri. Drainage Div. ASCE, **103**: 115-134.
- Matysik J., Alia A., Bhalu B., and Mohanty P. 2002. Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants. Curr. Sci., **82**(5): 525-532.
- Mayak S., Tirosh T. and Glick B. 2004. Plant growthpromoting bacteria confer resistance in tomato plant in salt stress. Plant Physio. Bioche., **42**: 565-572.
- Metwali E.M.R., Abdelmoneim T.S., Bakheit M.A. and Kadasa N.M.S. 2015. Alleviation of salinity stress in faba bean (*Vicia faba* L.) plants by inoculation with plant growth promoting rhizobacteria (PGPR). POJ 8(5): 449-460.
- Mielewczik M., Friedli M., Kirchgessner N. and Walter A. 2013. Diel leaf growth of soybean: a novel method to analyze two-dimensional leaf expansion in high temporal resolution based on a marker tracking

approach (Martrack Leaf). Plant Methods, 9: 30.

- Mielewczik M., Friedli M., Kirchgessner N. and Walter A. 2013. Diel leaf growth of soybean: a novel method to analyze two-dimensional leaf expansion in high temporal resolution based on a marker tracking approach (Martrack Leaf). Plant Methods, **9**: 30
- Minhas P.S. and Dagar J.C. 2016. Synthesis and way forward: agroforestry for waterlogged saline soils and poor quality waters. In: Agroforestry and management of water logged saline soils and poor quality waters. Adv. Agrofor. Series 13. Springer, New Delhi, pp 197-201.
- Minhas P.S. and Reddy G.P.O. 2017. Edaphic stresses and agricultural sustainability: An Indian perspective. Agric. Res., **6**(1): 8-21.
- Minhas P.S. and Sharma O.P. 2002. Management of soil salinity and alkaline problems in India. J. Crop Prod., **7**: 181-230.
- Moller I.S., Gilliham M., Jha D., Mayo G.M., Roy S.J., Coates J.C., Haseloff J., Tester M. 2009. Shoot Na+ exclusion and increased salinity tolerance engineered by cell type-specific alteration of Na⁺ transport in *Arabidopsis*.Plant Cell., **21**(7): 2163-2178.
- Moons A., Prinsen E., Bauw G., Van Montagu M. Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts in rice roots. Plant Cell 1997, **9**: 2243-2259.
- Mullan D.J., Colmer T.D., Francki M.G.2007. Arabidopsisrice-wheat gene orthologues for Na⁺ transport and transcript analysis in wheat-*L. elongatum* aneuploids under salt stress. Mol. Genet. Genomics: MGG, 277(2): 199-212.
- Munns R. 2005. Genes and salt tolerance: bringing them together. New Phytologist, **167**(3): 645-663.
- Munns R. and Tester M. 2008. Mechanisms of salinity tolerance. Annual Rev. Plant Biol., **59**: 651-681.
- Nazar R., Iqbal N., Syeed S. and Khan N. A. 2011. Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars. J. Plant Physiol., **168**(8): 807-815.
- Nounjan N., Nghia P. T. and Theerakulpisut P. 2012. Exogenous proline and trehalose promote recovery of rice seedlings from salt-stress and differentially modulate antioxidant enzymes and expression of related genes. J. Plant Physiol., **169**(6): 596-604.
- Otoch M. De Lourdes Oliveira, Menezes Sobreira A. C., Aragão Farias M. E. De, E. G. Orellano, Lima M. DaGuia Silva, and De Melo D. Fernandes. 2001. Salt modulation of vacuolar H⁺-ATPase and H⁺-Pyrophosphatase activities in *Vigna unguiculata*. J. Plant Physiol., **158**(5): 545-551.
- P. Krishna. 2003. Brassinosteroid-Mediated Stress

May, 2021]

Responses. J. Plant Growth Reg., **22**(4): 289-297.

- Pang Q., Chen S., Dai S., Chen Y., Wang Y. and Yan X. 2010. Comparative proteomics of salt tolerance in *Arabidopsis thaliana* and *Thellungiella halophila*, J. Proteome Res., **9**(5): 2584-2599.
- Peng H., Cheng H.Y., Chen C., Yu X.W., Yang J.N., Gao W.R., Shi Q.H., Zhang H., Li J.G., Ma H. 2009. A NAC transcription factor gene of Chickpea (*Cicer arietinum*), CarNAC3, is involved in drought stress response and various developmental processes. J. Plant Physiol., **166**(17): 1934-1945.
- Potters G., Pasternak T.P., Guisez Y., Palme K.J. and Jansen M.A.K. 2007. Stress induced morphoenic responses, growing out of trouble? Trends Plant Sci., **12**: 98-105.
- Rameshwaran P., Qadir M., Ragab R., Arslan A.Majid G.A., and Abdallah K. 2016.Tolerance of faba bean, chickpea and lentil to salinity: accessions' salinity response functions. Irrig. Drain, 65: 49-60. DOI: 10.1002/ird.1922.
- Rana D.S., Dass A., Rajanna G.A. and Kaur R. 2016. Biotic and abiotic stress management in pulses. Indian J. Agron., **61**: S238-S248.
- Reginato M., Sosa L., Llanes A., Hampp E., Vettorazzi N., Reinoso H., Luna V. 2014. Growth responses and ion accumulation in the halophytic legume *Prosopis strombulifera* are determined by Na₂SO₄ and NaCl. Plant Biol., **16**(1): 97-106.
- Romo S., Labrador E. and Dopico B. 2001. Water stressregulated gene expression in *Cicer arietinum* seedlings and plants. Plant Physiol. Biochem., **39**: 1017-1026.
- Rozema J. and Flowers T. 2008. Ecology: crops for a salinized world. Science, **322**(5907): 1478-1480.
- Saha P., Chatterjee P. and Biswas A.K. 2010. NaCl pretreatment alleviates salt stress by enhancement of antioxidant defence and osmolyte accumulation in mungbean (*Vigna radiata* L. wilczek). Ind. J. Exp. Biol., **48**: 593-600.
- Samineni S., Siddique K.M.H., Gaur P.M., Colmer T.D. 2011. Salt sensitivity of the vegetative and reproductive stages in chickpea (*Cicer arietinum* L.): Podding is a particularly sensitive stage. Environ. Exp. Bot., **71**(2):260-268.
- Samineni, S., Siddique K. H. M., Gaur P., and Colmer T. D. 2011. Salt sensitivity of the vegetative and reproductive stages in chickpea (*Cicer arietinum* L.): Podding is a particularly sensitive stage. Environ. Exp. Bot., **71**: 260-268.
- Saxena S. C., Kaur H., Verma P. et al. 2013. Osmoprotectants: potential for crop improvement under adverse conditions. In: Plant Acclimation to Environmental Stress, pp. 197-232, Springer, New York, NY, USA.

- Schmidt R., Mieulet D., Hubberten H.M. et al. 2013. SALT-RESPONSIVE ERF1 regulates reactive oxygen species-dependent signaling during the initial response to salt stress in rice. The Plant Cell, **25**(6): 2115-2131.
- Sehrawat N., Yadav M., Bhat K.V., Sairam R.K. and Jaiwal P.K. 2015. Effect of salinity stress on mungbean during consecutive summer and spring seasons. J. Agric. Sci., 60(1): 23-32.
- Shabala S. and Cuin T.A. 2008. Potassium transport and plant salt tolerance. Physiol. Plant., **133**(4): 651-669. https://doi.org/10.1111/j.1399-3054.2007.01008.x.
- Sharma B.R. and Minhas P.S. 2005. Strategies for managing saline alkaline water for sustainable agricultural production in South Asia. Agric. Water Manage, **78**: 136-151.
- Sharma S.K., Dua R.P. and Singh D. 2001. Mechanism of sodicity tolerance and genetic variability in wild and cultivated genotypes of pigeonpea. Indian J. Plant Physiol., 6(3): 275-278.
- Shavrukov Y., Gupta N. K., Miyazaki J., Baho M. N., Chalmers K. J. and Tester M.etal. 2010. HvNax3-a locus controlling shoot sodium exclusion derived from wild barley (*Hordeum vulgare ssp spontaneum*). Funct. Integ. Genomic, **10**: 277-291.
- Shevyakova N. I., Musatenko L. I., Stetsenko L. A. et al. 2013. Effects of abscisic acid on the contents of polyamines and proline in common bean plants under salt stress. Russian J. Plant Physiol., 60: 200-211.
- Shi H., Ishitani M., Kim C. and Zhu J.K. 2000a. The *Arabidopsis thaliana* salt tolerance gene SOS1 encodes a putative Na⁺/H⁺ antiporter. Proc. National Acad. Sci., U. S. A., **97**(12): 6896-6901.
- Shi H., Quintero F. J., Pardo J. M. and Zhu J.K. 2000b. The putative plasma membrane Na⁺/H⁺ antiporter SOS1 controls long-distance Na⁺ transport in plants. Plant Cell, **14**(2): 465-477.
- Shu S., Guo S. R. and Yuan L. Y. 2012. A review: polyamines and photosynthesis. In:Advances in Photosynthesis-Fundamental Aspects, (Ed.M. M. Najafpour), 439-464, InTech, Rijeka, Croatia.
- Singh D., Dikshit H.K. and Kumar A. 2014. Aluminium tolerance in lentl (*Lens culinaris* Medik.) with monogenic inheritance pattern, Plant Breed., **134**(1): 105-110. <u>https://doi.org/10.1111/pbr.12227</u>.
- Singh D. and Raje R.S. 2011a. Genetics of aluminium tolerance in chickpea (*Cicer arietinum* L.) Plant Breed., **130**(5): 563-568. https://doi.org/10.1111/j.1439-0523.2011.01869.x.
- Singh D., Raje R.S. and Chaudhary A.K. 2011b. Genetic control of aluminium tolerance in pigeonpea (*Cajanus cajan* L.). Crop Past. Sci., 62: 761-764. http:// /dx.doi.org./10.1071/CP11106.
- Singh D., Singh C. K., Kumari S., Tomar R. S. S., Karwa

S., Singh R., Singh R.B., Sarkar S.K. and Pal M. 2017a. Discerning morpho-anatomical, physiological and molecular multiformity in cultivated and wild genotypes of lentil with reconciliation to salinity stress. Plos ONE, **12**(5): e0177465. https//doi.org/101371/ journal.pope.0177465.

- Singh D., Singh C.K., Taunk J., Tomar R.S. 2016. Genetic analysis and molecular mapping of seedling survival drought tolerance gene in lentil (*Lens culinaris* Medik.). Mol. Breed., **36**(5): DOI: 10.1007/ s11032-016-0474-y.
- Singh D., Singh C. K., Tomar R. S. S., Sharma S., Karwa S., Pal M., Singh V., Sanwal S. K. and Sharma P.C. 2020a. Genetics and molecular mapping for salinity stress tolerance at seedling stage in lentil (*Lens culinaris* Medik) Crop Sci., **60**(3): 1254-1266..DOI: 10.1002/csc2.20030.
- Singh D., Singh C. K., Taunk J., Sharma S., Gaikwad K., Singh V., Sanwal S. K., Singh D., Sharma P.C. and Pal M. 2021. Transcriptome skimming of lentil (*Lens culinaris* Medikus) cultivars with contrast reaction to salt stress. Funct. Integr. Genomics, https://doi.org/ 10.1007/s10142-020-00766-5.
- Singh D., Singh C.K., Taunk J., Tomar R.S., Chaturvedi A.K., Gaikwad K. and Pal M. 2017b. Transcriptome analysis of lentil (*Lens culinaris* Medikus) in response to seedling drought stress. BMC Genomics 18:206. https://doi.org/10.1186/s12864-017-3596-7.
- Singh, J., Singh, V., Sharma, P.C., 2018. Elucidating the role of osmotic, ionic and major salt responsive transcript components towards salinity tolerance in contrasting chickpea (*Cicer arietinum* L.) genotypes. Physiol. Mol. Biol. Plants, **24**(3): 441-453. https:// doi.org/10.1007/s12298-018-0517-4.
- Soren K.R., Madugula P., Kumar N., BarmukhR.,Sengar M.S., Bharadwaj C.P.et al.. 2020. Genetic dissection and identification of candidategenes for salinity tolerance using Axiom®CicerSNParray in chickpea.Int. J. Mol. Sci., 21: 5058; doi: 10.3390/ ijms21145058.
- Srivastava S., Fristensky B. and Kav N.N. 2004. Constitutive Expression of a PR10 Protein Enhances the Germination of *Brassica napus* under Saline Conditions. Plant Cell Physiol., **45**: 1320-1324.
- Stratilová, B.; Rehulka, P.; Garajov á, S.; Rehulkov j á, H.; Stratilová, E.; Hrmova, M.; Kozmon, S. Structural characterization of the Pet c 1.0201 PR-10 protein isolated from roots of *Petroselinum crispum* (Mill.) Fuss. Phytochemistry 2020, **175**: 112368.
- Subbarao G.V. and Johansen C. 1994. Potential for genetic improvement in salinity tolerance in legumes: pigeonpe. In: M. Pessarkali (ed.) Handbook of Plant and Crop Stress, pp. 581-595. Marcel Dekker, Inc. N.Y.

Subbarao G.V., Johansen C., lana M.K. and Kumar Rao

J.V.D.K. 1991. Comparative salinity responses among pigeonpea genotypes and their wild relatives. Crop Sci., **31:** 415-418.

- Sugimoto M. and Takeda K. 2009. Proteomic Analysis of specific proteins in the root of salt-tolerant barley. Biosci. Biotechnol. Biochem., **73**: 2762-2765.
- Swaraj K. and Bishnoi N. R. 1999. Effect of salt stress on nodulation and nitrogen fixation in legumes. Indian J. Exp. Biol., 37: 843-848.
- Syam Prakash S.R. and Jayabaskaran C. 2006. Heterologous expression and biochemical characterization of two calcium-dependent protein kinase isoforms CaCPK1 and CaCPK2 from chickpea. J. Plant Physiol., **163**(11): 1083-1093.
- Takahashi T. and Kakehi J. I. 2010. Polyamines: ubiquitous polycations with unique roles in growth and stress responses. Annals Bot., **105**(1): 1-6.
- Tang L.L., Cai H., Zhai H., Luo X., Wang Z., Cui L. and Bai X. 2014. Overexpression of *Glycine soja* WRKY20 enhances both drought and salt tolerance in transgenic alfalfa (*Medicago sativa* L.). Plant Cell Tissue Organ Cult. (Pctoc), **118**: 77-86.
- Tavakkol E., Rengasamy P. and McDonald G.K. 2010. High concentrations of Na⁺ and Cl⁻ ions in soil solution have simultaneous detrimental effects on growth of faba bean under salinity stress. J. Exp. Bot., 61: 4449-4459.
- Tayyab, Azeemi M., Qasim M., Ahmed N., Hmedi and Ahmad R. 2016. Salt stress responses of pigeonpea (*Cajanus cajan*) on growth, yield and some biochemical attributes. Pak. J. Bot., 48(4): 1353-1360.
- Turner N.C., Colmer T.D., Quealy J., Pushpavalli R., Krishnamurthy L., Kaur J., Singh G., Siddique K.H., Vadez V. 2013. Salinity tolerance and ion accumulation in chickpea (*Cicer arietinum* L.) subjected to salt tress. Plant Soil., **365**(1): 347-361.
- Tuyen D.D., Lal S.K. and Xu D.H. 2010. Identification of a major QTL allele from wild soybean (*Glycine soja* Sieb. &Zucc.) for increasing alkaline salt tolerance in soybean. Theor. Appl. Genet., **121**: 229-236.
- Vadez V., Krishnamurthy L., Serraj R., Gaur P.M., Upadhyaya H.D., Hoisington D.A., Varshney R.K., Turner N.C., Siddique K.H. 2007. Large variation in salinity tolerance in chickpea is explained by differences in sensitivity at the reproductive stage. Field Crops Res., **104**(1-3): 123-129.
- Vadez V., Krishnamurthy L., Thudi M., Anuradha C., Colmer T., Turner N., Siddique K., Gaur P.M., Varshney R.K. 2012a. Assessment of ICCV 2 × JG 62 chickpea progenies shows sensitivity of reproduction to salt stress and reveals QTL for seed yield and yield components. Mol. Breed., 2012(30): 9-21.
- Vadez V., Rashmi M., Sindhu K., Muralidharan M.,

Pushpavalli R., Turner N.C., Krishnamurthy L., Gaur P.M. and Colmer T.D. 2012b. Large number of flowers and tertiary branches, and higher reproductive success increase yields under salt stress in chickpea. Eur. J. Agron., **41**: 42-51.

- Vincent D., Ergül A., Bohlman M.C., Tattersall E.A.R., Tillett R.L., Wheatley M.D., Woolsey R., Quilici D.R., Joets J., Schlauch K. et al. 2007. Proteomic analysis reveals differences between *Vitis vinifera* L. cv. Chardonnay and cv. Cabernet Sauvignon and their responses to water deficit and salinity. J. Exp. Bot., 58: 1873-1892.
- Vincente M.R. and Plasencia J. (2011). Salicylic acid beyond defence: its role in plant growth and development. J. Exp. Bot., 62(10): 3321-3338.
- Wang B., Lüttge U. and Ratajczak R. 2001. Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte *Suaeda salsa*. J. Exp. Bot., **52**(365): 2355-2365.
- Wang L., Wu X., Liu Y., Qiu Q.S. 2015. AtNHX5 and AtNHX6 control cellular K⁺ and pH homeostasis in *Arabidopsis*: three conserved acidic residues are essential for K⁺ transport. PLoS One, **10**(12): e0144716.
- Wang L., Wu X., Liu Y., Qiu Q.S. 2015. AtNHX5 and AtNHX6 control cellular K⁺ and pH homeostasis in *Arabidopsis*: three conserved acidic residues are essential for K⁺ transport. PLoS One, **10**(12): e0144716.
- Wang L., Wu X., Liu Y., Qiu Q.S. 2015. AtNHX5 and AtNHX6 control cellular K⁺ and pH homeostasis in *Arabidopsis*: three conserved acidic residues are essential for K⁺ transport. PLoS One, **10**(12): e0144716.

- Wang W.X., Vinocur B., ShoseyovO. and Altman A. 2001. Biotechnology of plant osmotic stress tolerance physiological and molecular considerations. Acta Hortic., 285-292.
- Wang Y. and Nii N. 2000. Changes in chlorophyll, ribulose bisphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in *Amaranthus* tricolor leaves during salt stress. J. Hort. Sci. Biotechnol., **75**(6): 623-627.
- War A.R., Paulraj M.G., War M.Y. and Ignacimuthu S. 2011. Role of salicylic acid in induction of plant defense system in chickpea (*Cicer arietinum* L.). Plant Signal. Behav., **2011**;6(11):1787–1785.
- Yadav R., Gaikwad K.B. and Bhattacharyya R. 2017. Breeding wheat for yield maximization under conservation agriculture. Indian J. Genet., 77(2): 185-198. DOI: 10.5958/0975-6906.2017.00026.8.
- Zepeda-Jazo I., Velarde-Buendia A.M., Enriquez-Figueroa R., Bose J., Shabala S., Muniz-Murguia J. and Pottosin I.I. 2011. Polyamines interact with hydroxyl radicals in activating Ca(2+) and K(+) transport across the root epidermal plasma membranes. Plant Physiol., **157**(4): 2167-2180.92.
- Zhang J. L. and Shi H. 2013. Physiological and molecular mechanisms of plant salt tolerance, Photosynthesis Res., **115**: 1-22.
- Zhou H. and Li W. 2013. The effects of oasis ecosystem hydrological processes on soil salinization in the lower reaches of the Tarim River, China. Ecohydrology, **6**: 1009-1020.
- Zhu J. K. 2003. Regulation of ion homeostasis under salt stress. Curr. Opinion Plant Biol., **6**(5): 441-445.