



# Salinity stress response and ‘omics’ approaches for improving salinity stress tolerance in major grain legumes

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## Abstract

**Key message** Sustaining yield gains of grain legume crops under growing salt-stressed conditions demands a thorough understanding of plant salinity response and more efficient breeding techniques that effectively integrate modern omics knowledge.

**Abstract** Grain legume crops are important to global food security being an affordable source of dietary protein and essential mineral nutrients to human population, especially in the developing countries. The global productivity of grain legume crops is severely challenged by the salinity stress particularly in the face of changing climates coupled with injudicious use of irrigation water and improper agricultural land management. Plants adapt to sustain under salinity-challenged conditions through evoking complex molecular mechanisms. Elucidating the underlying complex mechanisms remains pivotal to our knowledge about plant salinity response. Improving salinity tolerance of plants demand enriching cultivated gene pool of grain legume crops through capitalizing on ‘adaptive traits’ that contribute to salinity stress tolerance. Here, we review the current progress in understanding the genetic makeup of salinity tolerance and highlight the role of germplasm resources and omics advances in improving salt tolerance of grain legumes. In parallel, scope of next generation phenotyping platforms that efficiently bridge the phenotyping–genotyping gap and latest research advances including epigenetics is also discussed in context to salt stress tolerance. Breeding salt-tolerant cultivars of grain legumes will require an integrated “omics-assisted” approach enabling accelerated improvement of salt-tolerance traits in crop breeding programs.

**Keywords** Gene · Genomics · Genetic variation · QTL · Salinity · Stress · Tolerance

## Introduction

Salt stress causes considerable loss in agricultural production worldwide through severely impacting upon plant growth (Amitai et al. 1995; Banzai et al. 2002). Salinity-affected soils are prevalent in arable and irrigated lands in arid and semi-arid climates with considerable higher evapotranspiration (Shanon 1986; Sharifia et al. 2007; Manchanda

and Sharma 2008; Li et al. 2014; Kaashyap et al. 2017). Salinity remains one of the key drivers that contribute to soil toxicity in tropical Asia (Greenland 1984). The major factors that aggravate the challenge of soil salinity stress include low precipitation, high surface evaporation, depletion of ground water and inappropriate agricultural practices including improper ‘drainage in irrigated land’ (Jamil et al. 2011; Munns and Gilliam 2015). Wang et al. (2003) highlighted the growing expansion of salt-stressed area, with authors predicting nearly 30% loss in land due to salinity stress within next 25 years. In China, 9.2 mha area representing 6.62% of the total cultivated land is critically challenged by salinity stress (Yang et al. 2008). The global acreage constrained by salt stress includes a total of 45 mha irrigated and 32 mha hardy lands (Munns and Tester 2008; FAO 2015).

Grain legumes are important in relation to global food security (Zhu et al. 2005; Bohra et al. 2015), and their significance is attributable to higher contents of protein and other mineral nutrients (Broughton et al. 2003; Bohra et al. 2014;

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Foyer et al. 2016; Considine et al. 2017). Their ability to fix atmospheric nitrogen helps improving soil fertility and also contributes to sustainability of cereal–legume based cropping systems (Foyer et al. 2016). Like cereals, production of grain legume crops is also severely affected by salinity stress worldwide. Therefore, improved cultivars with higher salt tolerance are required to maintain their yield potential under salt-stressed condition (Kaashyap et al. 2017). Here, we discuss the impact of salinity stress on five major grain legumes viz. chickpea, common bean, cowpea, field pea and soybean together with describing the adaptive mechanisms against salinity stress. This is followed by a brief account on current knowledge about genetic resources, and genetics and genomics of salinity tolerance in these crops. Finally, we outline the scope of bridging the existing phenotype–genotype gap in light of the next generation plant phenotyping techniques.

## Effects of salinity stress on grain legumes

Plants stressed with salinity show perturbations in cellular metabolism and plant growth and development due to impaired CO<sub>2</sub> assimilation (Bayuelo-Jiménez et al. 2002a; Chen and Yu 2007; Khan et al. 2015, 2017), hindrance in nutrient uptake (Ahmed and Jhon 2005; Gama et al. 2007; Shahid et al. 2012), defective cytosolic enzymes, osmotic stress, ion toxicity (excess Na<sup>+</sup>/Cl<sup>-</sup>), hormonal dysfunction, oxidative stress (Essa 2002; Hernandez and; Almansa 2002; Bayuelo-Jiménez et al. 2003; Ahmad and Jhon 2005; Najafi et al. 2006; Shahid et al. 2012a, b), ultimately leading to cell death (Shabala 2009). Comprehensive reviews detailing impacts of salinity stress on grain legumes are made elsewhere (Manchanda and Garg 2008; Flower et al. 2010; Farooq et al. 2017).

## Adaptive mechanisms conferring salinity tolerance in grain legume crops

Plants respond to salinity stress through evoking a range of physiological, biochemical, and molecular mechanisms (Ashraf and Harris 2004; Munns and Tester 2008; Gupta and Huang 2014; Roy et al. 2014; Acosta-Motos et al. 2017; Liang et al. 2018), which can be categorized into three major classes (i) ‘ion exclusion’ to eliminate Na<sup>+</sup> and Cl<sup>-</sup> ions from roots when their accumulation becomes toxic, (ii) ‘tissue tolerance’ allowing ‘compartmentalized of toxic ions at cellular and intracellular level’ (Roy et al. 2014) and (iii) ‘osmotic tolerance’ (Parida et al. 2005; Munns and Tester 2008; Roy et al. 2014; Deinlein et al. 2014; Ismail and Horie 2017; Negrao et al. 2017). Mechanisms relying on ion exclusion and tissue tolerance against salinity have been reported

in soybean (Durand and Lacan 1994; Umezawa et al. 2000; Tsai 2003; Lee et al. 2004; Yu et al. 2005; Li et al. 2006; Sun et al. 2006; Wong et al. 2013; Guan et al. 2014a; Qi et al. 2014; Do et al. 2016; Liu et al. 2016; Patil et al. 2016) and in pea (Pandolfi et al. 2012). Salinity tolerance resulting from ‘osmotic tolerance’ mechanism has been reported in soybean (Phang et al. 2008; Ozge and Atak 2012; Wu et al. 2014), pea (Shahid et al. 2012), chickpea (Singh 2004) and in common bean (Chen et al. 2009). The physiological and biochemical processes leading to salinity tolerance are intensively investigated in model as well as industrial crops like soybean; however, the underlying mechanisms and pathways remain to be elucidated in the case of other grain legumes.

## Grain legume germplasm resources for improving salinity stress tolerance

Characterisation and utilization of genetic resources is key to genetic improvement of any crop. Significant progress has been achieved in crops for breeding salinity tolerance, notably in cereals like rice and wheat [for details see Ashraf and Wu (2011), Ismail and Horie (2017)]. However, relatively narrow genetic base of breeding programs of grain legume crops has hampered the progress of breeding against salinity (Sharma et al. 2017).

In recent years, efforts were made to explore the genetic variation for salinity tolerance in different legume crops. Chickpea genotypes show a wide range of variation in their response to salinity stress (Lauter and Munns 1986; Maliro et al. 2004; Serraj et al. 2004; Vadez et al. 2007; Krishnamurthy et al. 2011; Turner et al. 2013), and the variation in the level of salinity tolerance is reported across different growth stages. For instance, genotypes such as C 10, C 14, C 16, C 17, C 19, C 28 and C 29 could tolerate salinity up to 6 dSm<sup>-1</sup> at germination and seedling stage (Al-Mutawa 2003). The genotype L 550 showed tolerance under saline conditions on account of its ability to tolerate Na<sup>+</sup> toxicity (Lauter and Munns 1986). Similarly, two genotypes ICC 32 and ICCL 86446 were reported to show higher tolerance against Cl<sup>-</sup> ion toxicity (Dua 1992). Higher tolerance of kabuli chickpea than the desi types was demonstrated through analysis of 211 minicore collection (Serraj et al. 2004). By contrast, Vadez et al. (2007) found desi chickpea to be more tolerant than the kabuli types following evaluation of 263 germplasm lines under both salinity and controlled conditions. Yield under stressed conditions remains an important parameter for assessing stress tolerance of plants, and significant genetic variation has been reported for yield parameters in both desi and kabuli chickpea (Dua and Sharma 1995; Vadez et al. 2007, 2012; Turner et al. 2013). Turner et al. (2013) recorded upto 27-fold differences among 55 chickpea genotypes for seed yield at 40 mM NaCl. Given

the considerable impact of genotype  $\times$  environment (G  $\times$  E) interaction on plant salinity tolerance, multi-location testing has enabled identification of the salinity-tolerant chickpea such as ICC 9942 (Vadez et al. 2007; Krishnamurthy et al. 2011; Turner et al. 2013).

In common bean, analysis of 132 wild and 11 cultivated accessions using parameters like susceptibility index, root and shoot ratio demonstrated their differential response to salinity (Bayuelo-Jiménes et al. 2002). Various research groups have found significant variation for salinity tolerance among wild common beans (Bayuelo-Jiménes et al. 2002a, b; Bayuelo-Jiménes et al. 2003; Goerzt and Coons 1991). For example, higher germination of *Phaseolus* species like *P. filiformis*, *P. angustissimus*, *P. leptostachyus*, and *P. microcarpus* observed at 120 mM NaCl underscores the importance of wild species vis a vis pre-breeding programs (Bayuelo-Jiménes et al. 2002a). Based on the survival rate, *Phaseolus* genotype HRS 516 showed tolerance to varying NaCl concentrations such as 50 mM and 100 mM (Gama et al. 2007).

Analysis of 25 cowpea genotypes at 85 and 170 nmol NaCl L<sup>-1</sup> for germination percentage facilitated identification of the genotype CB 27 as the most salinity tolerant and others including CB 88, CB 3, CB 5, Tardon, Cuarenteno and CB 46 as moderately tolerant (Murillo-Amador et al. 2001). By examining Na<sup>+</sup> accumulation in root and shoot, and biomass production at varying NaCl concentrations, i.e., 0, 85, and 170 mM, four local cowpea accessions viz. Pacen'o, Tardon, Sonorens and Cuarenten'o and three accessions from California CB 46, CB 27 and CB 3 showed tolerance (Murillo-Amador et al. 2006). Interestingly, higher accumulation of Na<sup>+</sup> was recorded in roots in comparison to shoot in salt-tolerant genotypes. As shown in Table 1, greater tolerance of the cowpea genotypes 210856, 211557 and Asebot against salinity was evident based on root and shoot vigor under salinity stress (Gogile et al. 2013).

In pea, variation for traits such as plant height, plant growth rate, roots and shoot biomass was revealed following screening of 780 pea accessions under salinity stress (Leonforte et al. 2013a, b). Similarly, another study involving 30 pea genotypes reported variation for germination percentage, root and shoot weight and inorganic osmolytes (Shahid et al. 2012). The salt tolerance of the genotypes Samarina Zard, Climax, 9800-5 was found to be due to less accumulation of toxic Na<sup>+</sup> in leaf and a higher Na<sup>+</sup>/K<sup>+</sup> ratio, and abundant antioxidant enzymatic activities and osmolyte content under salinity stress (Shahid et al. 2012a, b).

In soybean, salinity tolerance traits exhibit a wide range of variation (Shao et al. 1986; Wang and Shannon 1999) in both cultivated (*Glycine max*) and wild relatives (*G. soja*, *G. tomentella* and *G. argyrea*) (Lenis et al. 2011). Tolerant soybean exhibited limited leaf scorching and retained higher chlorophyll content under salinity stress. Wide spectrum of

salinity tolerance was revealed in soybean encompassing various growth stages through analyzing a large collection of 1716 germplasm lines, representative of diversity in China provinces (Shao et al. 1986). The authors found seven genotypes showing tolerant reactions at all developmental stages. Later, the same group obtained eighty tolerant genotypes after screening more than 10,000 soybean lines under salinity stress (Shao et al. 1993). Similarly, significant variation for leaf Na<sup>+</sup> accumulation and biomass reduction was reported in three wild soybean species viz. *G. soja*, *G. tomentella* and *G. tabacina* under salinity stress (Kao et al. 2006). Perennial soybean displayed tolerance to NaCl up to 17.5 g L<sup>-1</sup> in comparison to *G. max* (5.2–8.0 g L<sup>-1</sup>), with former showing lower leaf chlorosis (Petalone et al. 1997). Higher level of salinity tolerance has been reported in BB 52 population derived from wild *G. soja* (Wu and Yu 2009). Examination of salinity tolerance of BB 52, cultivar N 23674 and their hybrid (BB 52  $\times$  N 23674) allowed authors to propose restricting Cl<sup>-</sup> to plant leaves as the possible mechanism imparting salt tolerance to soybean (Zhang et al. 2011). Likewise, the genotype BB 52 was reported as a promising source of salinity tolerance given the abundance of anti-oxidant enzymatic (Chen et al. 2013) and other physiological activities viz., higher relative water content (RWC) under salt stress (Wu et al. 2014). Additionally, contrasting mechanisms of salinity tolerance between *G. max* (preventing excess Cl<sup>-</sup> ions to leaf and shoot) and *G. soja* (prevention of excess Na<sup>+</sup> ions from root to leaf and stem) offer greater possibilities of broadening the genetic basis through interspecific hybridization (Luo et al. 2005). These studies highlight the significance of wild and perennial soybean to improving salinity tolerance of cultivated soybean.

### Crop wild relatives (CWRs) for harnessing novel variation for salinity tolerance traits

The bottleneck effects associated with crop domestication followed by intensive selection of high yielding lines have caused serious loss of genetic diversity in current crop breeding programs (Tanksley and McCouch 1997). The considerable loss in genetic diversity of food crops is evident at farmers's field also (Massawe et al. 2016). Therefore, novel allelic diversity must be introduced in breeding programmes to exploit genetic variations related to various resilience traits such as tolerance to salinity stress (Brozynska et al. 2016). Though the CWRs of grain legumes remain underutilized (Sharma 2017), efforts have been made in recent years to harness the variation for the traits relevant to salinity tolerance (Bayuelo-Jiménes et al. 2002a, b; Kao et al. 2006; Maliro et al. 2008; Wu and Yu 2009; Lenis et al. 2011). Recent genome sequencing attempts have allowed decoding whole genomes of CWRs, thus shedding new light

**Table 1** List of tolerant grain legume genotypes based on various growth stages under salinity stress

Crop	Name of genotype	Growth stage	Concentration of salt	References
Chickpea	L 550	Vegetative	50 mM NaCl	Lauter and Munns (1986), Tejera et al. (2006)
	H 355	Vegetative	6 dS m <sup>-1</sup> sulphate-salinized soil	Manchanda and Sharma (1989)
	BG 312	Vegetative	40 mM mixed salts	Sharma and Kumar (1990)
	Pusa 312, Pusa 212, Pusa 240	Vegetative (germination)	–	Saxena and Rewari (1991)
	CSG 88101, CSG 8927, CSG 8977	Vegetative and reproductive	–	Dua (1992), Dua and Sharma (1995)
	CM 663 and 10,572	Vegetative	80 mol m <sup>-3</sup> NaCl	Ashraf and Waheed (1993, 1998)
	CSG-88,101, CSG – 8890	Vegetative	7.8 dS m <sup>-1</sup> with mixed salts	Dua (1998)
	Amdoun I	Vegetative (root to shoot)	–	Slemi et al. (2001)
	JG 62, ICC 1431, ICC 15610, ICC 5003, ICC 4593, ICC 12155	Reproductive (seed yield)	80 mM NaCl	Vadez et al. (2007, 2012)
	CSG 8962 and ICCV 96836	–	–	Maliro et al. (2004)
	ICC 10755, ICC 13124, ICC 13357, ICC 15406, ICC 15697	Vegetative (shoot biomass)	100 mM NaCl	Serraj et al. (2004)
	ICC 30, ICC 8980, ICC 903, ICC 801, ICC 6671	Vegetative (biomass)	6 dS m <sup>-1</sup> NaCl	Maliro et al. (2008)
	Genesis 836	Reproductive	35 or 50 mM NaCl	Kotula et al. (2015)
	Genesis 836	Vegetative (photosynthetic rate)	30, or 60 mM NaCl	Khan et al. (2016)
	ICC 5003, ICC 15610 and ICC 1431	–	–	Vadez et al. (2007)
	INRAT 93 – 1	Vegetative (nodulation)	–	Ltaief et al. (2007)
	ICC 1431	Reproductive	80 mM NaCl	Samineni et al. (2011)
	SG-11 & DHG-84-11	Vegetative	8.0dSm <sup>-1</sup>	Singh (2004)
	Genesis 836, ICC 7323, ICC 95	Vegetative and reproductive	40 mM NaCl	Atieno et al. (2017)
	Common bean	HRS 516	Vegetative	100 mM NaCl
Wild <i>P. vulgaris</i>		Vegetative	180 mM NaCl	Bayuelo-Jiménes et al. (2002a, b)
<i>P. acutifolius</i>		–	–	Goerzt and Coons (1991) Bayuelo-Jiménes et al. (2003)
Cowpea	California Buckeye No. 5	Vegetative and reproductive	–	Mass and Poss (1989)
	Vita3, Vu15, and IT-85F-1380	Vegetative	75 mM NaCl	Win and Oo (2015)
	210856, 211557 and Asebot	Vegetative and reproductive	200 mM NaCl	Gogile et al. (2013)
	CB 27, CB 88, CB 3, CB 5, Tardon, Cuarenteno and CB 46	Vegetative (germination and emergence %)	85 and 170 mM NaCl	Murillo-Amador et al. (2001)
	‘Paceno’, ‘Tardo’n, ‘Sonorens’ ‘Cuarenteno	Vegetative (high biomass)	85 and 170 mM NaCl	Murillo-Amador et al. (2006)
	‘CB 46’, ‘CB 27’, and ‘CB 3’, ‘IT82D-889	–	–	–
	Pitiuba	–	–	Freitas et al. (2001)
	Diongoma, 58–78, and 58–191	Vegetative	200 mM NaCl	Thiam et al. (2013)
	Vita 3	Vegetative	100 mM NaCl	Costa et al. (2007)
EK 1, TZ 7 and B 23	Vegetative (germination)	12–16 dSm <sup>-1</sup> NaCl	Nabi et al. (2017)	
Pea	Granada	–	70 mM	Hernandez et al. (1993, 2000)
	ATC 1836	Vegetative (root and shoot)	–	Leonforte et al. (2013a, b)

**Table 1** (continued)

Crop	Name of genotype	Growth stage	Concentration of salt	References
Soybean	Green Arrow	Vegetative	70 mM NaCl	Najafi et al. (2007)
	Samarina Zard, Climax, 9800-5, 9800-10 and 2001-55	Vegetative	7.5 and 10 dS m <sup>-1</sup> NaCl	Shahid et al. (2012, b)
	2001-35, 2001-55 and Climax	Vegetative (shoot biomass)	NaCl 120 mM	Noreen and Ashraf (2009)
	<i>G. argyrea</i> 1626, <i>G. clandestina</i> 1388	Vegetative	10 g L <sup>-1</sup> NaCl	Pantalone et al. (1997)
	<i>G. clandestina</i> 1389			
	<i>G. microphylla</i> 1143 and 1195			
	Lee	Vegetative	8.5 dS m <sup>-1</sup>	Essa (2002)
	<i>G. tabacina</i> ; <i>Glycine tomentella</i>	Vegetative	0–85 mM NaCl	Kao et al. (2003, 2006)
	WF-7	Vegetative	200 mM NaCl	Ren et al. (2012)
	<i>G. max</i> , <i>G. soja</i> , <i>G. tomentella</i>	Vegetative	0–100 mM NaCl	Lenis et al. (2011)
	<i>G. argyrea</i>			
	S111-9	Vegetative	–	Lu et al. (2009)
	Manokin'	Vegetative	3 dS m <sup>-1</sup>	Wang and Shannon (1999)
	S-100, 'Lee-68', 'HBK R5528'	Vegetative	120–160 mM NaCl	Valencia et al. (2008)
	BB 52	–	200 mM NaCl	Chen et al. (2013)
	PI 483463	–	100 mM	Lee et al. (2009)
En-b0-1	Both reproductive and vegetative	70–100 mM NaCl	Yasuta and Kokubun (2014)	

on novel allele(s)/genomic information pertaining to salinity tolerance (Guan et al. 2014b; Qi et al. 2014; Brozynska et al. 2016; Munoz et al. 2017). Improving crop performance under increasing salinity stress warrants greater utilization of CRWs in breeding programs to allow untapped genetic variation flowing from CWRs to elite agronomic bases (Wang et al. 2017).

### Genetics of salt tolerance and efforts of conventional breeding for salinity stress breeding

Greater understanding of the genetic basis of traits having relevance to salinity stress is important for improving salinity tolerance in crops (Lee et al. 2009; Arzani and Ashraf 2016). Breeding for salinity tolerant crop varieties is time consuming given the multi-genic inheritance and 'multi-component nature' of salinity stress tolerance (DeRose-Wilson and Gaut 2011; Cabot et al. 2014; Negrao et al. 2017). Hence, direct selection for higher yield as a measure of salinity tolerance cannot be deemed very suitable (Ashraf 2004). Complexities in both genetic and physiological mechanisms of salinity tolerance in crop plants have been thoroughly discussed elsewhere (for details see Flowers 2004).

Classical genetics and conventional breeding approaches relying on phenotypic variation were implemented in grain legumes to understand salinity stress (Abel 1969; Dua and Sharma 1995; Serraj et al. 2004; Maliro et al. 2008; Xu and Tuyen 2010). Majority of these genetic analyses on salt tolerance are confined to only model legumes such as soybean. Examples include a classical genetics study by Abel (1969) that suggested a single dominant gene *Ncl* controlling salinity tolerance in soybean. This observation concurred with that of Shao et al. (1994) who proposed a single dominant gene for salt tolerance in soybean. Subsequently, a new allele from PI 483463, designated as *Ncl2* (Lee et al. 2009), was found to be different from the salinity tolerant gene reported from *G. max* line S100. Earlier, Luo et al. (2004) reported polygenic inheritance of salt tolerance in soybean based on the inheritance patterns inferred from crosses (Nannong 88–31 × Jackson and Nannong 1138–2 × Nannong 88–31). A list of genes contributing to salinity tolerance in soybean is given in Table 2. In chickpea, a diallel cross analysis revealed presence of both additive and dominance gene effects with higher dominance effects for the three traits (seed yield, pods per plant and seeds per plant) measured under salinity stress (Asraf and Waheed 1998). Similarly, generation mean analysis (GMA) in chickpea involving crosses derived from ICC 6263 (salt sensitive) × ICC 1431 (salt

**Table 2** List of salinity tolerance gene(s) and their putative function for salinity tolerance in soybean

Crop	Source/genotype	Name of gene	Function	References
Soybean	PI 483463 × Hutcheson	<i>Ncl2</i>	–	Lee et al. (2009)
Soybean	PI 483463 × Hutcheson, F <sub>2,3</sub>	Single dominant gene <i>Ncl2</i> allele	–	Lee et al. (2009)
Soybean	PI 483,463 × Hutcheson	<i>Glyma03g32890</i> <i>Glyma03g32900</i>	Encodes sodium/hydrogen exchanger family	Ha et al. (2013)
Soybean	Jackson × JWS156-1	<i>Glyma17g15000</i> <i>Glyma17g15150</i> <i>Glyma17g15520</i> <i>Glyma17g15580</i>	Transporter gene	Tuyen et al. (2013)
Soybean	Tiefeng 8 × 85–140, RIL, F <sub>2,3</sub>	One dominant gene	Lower accumulation of Na <sup>+</sup> in the shoot	Guan et al. (2014b)
Soybean	W05 × C08	<i>GmCHX1</i> <i>Glyma03g32890</i> <i>Glyma03g32900</i>	Having analogy to cation H <sup>+</sup> exchanger (CHX) gene	Qi et al. (2014)
Soybean	85–140 × Tiefeng 8	<i>GmSALT3</i> <i>Glyma03g32900.1</i>	Reduce salt transport to shoot tissues Encodes ‘cation/H <sup>+</sup> exchanger family based protein	Guan et al. (2014a)
Soybean	PI 483463 × Hutcheson, F <sub>8</sub> , RIL	<i>GmCHX1, Glyma03g32900</i>		Patil et al. (2016)
Soybean	FT-Abyara × C01, F <sub>8</sub> , RIL	<i>Ncl</i> <i>Glyma03g32900</i>	Low accumulation of Na <sup>+</sup> and Cl <sup>-</sup> accumulation and improve yield Lower accumulation of Na <sup>+</sup> , K <sup>+</sup> , and Cl <sup>-</sup> in the shoot under salinity stress	Do et al. (2016)
Soybean	–	SSAC (salt suppressed AP2 (domain-containing genes)	Relieving its protein inhibition on TH11 which encodes a positive regulator of salinity tolerance	Pan et al. (2016)
Soybean	85–140 × Tiefeng 8, NIL	<i>GmSALT3</i>	Regulate Na <sup>+</sup> and Cl <sup>-</sup> accumulation and improve yield	Liu et al. (2016)
Soybean	<i>Medicago sativa</i>	<i>MsWRKY11</i>	Increase in proline, superoxide dismutase, and catalase Activity	Wang et al. (2018)
Soybean	<i>Arabidopsis</i>	<i>AtSZF2</i>	Modulate ABA/stress responsive gene expression	Kim et al. (2017)

tolerant) for yield related traits (pods per plant, seeds per plant and seed yield) showed significant dominant effects under controlled condition, whereas additive effects were significant for the given yield traits under salinity stress (Samineni et al. 2011). Authors’ proposition of preponderance of additive effects for yield related traits under salinity stress, however, could not gather support from previous studies (Asraf and Waheed 1998). Availability of advanced mating designs such as nested association mapping (NAM), multi-parent advanced generation inter-cross (MAGIC) could play a larger role in resolving the complex genetic make up of such traits (Pandey et al. 2016).

## Discovery of QTLs/candidate genes controlling salt tolerance in grain legumes

Current advances in genotyping technologies have allowed discovery and assay of genome-wide genetic markers to locate QTL(s) controlling salinity tolerance in various legume crops (Vadez et al. 2012; Leonforte et al. 2013; Guan et al. 2014a, b; Qi et al. 2014; Pushpavalli et al. 2015; Do et al. 2016; Liu et al. 2016).

## Conventional QTL mapping

QTL mapping is an important technique to dissect the genetic architecture of complex traits like salinity stress that are governed by a variety of gene(s)/QTLs. In

chickpea, analysis of recombinant inbreds (JG 62×ICCV 2) enabled identification of one major QTL on LG03 governing 19% phenotypic variation (PV) for high seed yield under salinity condition (Vadez et al. 2012). Additionally, QTLs associated with seed number, pod number and 100-seed weight under both saline and non-saline conditions were mapped on LG06. Recently, two major QTLs controlling salinity tolerance were detected in chickpea on LGs05 and 07 from the population ICCV 2×JG 11 (Pushpavalli

et al. 2015). In parallel, the authors suggested a set of 48 putative candidate genes within the QTL-containing region, which encode various proteins including ion transport, ABA biosynthesis, and transcription factors (TFs). Table 3 enlists various QTLs associated with salinity tolerance-related traits in different grain legumes.

In soybean, one major QTL conferring salt tolerance was reported on LG (N) from an intra-specific population S100×Tokyo (Lee et al. 2004). Subsequent analyses based

**Table 3** List of QTLs/ gene conferring salinity tolerance in various grain legumes

Crop	Mapping population and type	QTL(s)	Chromosomal/LG group	PV%	Marker type	References
Chickpea	JG 62×ICCV 2, 126 F <sub>12</sub> RILs	QTL for seed number	3, 6	37	SSR	Vadez et al. (2012)
		QTL for seed yield				
	JG 62×ICCV 2, 126 F <sub>12</sub> RILs	QTL for 50% flowering	4	8.8–37.7	SSR	Vadez et al. (2012b)
		Seed number, shoot dry wt				
	JG 62×ICCV 2, 126 F <sub>12</sub> RILs	One major QTL for seed ratio	6	34.6	SSR	Vadez et al. (2012)
	ICCV2×JG11	2major QTLs	5, 7	12–17	SSR, SNP	Puspavalli et al. (2015)
Cowpea	<i>V. luteola</i> × <i>V. marina</i> subsp. <i>oblonga</i>	<i>Saltol1.1</i>	1	50	SSR	Chankaew et al. (2014)
Pea	Kaspa×Parafield RIL	4 QTLs	3, 7	12–19	SNP	Leonforte et al. (2013)
Soybean	S100 ×'Tokyo, F <sub>2:5</sub>	One major QTL	N	–	SSR	Lee et al. (2004)
	Kefeng No. 1×Nan-nong1138-2 ,RIL (184)	Eight putative QTLs	G, N, K, M, B1, B2	7.1–19.7	SSR	Chen et al. (2008)
	FT-Abyara×C01(RIL), F <sub>7</sub> (96)					Hamwiesh et al. (2011)
	Jin dou No. 6×0197 (RIL), F <sub>6</sub> (81)	One major QTL	N	44.0–47.1		
	F <sub>2</sub> , PI 548657×JWS156-1	One major QTL	–	68.7	SSR	Hamwiesh and Xu (2008)
	Jackson×JWS156-1, RIL	One major QTL	17	53.8	SSR	Tuyen et al. (2013)
	Jackson×JWS156-1, F <sub>6</sub> (112), F <sub>2</sub> (149)	One QTL	D2	13-50.2	–	Tuyen et al. (2010)
	PI 483,463×Hutcheson, RIL, F <sub>3</sub>	One QTL	3	47.8–56.5	SSR, SNP	Ha et al. (2013)
	Hong-feng11×Harosoy, BC	23 QTLs	–	–	–	Qiu et al. (2011)
	–	83 QTL by environment interaction interaction for salt tolerance index and 86QTL by interaction for alkaline tolerance index	–	–	SSR	Zhang et al. (2014)
	Kefeng1×Nan-nong1138-2, F <sub>7:11</sub> , RIL	11 QTLs	2, 7, 8, 10, 17, 18	25.9	SSR	Kan et al. (2016)
	Jidou 12' × 'Ji NF 58, F <sub>9:10</sub> , RIL	One major QTL	3	27–44.7	SSR	Shi et al. (2018)
<i>V. marina</i>	<i>V. luteola</i> × <i>V. marina</i> subsp. <i>oblonga</i> , F <sub>2:3</sub>	One major QTL	–	50	SSR	Chankaew et al. (2014)

on inter-specific (Jackson×JWS 156-1) and intra-specific (FT-Abyara×C 01) (Jin dou No. 6×0197) (Hamweih and Xu 2008; Hamweih et al. 2011) populations further supported presence of salt tolerance associated QTL on LGN. Chen et al. (2008) reported a total of eight putative salt tolerance QTLs explaining upto 19.7% PV. The QTLs viz. *qpsdG.1* (obtained from green house condition) and the *qtrG.1* (detected under field condition) detected on the same location on LG (G) flanked by the markers Sat\_164 and Sat\_358. Additionally, the QTL *qppsN.1* co-localized with same genomic region on LG (N) as suggested earlier by Lee and colleagues.

In soybean, Ha et al. (2013) found one major QTL for salinity tolerance on chromosome 3 by analyzing a RIL population (PI 483463×Hutcheson) with simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) markers. This QTL region corresponded with the genomic region suggested earlier by Lee et al. (2004) as associated with salinity tolerance in soybean. Considering tolerance at germination stage, 11 QTLs (related to germination indices) contributing to salt tolerance were mapped in a population (Kefeng1×Nannong1138-2) (Kan et al. 2016), with the QTL-containing regions showing agreement with previous reports in soybean (Lee et al. 2004; Chen et al. 2008; Hamwieh and Xu 2008; Hamwieh et al. 2011; Ha et al. 2013; Kan et al. 2015).

In pea, two QTLs *Salt index\_QTL 1* (flanked by SNP\_100000313 and SNP\_100000353) and *Salt index\_QTL 2* (flanked by SNP\_100000318 and SNP\_100000130) were reported on LGs Ps III and Ps VII, respectively (Leonforte et al. 2013). The authors also identified a candidate gene *Medtr3g073300.1* that codes for a protein associated with salt tolerance. An updated list of QTLs pertaining to salinity tolerance in various crops is available at PLANTSTRESS site (<http://www.plantstress.com/biotech/index.asp?Flag=1>).

Highly saturated genetic linkage maps enabled by high-density genotyping assays allow better prioritization of candidate gene(s) for downstream analyses and finally, pinpointing the causative locus and its cloning. A major effect QTL for alkaline salt tolerance was fine mapped to a 3.33-cM region on LG17 in soybean (Tuyen et al. 2013), and further analysis of this genomic region led to the identification of four putative candidate genes *Glyma17g15000*, *Glyma17g15150*, *Glyma17g15520*, and *Glyma17g15580* (Tuyen et al. 2013). Similarly, Ha et al. (2013) narrowed down a major QTL on LG03 to a 658-kb region harbouring two candidate genes viz. *Glyma03g32890* and *Glyma03g32900*. Interestingly, different research groups have confirmed the presence of salt tolerance-controlling gene (*GmCHX1/GmSALT3/Ncl*) on chromosome 3 (Guan et al. 2014a, b; Qi et al. 2014; Do et al. 2016; Liu et al. 2016). By further narrowing down the *GmCHX1* locus to a 388-Kb region, Qi et al. (2014) identified two candidate

genes *Glyma03g32890* and *Glyma03g32900* having analogy to cation H<sup>+</sup> exchanger (CHX) gene. The salt tolerance of W05 was attributed to the absence of a retrotransposon element in ion transporter gene *GmCHX1* as compared to the salt sensitive genotypes C08 and William 82 having retrotransposon inserted within the gene. Similarly, a 17.5-kb region (*GmSALT3* locus) on chromosome 3 harbours a candidate gene *Glyma03g32900.1* coding for 'cation/H<sup>+</sup> exchanger family and contributes to salt tolerance via reducing shoot accumulation of Na<sup>+</sup> in soybean (Guan et al. 2014a). A single dominant gene for salinity tolerance was mapped on chromosome 3 within a 209-kb region (Hamwieh and Xu2008), and the observation showed agreement with earlier report of Lee et al. (2004). Later, the *Ncl* locus was assigned to a 16.6-kb region and enabled delineation of the candidate gene *Glyma03g32900* (Do et al. 2016). Unlike the major grain legume crops discussed above, limited progress has been achieved towards identification of salinity tolerant QTL(s) in lesser-studied legumes like cowpea. Nevertheless, improving capacities of genotyping and phenotyping technologies could further enable high-resolution trait mapping and cloning of QTLs responsible for salinity tolerance in grain legumes.

## Genome wide association studies (GWAS)

Association mapping/GWAS is receiving greater attention due to its ability to improve the resolution of the QTL detection without investing extra efforts on population development (Bohra 2013). Higher precision and allelic richness of GWAS has permitted access to functional genetic variants for salt tolerance traits in genetically diverse germplasms of grain legumes (Guan et al. 2014b; Qi et al. 2014; Kan et al. 2015, 2016; Moghaddam et al. 2016; Patil et al. 2016; Zhang et al. 2016; Hoyos-Villegas et al. 2017; Ravelombola et al. 2017; Xu et al. 2017). For instance, SSR-based association analysis of 196 soybean landraces revealed four significant marker trait associations (SMTAs) for salt tolerance imbibition rate (ST-IR) trait on LGs06 and 07, five SMTAs for salt tolerance germination index (ST-GI) on LGs 07 and 19, and eight SMTAs for ST-GR traits on LGs 01, 02, 03, 06, 07, and 19 (Kan et al. 2016). Interestingly, the reported SMTAs overlapped with the genomic regions reported earlier for having association with salinity tolerance in soybean (Lee et al. 2004; Hamwieh and Xu 2008; Ha et al. 2013; Guan et al. 2014b; Zhang et al. 2014; Kan et al. 2015). Likewise, Kan et al. (2015) detected one SMTA for salt tolerant index at germination stage through GWAS of 191 soybean landraces with 1,142 SNPs, thus offering a set of nine candidate genes. Similarly, GWAS of 106 soybean lines with SoySNP50Kchip (Song et al. 2013) revealed SMTAs on chromosome 3 for physiological parameters like leaf chlorophyll



content and leaf scorch ratio (Patil et al. 2016). Importantly, this genomic region overlapped with the *GmCHX1* locus known to control salinity tolerance in soybean (Guan et al. 2014a; Qi et al. 2014). Another GWA study on 283 soybean lines using SoySNP50K chip revealed nine genomic regions showing significant association with leaf chloride concentration and leaf chlorophyll content (Zeng et al. 2017). Likewise, six genomic regions could be associated with salinity tolerance through analyzing soybean with SoySNP50K iSelect BeadChip (Huang et al. 2018). A more recent genotyping-by-sequencing (GBS) analysis in cowpea led authors to discover association of SNP markers with salinity tolerance at germination and seedling stages (Ravelombola et al. 2017). Large-scale and accurate phenotyping protocols may further increase the efficiency of GWAS and, the stable and consistent SMTAs could be deployed in genomics-assisted breeding for improving salinity tolerance in various grain legumes.

### Genome sequencing/re-sequencing to reveal novel functional variants

Latest developments in genome sequencing/ re-sequencing motivated by next generation sequencing (NGS) chemistry have opened up promising avenues to uncover functional genetic diversity associated with traits of agricultural significance (Bohra and Singh 2015; Jha et al. 2016). Sequencing whole genomes holds great importance for capturing the genetic diversity harboured particularly in the wild accessions or landraces, which might have lost during domestication (Qi et al. 2014; Patil et al. 2016). Noteworthy progress has been made to elucidate novel genomic variants associated with the traits of breeding interest in different grain legumes through genome sequencing (Lam et al. 2010; Li et al. 2013, 2014; Varshney et al. 2013; Qi et al. 2014; Schmutz et al. 2014; Zhou et al. 2015; Patil et al. 2016; Rendón-Anaya et al. 2017). A recent sequencing attempt of 31 landraces and 22 wild soybeans elucidated nine haplotypes containing two salt-tolerant and seven salt-sensitive (Guan et al. 2014a). The authors also confirmed the widest geographical distribution of salt tolerance causative H1 haplotype in soybean. Furthermore, re-sequencing of more than 100 soybean lines enabled identification of three major structural variants namely SV1, SV2 and SV3 in the promoter and coding sequences of *GmCHX1* gene (Patil et al. 2016). Importantly, the SV1 manifested by the salt-sensitive genotypes W 82 and C 08 contained Ty1/copia retrotransposon in the given locus (Qi et al. 2014), while salt tolerant SV-2 lacked Ty1/copia retrotransposon. Interestingly, the structural variant SV-3 having no retrotransposon showed salt sensitive reaction. In *M. truncatula*, whole genome re-sequencing of 39 wild accessions provided novel insight into the genetic basis

of adaptation under salinity stress (Friesen et al. 2014). Participation of candidate gene(s) including *Medtr3g098090.1* (orthologous to *AtCIPK21*) in abscisic acid and jasmonic acid signal transduction pathway was shown (Friesen et al. 2014). Availability of sequenced reference genomes in various grain legumes including chickpea (Jain et al. 2013; Varshney et al. 2013), soybean (Schmutz et al. 2010), common bean (Schmutz et al. 2014), cowpea (Munoz-Amatriain et al. 2017) and current progress in sequencing pea genome will delineate hitherto unknown salt responsive structural variants and genes.

Availability of reference genome sequences along with re-sequencing multiple genomes of diverse lines including CWRs and landraces could help delineate novel genomic segments associated with salinity tolerance. This will eventually offer more suitable targets for genome editing techniques such as CRISPR/Cas9 (Pennisi 2013).

### Diverse omics platforms to obtain causative loci

Improvements in understanding other “omes” beyond genome have helped assigning functional role to candidate gene(s)/QTL(s) that relate to complex abiotic stress including salinity stress in crop plants (Salt et al. 2008; Baxter 2009; Liu et al. 2014; Kim et al. 2015; Ahmed et al. 2016b; Conesa et al. 2016; Rathi et al. 2016).

### Transcriptomic approaches to discover candidate gene(s) for salinity tolerance

Recent shift from microarrays to high-throughput RNA sequencing (RNA-seq) technology has accelerated global expression profiling of the candidate gene(s) that respond to stress (Liu et al. 2014; Vu et al. 2015; Conesa et al. 2016). These technologies enhance possibilities to decipher transcripts/genes that play pivotal role in “regulation of transcriptional and translational machineries” under salt stress (Sahi et al. 2006a, b; Jamil et al. 2011).

An array of functional genomic resources have been established for analyzing the expression patterns of various salinity tolerance genes in chickpea; such as cDNA- microarray (Mantri et al. 2007), expressed sequenced tags (ESTs) (Varshney et al. 2009) and deep super serial analysis of gene expression (SAGE) (Molina et al. 2011). Subsequently, RNA-seq analysis of root tissue at vegetative and reproductive stages under salt stress revealed 1376 and 3660 DEGs, respectively in chickpea. Concerning gene function, majority of these differentially expressed genes (DEGs) were associated with cellular metabolic processes (carbohydrate and lipid metabolism), and cell redox homeostasis to ethylene

hormone signaling under salinity stress (Garg et al. 2016). Expression analysis of *GmPAP3* gene induced under salt stress suggested its possible contribution to salt tolerance in soybean through reactive oxygen species (ROS) scavenging (Liao et al. 2003). Higher induction of cellular antioxidant genes and differential expression of *alternative oxidase 1 (Aox1)* gene in root of *M. truncatula* could play significant role in salt stress adaptation (Mhadhbi et al. 2011, 2013). Differential expressions of TF genes such as *bHLH*-type, *ZFP*, *bZIP*, *YABBY*, *HD-Zip*, *ERF/AP2*, *WRKY* are notable owing to their role in regulating plant response to abiotic stresses including salinity stress (de Lorenzo et al. 2007; Merchan et al. 2007; Sanchez et al. 2009; Song et al. 2012; Zahaf et al. 2012; Chen et al. 2014; Deinlein et al. 2014; Zhao et al. 2017). Notably, over expression of *MtCBF4* in *M. truncatula* (Li et al. 2011) and higher expression of *Zpt2-2* and *CBF4* TFs in three annual *Medicago* genotypes (Mokhtari et al. 2017) rendered them salinity tolerant. In common bean, Hiz et al. (2014) obtained differential expression of 6422 and 4555 unigenes from leaf and root tissues,

respectively along with 441 salt responsive TFs from 2678 putative TFs under salinity stress (Table 4). A total of 155 *bHLH* genes were recovered via comprehensive genome wide analysis in common bean (Kavas et al. 2016). Importantly, expression analysis confirmed differential expression of 63 *PvbHLH* genes under salinity stress. Additionally, the authors employed RNA-seq analysis to illustrate the participatory role of miRNA belonging to *PvHLH-22* and *PvHLH-44* genes under salt stress. Gene expression profiling under salt stress revealed up regulation of 65 *GmWRKY* genes and down regulation of *WRKY71* gene in soybean (Yu et al. 2016). While, 47 *GmWRKY* and two *WRKY* genes showed down and up regulation, respectively in RNA-seq analysis of aerial part of plant under salt stress in soybean. Similarly in chickpea, differential expression was observed for *WRKY*-TF genes under salinity stress (Garg et al. 2016). More recently, function of miR156 in response to salinity stress was demonstrated in alfalfa (Arshad et al. 2017). Authors proposed that miR156 led suppression of *SPL* TFs in miR156-overexpressing alfalfa possibly serves as

**Table 4** List of differentially expressed gene(s) related to salinity stress tolerance recorded from transcriptome analysis

Crop species	Genotype	Differentially expressed gene/candidate gene(s)	References
Chickpea	JG 11, JG 62	3798 and 4460 ESTs	Varshney et al. (2009)
Chickpea	INRAT-93	363 and 106 transcripts	Molina et al. (2011)
Chickpea	–	1376 and 3660 DEGs	Garg et al. (2016)
Chickpea	ICC 4958	miRNAs miR156_1 and miR156_10	Kohli et al. (2014)
		Car-miR008, car-miR011 and car-miR015	
Chickpea	JG11 and ICCV 2	Upregulation of cationic peroxidase Aspartic ase, NRT1/PTR Calcium-transporting ATPase Phosphatidylinositol phosphate kinase genes DREB1E, NAC, WRKY, bHLH, and ERF genes, protein kinase genes Phytohormone-related genes and transmembrane Transported genes	Kashyap et al. (2018)
Common bean	–	6422 and 4555 unigenes, 441 TFs	Hiz et al. (2014)
Common bean	–	63 <i>PvbHLH</i> genes	Kavas et al. (2016)
Common bean	–	<i>PvAP2-ERFs</i>	Kvas et al. (2015)
Common bean	Zulbiye	<i>PvHSP70</i>	Buyuk et al. (2016)
Soybean	–	<i>Glyma.10G116600</i> , <i>Glyma.02G087400</i> <i>Glyma.13G329700</i> <i>Glyma.12G073300</i> , <i>Glyma.15G044400</i> and <i>Glyma.11G053800</i>	Pan et al. (2016)
Soybean	–	<i>HD-Zip</i> genes	Chen et al. (2014)
Soybean	–	12 salt-responding F-box genes	Jia et al. (2017)
Soybean	–	Genes involved in carbon and nitrogen metabolism	Liu et al. (2018)
Soybean	RA-452 × Osage	154 common DEGs and <i>Glyma.02G228100</i> , <i>Glyma.03G031400</i> <i>Glyma.04G180300</i> , <i>Glyma.04G180400</i> <i>Glyma.05G204600</i> , and <i>Glyma.17G173200</i>	Zeng et al. (2018)

an activator for expression of non-*SPL* TFs. This in turn causes over-expression of various downstream genes including *NHX1*, *HK1 HC-ATPase* and *SOS1*, which eventually improves salinity tolerance of alfalfa *via* increased biomass, reduced Na<sup>+</sup> toxicity, etc. With growing refinements in sequencing technologies, contribution of non-coding RNA (nc RNA) molecules including both long non coding RNA (lnc RNA) and small RNA (sRNA) or micro RNA (miRNA) in acclimatization of plants to a range of abiotic stresses is evident (Long et al. 2015; Liu et al. 2015). A plethora of salt responsive sRNAs regulating plant gene expression programme in response to salinity stress have been disclosed (Liu et al. 2015; Long et al. 2015). Recently, Pan et al. (2016) unveiled six target genes namely *Glyma.10G116600*, *Glyma.02G087400*, *Glyma.13G329700*, *Glyma.12G073300*, *Glyma.15G044400*, and *Glyma.11G053800* for miR172a expressed under salt stress in soybean (Table 4). It was also postulated the underlying mechanistic role of miR172a in salt tolerance *via* cleaving *AP2/EREBP*-type TF gene *SSAC1*, triggering induction of thiamine biosynthesis gene *TH11* encoding positive regulator for salt tolerance. Majority of the regulatory genes are involved in basic biological metabolic processes covering photosynthesis, biosynthesis of unsaturated fatty acids to phenylalanine metabolism. By employing a comparative genomics approach in cowpea, 18 conserved miRNAs and corresponding 15 target genes were recovered under salt stress (Paul et al. 2011). Of these 15 genes, upregulation of seven genes under salt stress was validated through qRT-PCR assay. While, Kohli et al. (2014) recovered miRNAs miR156\_1 and miR156\_10 showing low up regulation and, novel miRNAs *viz.*, car-miR008, car-miR011 and car-miR015 showing three fold up regulation under salt stress in chickpea using high throughput sequencing of ICC 4958 RNA. The target gene of miR156 was reported to encode squamosa promoter-binding protein. To quantify and localize gene expression simultaneously, Lieben et al. (2017) suggested ‘spatial transcriptomic’ approach that combines data from histological imaging and RNA sequencing. The global transcriptome profiling improves our capacity to understand the gene expression networks, regulatory molecules including TFs and the crosstalk between different pathways that participate to impart salinity tolerance in plants.

## Proteomics

Proteomics allows comprehending the changes in proteins participating in essential biological pathways and post translational modifications of ‘stress-induced’ proteins, essentially needed by plants to acclimatize themselves to various abiotic stresses (Kosová et al. 2011; Hossain et al. 2013; Ramalingam et al. 2015). Thus, it could be of paramount

significance to capture the entire proteins produced in response to various abiotic stresses including salt stress, thus furthering our knowledge about the protein networks associated with salt responsive signaling pathways (Ji et al. 2016). Importantly, various strategies deployed by plants to adapt themselves under salt stress at cellular, metabolic and whole plant level could be deciphered *via* proteomics (Ahmad et al. 2016; Silveira and Carvalho 2016; Zargar et al. 2017). Among legume crops, comprehensive proteomic studies are mostly available in two major legume crops *viz.*, soybean and *M.truncatula* (Rathi et al. 2016). Following salinity stress changes occur in crucial proteins including those related to photosynthesis, carbohydrate and energy metabolism, anti oxidant/ROS scavenging, and signal transduction pathways (Long et al. 2016) (for details see Kumari et al. 2015). Concerning changes in proteins in photosynthesis, differential expression was noted in soybean leaves, hypocotyls, and roots in response to salt stress (Sobhanian et al. 2010). Down regulated proteins included ‘glyceraldehyde-3-phosphate dehydrogenase’ (expressed in leaf/hypocotyls), ‘fructokinase 2’ (expressed in hypocotyls/root) that participate in photosynthesis and other metabolic processes under salinity stress (Sobhanian et al. 2010). In case of cowpea, a total of 22 differentially regulated proteins under salt stress were recovered from two contrasting genotypes (de Abreu et al. 2014). Important proteins such as ‘rubisco activase, ribulose-5-phosphate kinase (Ru5PK), oxygen-evolving enhancer (OEE) protein 2’ that participate in vital processes like energy metabolism and photosynthesis showed abundance in salt tolerant genotypes, contrary to which these key processes are negatively affected in salt sensitive cultivar limiting their growth (de Abreu et al. 2014).

MALDI-TOF/TOF mass spectrometry aimed to identify proteins pertaining to changes in cellular metabolism in salt-stressed soybean unearthed a set of 43 responsive proteins. A total of 29 proteins showed up-regulation, while 8 proteins showed down regulation and 6 proteins were recorded to be novel under salt stress (Alam et al. 2011). Importantly, understanding the role of phosphoproteins in connection to salt tolerance, proteomic analysis at various time intervals identified 2692 phosphoproteins and 5509 phosphorylation sites in contrasting soybean cultivars under salt stress (Pi et al. 2016). Additionally, phosphorylation of various TFs including MYB/MYB TF like proteins regulate the salt responsive gene(s), involved in chalcone metabolism (chalcone synthase) causing salt tolerance in soybean were recovered. Moreover, 278 and 440 salt responsive differentially expressed proteins from leave and root, respectively, were identified *via* iTRAQ assay in soybean under salt stress (Ji et al. 2016). Concerning their functional role, all the recorded proteins could be assigned to 13 categories covering carbohydrate metabolism, stress and defense, signaling, membrane transport to

cell division. Additionally, up regulation of late embryogenesis-abundant protein, beta-conglycinin, elicitor peptide three precursor, and basic/helix-loop-helix protein, while down-regulation of protease inhibitor and lectin proteins was observed in hypocotyls and root of soybean (Aghaie et al. 2009).

Integrating proteomic data with genomic or transcriptomic data could illustrate underlying candidate gene(s) and the complex regulatory mechanisms and key signaling players involved in salinity response and tolerance in grain legumes (Ngara and Ndimba 2014).

## Metabolomics

Transcriptomics and proteomics based approaches are not adequate to illuminate the global landscape of cellular response shown by plants under abiotic stress, as plant response might involve a variety of metabolites produced under stress (Hall et al. 2002; Sumner et al. 2003; Bhalla et al. 2005; Shulaev et al. 2008; Kumar et al. 2017a, b). Therefore, metabolomics is receiving increasing attention to adequately explain the “ultimate phenotype” emanating from “complex gene network and their interaction with environment” (Hill et al. 2013; Dias et al. 2015). In grain legumes, implementation of metabolomics approach, however, has remained confined to model legumes to comprehend plant stress response (Farag et al. 2008; Sanchez et al. 2008, 2010; Komatsu et al. 2011; Ramalingam et al. 2015). Like proteins, significant changes occur in various metabolites involved in carbohydrate metabolism, amino acids biosynthesis in TCA and glycolysis cycle and at other protective antioxidation system levels (Kumari et al. 2015; Jiao et al. 2018).

A comparative analysis of wild soybean W05 and cultivated soybean C08 at metabolic level suggested abundance of several compounds such as disaccharides, sugar alcohols, and acetylated amino acids in wild type than the cultivated types (Lu et al. 2013). Likewise, Zhang et al. (2016) suggested a relation between elevated levels of metabolites (phenylalanine, asparagine, citraconic acid and other metabolites derived from TCA cycle and glycolysis process) with salinity tolerance of wild type soybean (*G. soja*) than the cultivated type (*G. max*). Additionally, enhanced production of several metabolites ranging from amino acids like isoleucine, serine, l-allothreonine, glutamic acid, phenylalanine, asparagines, aspartic acid, and other fatty/organic acids and anti oxidants provides higher tolerance to salinity stress in wild soybean seedlings in comparison to cultivated soybean (Li et al. 2017b). A comparative metabolomic study in W1 common wild type soybean and W2 salinity tolerant wild type soybean revealed enhanced accumulation of different organic acids, TCA cycle metabolites and various amino acids in the root of W2 type, which in turn conferred higher

salinity tolerance to W2 than W1 (Jiao et al. 2018). Thus, specific metabolites produced under salinity stress could act as biomarker for distinguishing salt tolerant and sensitive genotype (Sanchez et al. 2011). However, reports on elucidating the role of various metabolites involved in salinity acclimation are limited in grain legumes.

## Ionomics

Ionomics is one of the emerging ‘omics’ approaches that facilitates ‘high throughput elemental profiling’ of an organism (Salt et al. 2008; Baxter 2009). Ionomics could decipher the role of mineral nutrients dynamics causing plant toxicity/deficiency and thus, negatively affecting different plant growth stages under various abiotic stresses including salinity (Shelden and Roessner 2013). Also, ionomics can be employed as both forward and reverse genetic tool for investigating gene(s) function in plant (Baxter 2009). A number of high throughput techniques such as inductively coupled plasma-mass spectrometry (ICP-MS), inductively coupled plasma-atom/optical emission spectrometry (ICP-AES/OES), X-ray fluorescence (XRF), laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), neutron activation analysis (NAA) have been used for studying ionomes (Becker 2010; Sanchez et al. 2011; Wu et al. 2013). Ionomics has also been applied to elucidate ion detoxification and ion homeostasis in response to salinity in cereals (Wu et al. 2013) and legumes such as *Lotus creticus*, an extremophile and *L. corniculatus* and *L. tenuis*, glycophytic legume species (Sanchez et al. 2011). The study showed differential expression of Ca, Mg, Mn, Fe, and Zn in plants in response to salinity stress. In parallel, considerable elemental changes such as an increase in S, P and Zn was shown by salinity tolerant genotypes in comparison to salinity sensitive genotypes. Changes in  $\text{Na}^+$ ,  $\text{Zn}^{+2}$ ,  $\text{Ca}^{+2}$ , and  $\text{Mg}^{+2}$  ions in miR156-overexpressing alfalfa genotypes at different levels of salinity stress led authors to propose that overexpressive miR156 alfalfa accumulate lower  $\text{Na}^+$  to manifest salinity tolerance (Arshad et al. 2017). In recent years, association between altered content of various elements and salinity response has been demonstrated in various crops. For example, in maize dynamics of various essential nutrient elements ranging from K, Na, Ca, Zn, Fe, Cu, Mn to B in root and shoot seedling under salinity was reported (Guo et al. 2017). Importantly, abundant  $\text{Na}^+$  and  $\text{Cl}^-$  content in both old and young leaves and a decrease in K content in older leaves were noticed. The content of Ca was highest in old leaves, while K content was highest in the young leaves under alkali stress in cotton (Guo et al. 2016). The immense potential of ionomics

techniques in deciphering salinity stress tolerance remains to be seen in case of grain legumes.

## Phenomics to describe physiological response to salinity stress

Despite unprecedented progress in genomic data generation, phenotyping capacity still offers a key bottleneck to understand the quantitatively inherited complex traits that are highly influenced by the environment (Furbank and Tester 2011). Enhanced precision and throughput of trait phenotyping including response to salinity, high-throughput phenotyping platforms have been recently established; examples include The Plant Accelerator in Adelaide, Australia and International Plant Phenotyping Network (<http://www.plant-phenotyping.org/>) and so forth. These next-generation phenotyping techniques offer several advantages over conventional phenotype recording such as non-destructive measurement/ non-invasive phenotyping, automation of data, spectral imaging of complex traits, generating precise records such as ‘ionic responses’ under salinity stress (Berger et al. 2012; Campbell et al. 2015; Al-Tamimi et al. 2016; Negrao et al. 2017). Image-based phenotyping approach including thermal infrared imaging, fluorescence imaging, 3D imaging (James and Sirault 2012; Li et al. 2014; Campbell et al. 2015; Fahlgren et al. 2015; Atieno et al. 2017) is emerging as one of the important high throughput phenotyping platforms to record the minute changes in morphological and physiological responses at ‘high time and spatial resolution’ (Negrao et al. 2017). These responses range from ‘chlorophyll fluorescence and leaf water content’, relative growth rate to leaf senescence under salinity stress in large set of germplasm or in mapping population at a time (Berger et al. 2012; Hairmensis et al. 2014; Campbell et al. 2015; Awlia et al. 2016). In this regard, relative growth rate dynamics measured at various time scales using high-resolution imaging system (fixed 5 megapixel visible/RGB camera) under the salinity stress in chickpea is noteworthy (Atieno et al. 2017). As discussed by Negrao et al. (2017), high throughput phenotyping in plants enables accurate assessment of effects of salt stress at various physiological levels including photosynthesis, transpiration, ionic relation, plant senescence and also on yield and other traits relevant to salinity tolerance. Advances in plant phenomics including automated and digital imaging may further increase our understanding of the diverse temporal response of genotype under salinity stress. In this regard, ‘deep learning’ (Singh et al. 2018), ‘active vision cell’ (AVC) image-acquisition (Gibbs et al. 2018) and other modern phenotyping tools could be employed

for identifying, quantifying and predicting plant salinity response with enhanced precision.

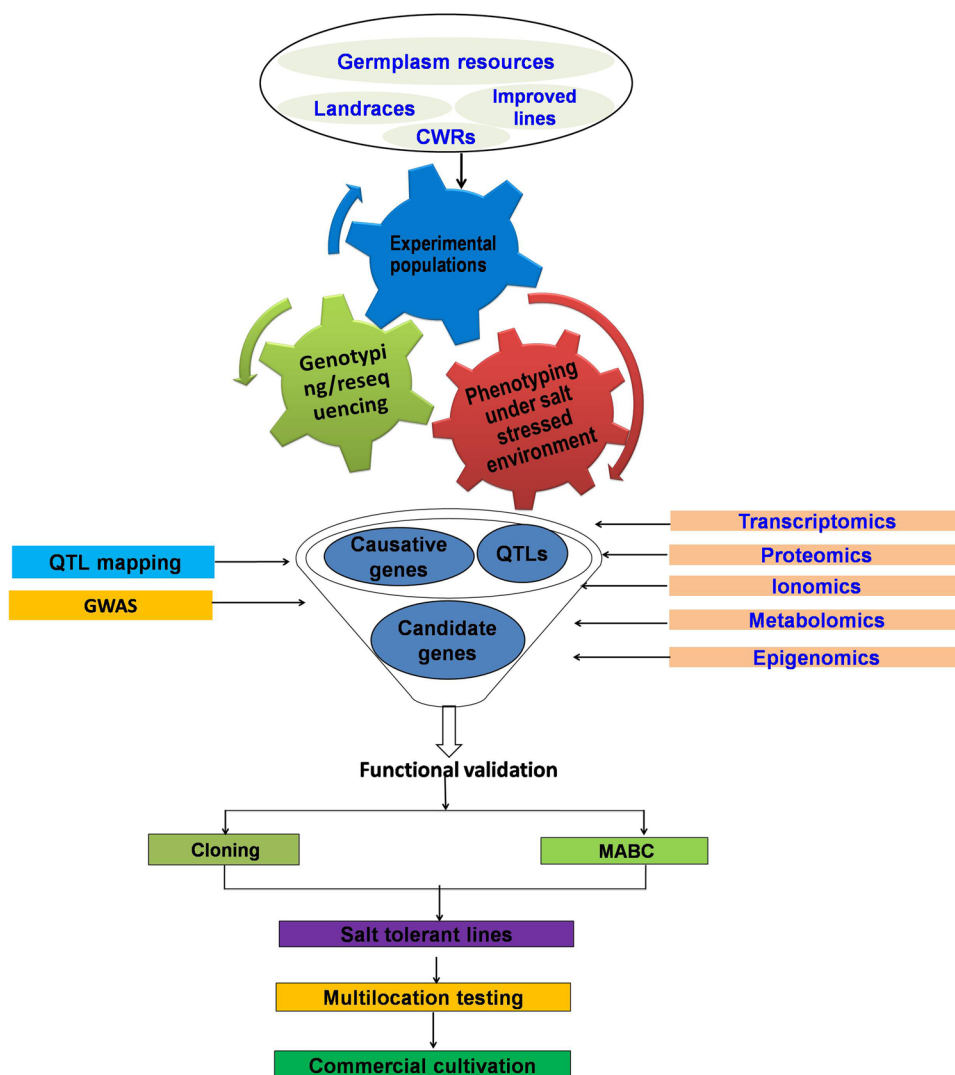
## Marker-assisted selection (MAS) for salinity tolerance: some examples in grain legumes

Trait mapping studies in grain legumes have led to development of breeder-friendly genotyping assays to allow QTL introgression into elite cultivars through simple MAS or marker assisted back crossing (MABC) technique (Collard and Mackill 2008). With regard to MAS for salinity tolerance, noteworthy examples are now available across different crops (for details see Asraf and Foolad 2013; Arzani and Ashraf 2016). MABC enabled transfer of *Ncl* gene from wild soybean JWS 156-1 to salt sensitive cultivar Jackson underscores the immense potential of DNA marker technology for targeted and accelerated improvement of salt stress tolerance in grain legumes (Do et al. 2016). The resulting introgression lines with the *Ncl* gene introgressed in them showed up to 5.5 times higher yield under salinity stress. Greater efficiency of MAS for enhancing salt tolerance was demonstrated in soybean breeding programs with DNA markers Barcsoyssr\_3\_1306, Barcsoyssr\_3\_1310 and QS080465 InDel registering 76.2%, 90.1% and 94.3% efficiencies, respectively (Guan et al. 2014b). Similarly, Liu et al. (2016) successfully employed MAS for differentiating between salt-tolerant and salt-sensitive ILs (Tiefeng 8 × 85–140) using an InDel marker. Though cases of MAS for improved salinity tolerance have been reported only in soybean, growing number of MTAs reported in different grain legumes hold promise to extend usage of these technologies to other less researched crops (Do et al. 2016; Liu et al. 2016).

## Emerging role of epigenetics in understanding salinity stress

Recent technological advancement has greatly supported epigenetic regulation as “mechanistic basis of stress memory” that plays a greater role in regulating various stress responsive gene(s) for plant survival under various environmental stresses including salinity stress (Kim et al. 2010, 2015; Pandey et al. 2016a, b; Lamke and Baurle 2017). Role of epigenetics in conferring ‘phenotypic plasticity’ to plants to adapt themselves to various abiotic stresses has been critically reviewed (Gallusci et al. 2017). Regulation of various important TF coding genes via epigenetic modification (methylation and histone modification) could play significant role in adapting

**Fig. 1** Integrated ‘omics’ approaches for development of salinity tolerant genotypes



soybean under salinity stress (Song et al. 2012). Out of 10 TFs, significant up regulatory induction in four TFs (one *MYB*, one *b-ZIP* and two *AP2/DREB*) gene such as *Glyma11g02400*, *Glyma08g41450*, *Glyma16g27950* and *Glyma20g30840* were noted due to changes in methylation pattern in the promoter regions of the given genes under salinity stress (Song et al. 2012). Methylation and demethylation status of H3K4me3, H3K9me2 and H3K9ac control the expression of these genes under salinity stress (Song et al. 2012). Differentially methylated regions and their relevant role in expression of various genes related to abiotic stresses including salinity stress has been recently uncovered via whole genome bisulphate sequencing in rice (Garg et al. 2015; Wang et al. 2015), wheat (Wang et al. 2014; Kumar et al. 2017a, b), brassica (Marconi et al. 2013), maize (Forestan et al. 2016). More research on epigenetics will increasingly uncover the association between ‘epigenetic biomarker’ and alterations in gene expressions in response to salinity stress.

However, progress of understanding of salinity stress response in grain legume at epigenetic level remains limited.

### Integration of “omics” to sustain grain legume yield under salinity stress

With the deluge of high-throughput ‘omics’ data, bioinformatics/computational biology is receiving greater attention to derive better inferences from the large-scale datasets (Colmsee et al. 2012; Deshmukh et al. 2014; Jha et al. 2017). However, integration of these vast ‘omics’ data to resolve the complex traits at functional level poses a big challenge (Deshmukh et al. 2014). A complex network of signal transduction pathways and several levels of regulations occurring at gene regulation, transcription, post-transcription and post-translational render salinity a

complex trait (Li et al. 2017a, b). Thus, ‘omics’ including transcriptomics, proteomics, metabolomics, ionomics, and epigenomics level ultimately, decides the phenotypic expression of gene(s) contributing in salinity stress tolerance. To retrieve information pertaining to gene, genomics, transcriptomics, proteomics and other ‘omics’, several web-based resources have been established in various legume such as Chickpea Transcriptome Database (CTDB) in chickpea (Verma et al. 2015), Cowpea Genespace/Genomics Knowledge Base (CGKB) in cowpea (Chen et al. 2007), Soybean Knowledge Base in soybean (SKB, <http://soykb.org>), and Legume information system (LegumeInfo.org) (Dash et al. 2016). To expeditiously breed tolerant cultivars in grain legumes, deployment of candidate gene(s)/QTL(s) contributing salinity tolerance through effective integration of multilayer ‘omics’ science and breeding techniques is illustrated in Fig. 1.

## Conclusion and future directions

Yield gains of grain legume crops need incremental increase in the face of growing food demands coupled with an expansion in salt affected area (Alexandratos and Bruinsma 2012). Large-scale deployment of CWRs is imperative to bring ‘salinity adaptive traits’ into the cultivated pool. This, however, will require: (a) reliable evaluation of germplasm resources for salinity tolerance (b) monitoring precise phenotypic response of genotypes at various growth stages under salinity stress (Atieno et al. 2017) and (c) multi-location field testing of tolerant genotypes under salinity stress. To support crop improvement programs, ‘multi-layered omics science’ could play a significant role in deciphering plant salinity response. In addition, new breeding techniques such as ‘speed breeding’ (Li et al. 2018), genomic selection (Goddard and Hayes 2007) and genome editing via CRISPR-Cas9 (Pennisi 2013) could enable faster development of stress tolerant plants. The improved knowledge about plant salinity response coupled with more efficient breeding programs will certainly contribute to sustain productivity levels of grain legume crops under salt-stressed scenario.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interests.

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