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REVIEW

IMPORTANT ANALYZING PARAMETERS IN THE ASSESSMENT OF SALT TOLERANCE IN PLANTS

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SUMMARY

Maximal crop performance potential and land area suitable for cultivation are usually restricted by adverse environmental conditions. Among the abiotic factors, salinity stress is considered as one of the main threats, which causes ionic toxicity, dehydration and oxidative stresses on the plants. Alarmingly, the impact of salinity is predicted to be more severe in the forthcoming years due to global warming. Therefore, development of new cultivars with better salinity resistance with mimimized yield penalty under the adverse condition, either by breeding or genetic engineering approach, has attracted a great attention from the scientists. In this review, important parameters used in evaluation of plant resistance ability against salinity stress are discussed, which highlights the necessity to obtain multi-sets of biological data ranging from analyses of morphological alterations to physiological, biochemical and molecular responses, as well as by performing -omics studies to find out network of salinity-responsive pathways. Literature review also demonstrates that the relevance of salinity condition setup in terms of concentration and duration is required in experimental design. Furthermore, recent investigations on genome duplication, activities of non-coding sequence or epigenetics also reveal their regulatory roles in shaping plant response and tolerance degree toward salinity stress. Collection of such data not only contributes to widen scientific understanding of plant response mechanisms and adaptation to this stress factor but also facilitates the identification of important genes associating with plant tolerance to salinity. Therefore, the presented information could be used as a reference for the salinity stress-related studies serving for crop innovation and transgene function characterization.

Keywords: *analyzing parameters, gene function characterization, osmotic stress, plant resistance, salinity stress*

INTRODUCTION

In addition to drought, salinity has emerged as another major abiotic threat that agriculture production is currently facing with. Presence in high concentration of either sodium bicarbonate $NaHCO_3$ (i.e. alkaline soil) or sodium chloride NaCl (i.e. saline soil) is the main cause for soil becoming "salinized", which contains excessive level of Na^+ ions (Chen *et al*., 2014). Under effects of climate change and global warming, area of saline soil has been critically expanded due to aggressive intrusion of the sea water onto mainland in recent years (Li *et al.,* 2009). Furthermore, human cultivation activities such as inappropriate water management and fertilizer

usage have worsen the situation (Pessarakli, Huber, 1991; Wanjogu *et al.,* 2001). Excessive salts in soil cause negative effects on growth and productivity of crop plants, which mainly belong to the group glycophyte with the character of low resistance to salinity (Flowers 2004; Munns, Tester, 2008).

Under this adverse condition, plants suffer stunted growth, leaf chlorosis, reduced photosynthesis, cellular water loss, disrupted cellular ionic homeostasis and cell damage due to accumulation of reactive oxygen species (ROS) (Kumar *et al*., 2013; Golldack *et al*., 2014) (Figure 1). If the stress is prolonged or too severe, plants even cannot maintain their survival. Following the progress events of salinity stress effects on plants, in the early stage, plants experience with physiological drought (i.e. hyperosmotic stress) due to the difficulties in absorbing water from the soil with high concentrations of ions by the root systems. Following this, accumulation of cellular Na^+ and Cl^- results in ionic toxicity (i.e. hyperionic stress) to plant cells. Osmotic and ionic stresses can then trigger the oxidative stress with increased production of cellular ROS contents (Gupta, Huang, 2014) (Figure 1). It is noted that apart from direct effects on plants, salinity stress also disturbs the environment in the rhizosphere (i.e. the soil vicinity surrounding the root system), thus preventing the plants from establishment with beneficial microorganisms and uptaking nutrients (Kulkarn *et al*., 2000; Rao *et al*., 2002).

In this review, we summarize parameters that the researchers can rely on in evaluating plant resistance capacity to salinity, which will be discussed in connection with current understanding of plant response to this adverse condition and progress in advancement of technologies and methodologies. The information presented here could be used as a reference in designing a relevant and sufficient set of assessment criteria for comparative studies, which serve for the selection or development of salinity-tolerant cultivars and for gene function characterization purpose.

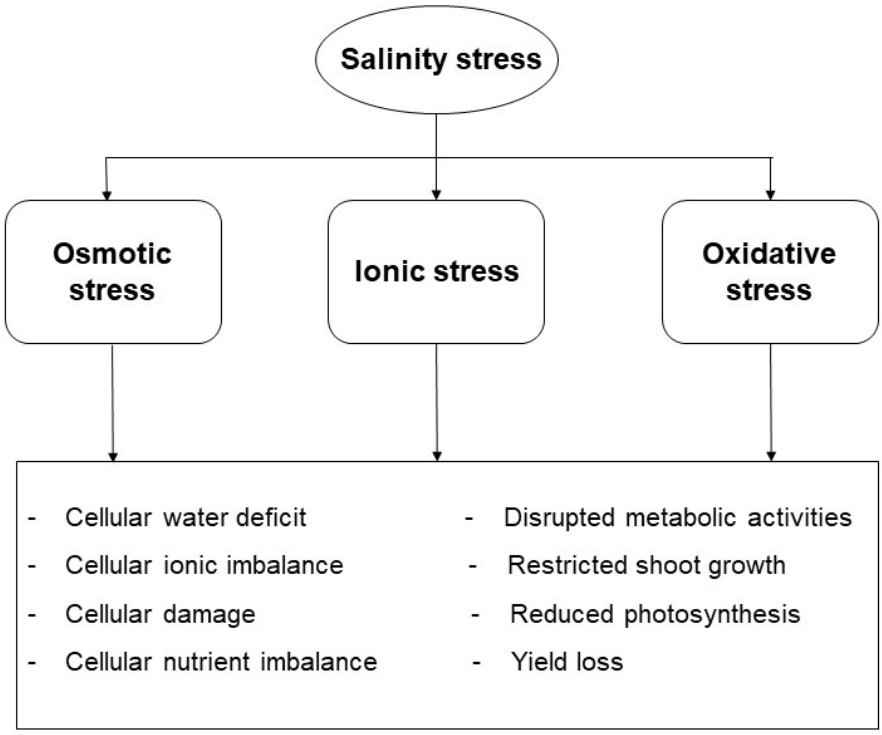

Figure 1. Salinity effects to plant growth, development and productivity.

ANALYZING PARAMETERS ASSOCIATING WITH MORPHOLOGICAL, PHYSIOLOGICAL AND BIOCHEMICAL TRAITS

Evaluate morphological characters and overall plant performance under salinity stress

Examining survival rate upon salinity stress exposure is an indispensable experiment as its results will provide an overall evaluation on the salt tolerance capacity of a plant genotype before its tolerance mechanisms are investigated (Table 1). The assay can be divided into three main stages, which are (i) growing plants under normal condition, (ii) stress application, and (iii) recovery and survival rate calculation. For example, two-week-old *Arabidopsis* can be treated with 200 mM NaCl solution daily over a three-week-duration, followed by three-day normal irrigation with water prior to calculating the proportion of alive plants (Li *et al*., 2019). It is noted that the duration and procedure of the stress treatment can be modified depending on plant species, plant age, plant density per container, salt concentration and volume, as well as frequency of the salt solution application (Table 2). In study of Li *et al*. (2018), four-week-old *Arabidopsis* seedlings were used for application of 300 mM NaCl solution every three days until the stress effects could be visualized. Meanwhile, salt treatment for rice (*Oryza sativa*) can be set up by exposing the seedlings to ten-day-stress duration using 150 mM NaCl solution (Zhu *et al*., 2015). Generally, dicot plants have a greater variation in salinity tolerance than the monocot plants (Munns, Tester, 2008). Furthermore, this method can be used to analyze the salt effects on plant productivity by investigating the reproduction-related traits rather than survival rate (Table 1). The agronomic traits are very important in agricultural and economic perspectives in selecting elite cultivars not only with enhanced stress tolerance but also with high productivity (Liang *et al*., 2016). Singh and others (2015) have demonstrated that among the tolerance indices that can be used to assess the salt resistance associated with plant productivity, mean productivity, geometric mean productivity, and stress tolerance index were more reliable parameters than others such as tolerance index, yield index and yield stability index (read original paper for information of each index calculation).

As salinity stress inhibits early seed development, examination on germination rates as well as shoot- and/or root-associated traits over a range of different salt concentrations is usually conducted (Table 1). For *Arabidopsis*, the sterilized seeds are placed on half strength Murashige and Skoog (1/2 MS) medium (Murashige, Skoog, 1962) containing NaCl 100 mM under relevant growing condition and the rate of seeds with radicle emergence (i.e. successful germination) can be monitored every 24 hours within five consecutive days since seeding (Li *et al*., 2019). Germination test using higher salts (e.g. 250 mM) and MS medium has also been reported (Lee *et al*., 2006). In addition, this test is commonly conducted over a range of different NaCl concentrations. For example, sterilized soybean (*Glycine max*) seeds can be placed on the medium containing 0, 100, 200 and 300 mM NaCl (Li *et al*., 2017).

This *in vitro* assay system (100-125 mM NaCl) can also be used to assess root length and fresh weight of *Arabidopsis* seedlings that has been grown on medium with salt supplementation for a week (Qin *et al*., 2017; Li *et al.,* 2019). For studies in tobacco (*Nicotiana tabacum*), NaCl solution with concentrations of 100-200 mM has been applied for germination and growth assays (Kobayashi *et al*., 2008; Yang *et al*., 2017). With bigger plants like soybean, growing plants in hydroponic system using half-strength Hoagland solution can make it easier for salt treatment, simply by adding the desired salt amount into the nutrition solution and immersing the root part into this liquid (Li *et al*., 2017) (Table 1). In addition, certain measurements can be categorized for specifically ranking the plant tolerance capacity. For example, depending on the visualized damage and necrotic degree that the studied plants can be placed in a five-point

scale, with level 1 for no sign of necrosis and level 5 with the highest score of injured areas (75-100%) (Sabra *et al*., 2012). Similarly, degree of reduction in relative growth rate under salinity stress condition, of which calculation is based on the dry weight recorded at different time points, can be used to divide plants into groups of salt-tolerant, moderately salt-tolerant, moderately salt-sensitive and salt-sensitive species (Cassaniti *et al*., 2012).

Table 1. Common parameters used for analyses of morphological, physiological and biochemical traits to evaluate plant resistance capacity to salinity stress.

Assay name	Analyzing parameters	References
Survival rate assay	post-stress survival rate	Li *et al*., 2018; Li *et al*., 2019
Germination assay	germination rate	Li *et al*., 2017
Vegetative growth assay	root length, shoot length, fresh and dry biomass	Wang *et al*., 2016; Li *et al*., 2017
Analysis of reproductive traits	flowering time, number of flowers/pods/fruits/fruit branches, yield per plant	Liang *et al*., 2016; Wang *et al*., 2017
Analysis of accumulated reactive oxygen species	superoxide anion and hydrogen peroxide contents	Wang *et al*., 2017
Analysis of membrane damage	ion leakage and malondialdehyde content	Orellana *et al*., 2010; Wang *et al*., 2016
Analysis of antioxidant enzyme activities	superoxide dismutase, peroxidase, catalase and glutathione transferase activities	Li *et al*., 2017; Wang *et al*., 2017
Measurement of hormonal contents	abscisic acid and jasmonic acid	Yang *et al*., 2001
Measurement of osmolyte contents	Proline, trehalose and soluble sugar contents	Wang *et al*., 2017
Measurement of intracellular ion contents	Na^+, K^+ and Cl^- contents	Xu *et al*., 2016; Li *et al*., 2017
Evaluation of photosynthetic performance	Chlorophyll content, stomata aperture and density	Orellana *et al*., 2010; Liang *et al*., 2016; Wang *et al*., 2017

Table 2. Concentrations of sodium chloride that have been applied to different plant species in salinity stress-related studies.

Plant species	Applied NaCl concentration	Duration	Studied system	Studied parameters	References
Arabidopsis thaliana	250 mM	2 weeks	Soil and irrigation	Survival rate, chlorophyll content	Cao *et al*., 2017
		4, 10, 12, 14 and 16 days		Fv/Fm values	
	100 and 150 mM	7 days	Half-strength MS	Root length	He *et al*., 2019
	200 mM	12 days (4-d intervals)	Soil and irrigation	Survival rate, fresh weights, Fv/Fm, MDA, proline and H_2O_2 contents,	

				antioxidant enzyme activities	
	50, 100 and 150 mM	5 days	Half-strength MS	Seed germination	
Boehmeria nivea (ramie)	250 mM	7 days	Half-strength Hoagland	Photosynthesis, relative water content, MDA and proline contents, peroxidase activity	An *et al*., 2015
	300 mM	12 days	Soil and irrigation	Total plant fresh and dry weights	
	350 mM	11 days		Fresh and/or dry weights of shoot/root/bast; transpiration	
Glycine max (soybean)	200, 250 and 300 mM	7 days	Half-strength MS medium	Germination rate	Zhang *et al*., 2013
	300 mM	48 hours	Hydroponic	Root characters	
	200 and 300 mM	2 weeks (3 times/week)	Soil and irrigation	Growth characters	
	300 mM	9 days (3 times/week)		Proline and sugar contents	
Gossypium hirsutum (cotton)	250 mM	7 days	Hoagland solution	Fresh and dry weights	Liu *et al*., 2014
		2 weeks		Proline and MDA contents	
	100 and 250 mM	20 days (5- or 10d-intervals)	Soil and irrigation	Photosynthesis, stomatal conductance and transpiration	
Musa acuminata (*banana*)	100, 200 and 250 mM	6 days	Salt solution	Leaf disc assay for chlorophyll content determination	Tak *et al*., 2017
	250 mM	15 days	Soil and irrigation	MDA, Fv/Fm, proline contents	
Nicotiana tabacum (tobacco)	100 mM	30 days	Half-strength MS medium	Root lengths and weights	Li *et al*., 2018
Oryza sativa (Rice)	150 mM	6 days	Hoagland solution	Na^+ content	Hong *et al*., 2016
			Half-strength MS medium	Shoot height, fresh weight, number of later roots	
	200 mM	12 days	Soil and irrigation	Survival rate	Hu *et al*., 2006
	100 mM	5 days	Hydroponic	Fresh weight	

		10 days	MS medium	Shoot and root growth measurements	
Solanum lycopersicum (tomato)	100 mM	4 days	Salt solution	Leaf disc assay for chlorophyll content determination	Zhu *et al*., 2014
	400 mM	21 days (72-hour interval)	Soil and irrigation	Growth characters	
Triticum aestivum (bread wheat)	2%	7 days	Hoagland solution	Survival rate, fresh and dry weights	Saad *et al*., 2013

Evaluate physiological and biochemical traits of plants under salinity stress

It has been known that oxidative stress is the secondary stress induced by osmotic and ionic disturbance, with increased production of ROS contents (Gupta, Huang, 2014). Accumulation of species such as superoxide ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2) in plants can cause damage of cellular membrane and molecules, as well as interruption of metabolic activities (Gill, Tuteja, 2010). Knowing accumulation degree of these ROS can be used as indicators for the estimation of cellular oxidative stress level. Detection of ROS in the leaf tissues can be achieved by staining methods using nitro blue tetrazolium (NBT) for $O_2^{\bullet-}$ (Shi *et al*., 2010) and 3,3'-diaminobenzidine (DAB) for H_2O_2 (Liu *et al*., 2014). Although total ROS production in intact cells can be visualized by staining with 2,7-dichlorofluorescin diacetate (H_2DCF-DA) (Zhang *et al*., 2011; Yang *et al*., 2017), this method has been claimed not to be accurate due to non-specificity in substrate binding of the chemical reagent (Jakubowski, Bartosz, 2000; Chen *et al*., 2010). Apart from these histochemical staining assays, H_2O_2 content can be quantified by spectrophotometric approach (Patterson *et al*., 1984) (Table 1). In addition, oxidative stress-induced damage of cellular membrane can be estimated based on the measurement of electrolyte leakage or malondialdehyde (MDA) contents (Campos *et al*., 2003; Li *et al*., 2015) (Table 1). In some studies, examination on cell death by Evans blue staining is also conducted (Zhang *et al*., 2011; Qin *et al*., 2017; Yang *et al*., 2017). In other papers, measurement of Na^+ and K^+ contents is addressed as the plant growth is negatively affected by the high level of Na^+ in the cytosol but supported by the presence of K^+ (Munns *et al*., 2006; Chen *et al*., 2014; Xu *et al*., 2016; Li *et al*., 2017) (Table 1). Therefore, under salinity stress conditions, maintaining a low cytosolic Na^+/K^+ ratio is important for normal metabolic activities to take place (Munns *et al*., 2006; Chen *et al*., 2014). In certain species that are able to effectively prevent the Na^+ accumulation on leaves, measurement of Cl^- should be conducted as its concentration might be enhanced to a toxic dose level along with potassium ions (Munns, Tester, 2008).

Plants use both enzymatic and non-enzymatic pathways to protect themselves from oxidative stress effects, mainly by scavenging ROS or by using molecules functioning as antioxidants. Regards to the enzyme-mediated defense, superoxide dismutase (SOD) plays in the first line by converting superoxide into H_2O_2. The generated H_2O_2 will be further detoxified by peroxidase (POD) and catalase (CAT) enzymes. In the non-enzymatic defense pathway, certain molecules such as proline, soluble sugars (e.g. trehalose, glucose and fructose) and glycine betaine will play a role in antioxidative protection (Ashraf, Foolad, 2007; Gupta, Huang, 2014; Qin *et al*., 2017; Wang *et al*., 2017). The main functions of these compounds are to enhance water retention capacity by lowering cellular water potential under osmotic stress as well as stabilize cellular environment to maintain

metabolic activities (Ashraf, Foolad, 2007). Therefore, analyzing enzymatic activities or contents of these antioxidant/osmoprotectant molecules would provide important information on plant defense capacity to salinity (Li *et al*., 2018; Li *et al*., 2019) (Table 1).

As salinity stress also causes adverse effects on photosynthetic molecules and performance, measurement of chlorophyll content is usually included in the study. To do this, in small plants like *Arabidopsis*, aerial part of different plants can be pooled together for being used as a biological replicate (Li *et al*., 2018) and in bigger plants, individual leaf samples can be analysed separately (Liang *et al*., 2016). In addition, investigation of stomata-related traits such as aperture size and density also reveal useful information for evaluation of photosynthetic activity potential (Orellana *et al*., 2010; Liang *et al*., 2016; Wang *et al*., 2017).

Hormone-mediated plant response to salinity stress, including abscisic acid (ABA) and jasmonate acid (JA), has also been well documented (Tuteja, 2007; Zhang *et al*., 2017). A number of transcription factors regulating plant response to salinity has been found to work in ABA-dependent manner (e.g. tomato (*Solanum lycopersicum*) JERF1), or in both pathways (e.g. *Arabidopsis* ERF1 and AtMYC2) (Cheng *et al*., 2013; Zhao *et al*., 2014). Therefore, quantification of ABA and JA contents by enzyme-linked immunosorbent assays (ELISAs) can be considered (Yang *et al*., 2001) (Table 1).

TARGET GENES FOR EXPRESSION ANALYSIS BY QUANTITATIVE REVERSE TRANSCRIPTION PCR (RT-qPCR) METHOD

Over the last decade, RT-qPCR has become a more widely used method than RNA gel blotting in detecting differential gene expression between conditions (e.g. stressed versus normal conditions) or genotypes, from which important gene activities in connection with salt tolerance capacity can be identified. RT-qPCR is also employed to validate the transcriptomic analyses. In addition, gene expression data would provide complementary evidence for supporting the phenotypic, physiological or biochemical results, making the conclusion more reliable. For example, transgenic *Arabidopsis* ectopically expressing sweet potato (*Ipomoea batatas*) *IbRAP2-12* acquired better salt tolerance, with higher proline content and in consistency with higher expression of *pyrroline-5-carboxylate synthase 2* (*P5CS2*) (Li *et al*., 2019). This gene encodes the key enzyme in biosynthesis of proline, a molecule functioning as an osmolyte used for osmotic adjustment and as an antioxidant in protecting bio-macromolecules and scavenging ROS (Ashraf, Foolad, 2007; Li *et al*., 2019). In another example, increased trehalose content coupled with up-regulation of genes *ThTPS1-3* and *ThTPPA* encoding the key enzymes 3 trehalose-6-phosphate synthase (TPS) and 1 trehalose-6-phosphate phosphatase (TPP), respectively, in the biosynthetic pathway of trehalose is observed in the transgenic *Tamarix hispida* overexpressing *cytokinin response factor 1* (*CRF1*) (Qin *et al*., 2017).

Table 3 presents important pathways and functional groups whose gene expression could be regulated in mediating plant response to salinity stress. In general, expression of genes encoding the enzymes working in the biosynthesis of hormones (e.g. ABA and JA), osmoprotectant (e.g. proline, trehalose), as well as in ROS removal (e.g. CATs and PODs) is induced upon salinity stress challenging. For example, increase in expression of *Arabidopsis* dehydroascorbate reductase 1-encoding gene (*DHAR1*) under this adverse condition, was reported (Li *et al*., 2019). DHAR1 is an enzyme belongs to glutathione S-transferase superfamily and responsible for the regeneration of ascorbate, an antioxidant molecule (Ding *et al*., 2020). Therefore, activity of this enzyme also plays an important role in plant defense. Dehydrin proteins such as late embryogenesis abundant (LEA) proteins, responsive-to-ABA (RAB) proteins and cold-regulated (COR) proteins are well-known members functioning in

cellular protein protection and membrane stabilization under osmotic stress (Verslues *et al*., 2006; Jia *et al.,* 2014; Shinde *et al*., 2019). Therefore, expression study of their corresponding encoding genes is an interest. It is found out that the transgenic tomato (*Solanum lycopersicum*) overexpressing *SlAREB1* had increased expression in two dehydrin encoding genes *TAS14* and *LE25*, suggesting their contribution to the enhanced tolerance of the transgenic tomato under salinity stress (Orellana *et al*., 2010).

As saline conditions cause ionic and osmotic imbalance, it is important to study the expression levels of genes encoding transporter proteins in the root tissue. Particularly, attention should be paid to genes coding for Na^+ transporters [e.g. *salt overly sensitive 1* (*SOS1*), *cation/H^+ exchanger* (*CHX1*) and *Na^+/H^+ antiporters 1* (*NHX1*), and K^+ transporters [e.g. *CHX1* and *high-affinity potassium transporter 1;4* (*HKT1;4*)], as well as water channels (known as "aquaporin") [e.g. *plasma membrane intrinsic protein 1;6* (*GmPIP1;6*)]. SOS1 is a well-known Na^+/H^+ antiporter working in the SOS-signaling pathway for regulating cellular Na^+ efflux (Cellier *et al*., 2004; Chen *et al*., 2014; Gupta, Huang, 2014; Qi *et al*., 2014; Zhou *et al*., 2014; Li *et al*., 2017). SOS1 and NHX1 are known to reside on the plasma membrane and tonoplast (vacuole) membrane, respectively, and responsible for the prevention of intracellular Na^+ accumulation, either by Na^+ exclusion or compartmentalization (Apse *et al*., 2003; Shi *et al*., 2000).

For transgenic studies using transcription factor-encoding genes as the transgenes, analyzing the *cis*-motifs present in the promoter region of target genes could help compiling the list of potential genes whose expression should be prioritized for investigation. Of course, it is possible that genes without the *cis*-acting elements for the transcription factor binding are also its downstream target genes, as an outcome of indirect regulation/interaction. Salinity stress-related studies have identified participation of various transcription factors that belong to different families, such as dehydration-responsive-element (DRE)-binding proteins (DREBs), zinc finger proteins (ZFPs), ethylene response factor proteins (ERFs) and myeloblastosis proteins (MYBs) (Xu *et al*., 2016; Wang *et al*., 2017). As drought and salinity stresses cause osmotic stress, similar strategies and components are used by plants in response to drought and high salinity conditions (Ashraf, Foolad, 2007; Gill, Tuteja, 2010; Golldack *et al.,* 2014; Li *et al.,* 2017).

Table 3. Main pathways that might be under regulation in mediating plant response to salinity stress, based on studies of transgenic plants with improved salinity tolerance and analyzed by RT-qPCR method. Examples for genes with altered expression in each pathway are included.

Function	Transgenic plants	Transgene	Responsive genes	References
Abscisic acid biosynthesis-related pathway	*Arabidopsis*	*Ipomoea batatas IbRAP2-12*	*abscisic aldehyde oxidase 3* (*AAO3*)	Li *et al*., 2019
	Gossypium hirsutum	*Zea mays ABP9*	*nine-cis-epoxycarotenoid dioxygensase 2* (*GhNCED2*)	Wang *et al*., 2017
Jasmonic acid biosynthesis-related pathway	*Arabidopsis*	*I. batatas IbRAP2-12*	*lipoxygenase 2* (*LOX2*) *allene oxide synthase* (*AOS*)	Li *et al*., 2019
Proline biosynthesis-related pathway	*Arabidopsis*	*Tamarix hispida ThCRF1*	*pyrroline-5-carboxylate synthase 1* (*P5CS1*)	Qin *et al*., 2017

Trehalose biosynthesis-related pathway	*T. hispida*	*T. hispida ThCRF1*	*3 trehalose-6-phosphate synthase* (*ThTPS1-3*); *1 trehalose-6-phosphate phosphatase* (*ThTPPA*)	Qin *et al*., 2017
Reactive oxygen species removal	*Arabidopsis*	*I. batatas IbRAP2-12*	*glutathione peroxidase 7* (*GPX7*), *ascorbate peroxidase 1* (*APX1*), *dehydroascorbate reductase 1* (*DHAR1*), *catalase 1* (*CAT1*)	Li *et al*., 2019
	T. hispida	*T. hispida ThCRF1*	superoxide dismutase-encoding genes *(ThSOD1, ThSOD2, ThSOD3)*	Qin *et al*., 2017
	G. hirsutum	*Z. mays ABP9*	*Superoxide dismutase* (*GhSOD*), *peroxidase* (*GhPOD*), *catalase* (*GhCAT*), *Glutathione-S-transferase* (*GhGST*)	Wang *et al*., 2017
Transporter proteins	*Glycine max*	*G. max GmFDL19*	*Cation/H$^+$ exchanger* (*GmCHX1*), *plasma membrane intrinsic protein 1;6* (*GmPIP1;6*); *Na$^+$/H$^+$ antiporters 1* (*GmNHX1*), *GmHKT1;4*; *salt overly sensitive* (*GmSOS1*)	Li *et al*., 2017
Dehydrin proteins (e.g. LEA, RAB and COR subfamilies)	*Solanum lycopersicum*	*S. lycopersicum*	*TAS14, LE25*	Orellana *et al*., 2010
Transcription factors	*G. max*	*G. max GmFDL19*	*GmbZIP1*, *GmNAC11*, *GmNAC29*, *GmDERB2A;2*, *GmWRKY27*, *GmERF5*, *GmMYB174*	Li *et al*., 2017
	G. hirsutum	*Z. mays ABP9*	*dehydration-responsive-element (DRE)-binding protein 2* (*GhDBP2*), *zinc finger protein 1* (*GhZFP1*), *ethylene response factor 1* (*GhERF1*)	Wang *et al*., 2017

RECENT ANALYTIC APPROACHES CONTRIBUTING TO COMPREHENSIVE UNDERSTANDING OF PLANT TOLERANCE TO SALINITY

With rapid progress in developing novel technologies and advanced instruments, in addition to transgenic/mutant-based systems, other approaches can be utilized to comprehensively understand the plant tolerance to salinity. It has been shown that microRNA (miRNA) molecules also play a role in determining the plant tolerance capacity (Genie *et al*., 2019) (Table 4). For example, increasing transcript abundance of certain miRNAs could make the transgenic rice more vulnerable to salinity stress (Gao *et al*., 2010; Gao *et al*., 2011). Other studies have indicated that the salt tolerance of plants can be also affected by epigenetic changes such as post-translational modification *via* activity of ubiquitin ligases or degree of DNA methylation (Park *et al*., 2010; Feng *et al*., 2012) (Table 4). With the reduction in cost and time as well as improved instrument versality, analysis at systemic scale can provide global information for the salinity stress-induced changes in transcript profile, protein profile or metabolite profile (Hernández, 2019). It must be emphasized that genome-wide studies remain as an important approach as the tolerance capacity among different cultivars can be compared and assessed based on genetic variants or polyploidy status (Tu *et al*., 2014; Ganie *et al*., 2019).

Furthermore, using molecular markers also contributes to the identification of important salinity-related genes and establishment of QTL (quantitative trait locus) mapping of these genes (Ky *et al*., 2018; Lang *et al*., 2019; Le *et al*., 2021) (Table 4). Previously, an important QTL for salinity tolerance in rice, known as *Saltol*, is reported (Vu *et al*., 2012).

Table 4. Other data for comprehensive understanding on plant tolerance capacity toward salinity.

Targets	Examples	Added information value	References
Non-protein-coding genes	miRNA	Novel mechanism of plant responses to salinity	Gao *et al*., 2010; Gao *et al*., 2011
Epigenetics	Ubiquitination genes, DNA methylation	Affecting protein stability and expression degree	Park *et al*., 2010; Feng *et al*., 2012
Genome duplication	Genome-wide analysis	To examine polyploidy status in association with salt tolerance capacity	Tu *et al*., 2014
-Omic studies	Transcriptomic profiling, proteomic profiling, metabolic profiling	To obtain global salt responsive-network and identify important participants	Ganie *et al*., 2019; Hernández, 2019
DNA markers	Simple sequence repeats, expressed sequence tag markers, SNPs	Locate important salinity-related genes and quantitative trait loci (QTL mapping)	Ky *et al*., 2018; Lang *et al*., 2019; Le *et al*., 2021

SALINITY STRESS TOLERANCE STUDIES IN VIETNAM

In Vietnam, salinity has not been considered a major threat to agricultural production until recent years, when a higher rate of seawater intrusion to the coastal region and river has been observed. Particularly, the rise in sea level due to climate change makes the agricultural production in Mekong River Delta become vulnerable more than ever. To cope with this, various measures have been suggested or deployed, including infrastructural establishment to prevent the invasion of seawater into the mainland, changes in agronomic practices and cropping pattern (Dam *et al*., 2021). Regarding development of elite salinity-tolerant culivars, so far this has been an interest for rice only. This is easily understood as Vietnam is one of the main global rice suppliers and its economy heavily depends on the rice productivity. In fact, research on improvement of rice tolerance to salinity has been conducted many years ago using conventional breeding and the application of marker-assisted selection (MAS) has accelerated this breeding process (Lang *et al*., 2019). Similarly, marker-assisted backcrossing (MABC) is also adopted to speed up the development of salt-tolerant rice varieties in comparison with the traditional backcrossing method (Vu *et al*., 2012). Following this, introgression lines with improved salt tolerance were generated by introduction of *Saltol* QTL into BT7, a rice variety carrying certain desired agronomic traits, by crossing this with a salt-tolerant donor variety, FL478-*Saltol* (Linh *et al*., 2012).

Other studies focus on evaluating the salinity tolerance of different rice cultivars (Ky *et al*., 2018; Lang *et al*., 2019), including the mutant rice lines (Huong *et al*., 2020). For example, twelve different rice varieties in Tra Vinh have been analyzed for their salinity tolerance capacity to NaCl 6‰ based on three SSR (Simple sequence repeat) markers (RM336, RM10793 and RM10825) and ratio of K^+/Na^+ uptake (Ky *et al*., 2018). Phenotype-based parameters, including plant height, root length, survival rate and biomass, have been also

employed to screen for the rice germplasms with higher salt tolerance (Lang *et al*., 2019). Meanwhile, another study unraveled the salinity tolerance of different rice varieties based on yield-related properties including productiviy, amylose and protein contents (Quan, Vo, 2017). Recently, a transcriptomic analysis has been conducted for two rice varieties with contrasting salinity tolerance, in order to identify pathways and genes associating with the plant tolerance (Ky *et al*., 2021).

In other plant species, the gained information and outcomes remain limited as only a handful studies have been conducted in relation to salinity stress in Vietnam. Among of these studies, it has been demonstrated that exogenous application of salicylic acid and/or calcium can enhance the salinity tolerance of amaranth (*Amaranthus tricolor*) via promotion of Na^+ exclusion from roots, accumulation of phenolic and flavonoid compounds as well as increased antioxidant activities (Hoang *et al*., 2020). Tolerance of various chili pepper genotypes against different concentrations of NaCl or $CaCl_2$ (ranging from 0-300 mM) has been also explored, which was based on germination rate, plant height, number of leaves, branches and flowers, leaf area, phenolic compound contents and antioxidant activities (Ai *et al*., 2021). In another research, comparison for suitability of growing soybean versus *Sesbania rostrata* for saline land improvement purpose was conducted, with the assesesment of plant height, root length, biomass, proline content coupled with endogenous Na^+ accumulation, and SPAD (Soil-Plant Analyses Development) index to estimate the chlorophyll content (Phuong *et al*., 2018a). Similar investigations have been performed for mustard (*Brassica juncea*) (Phuong *et al*., 2018b) and quinoa (*Chenopodium quinoa*) (Long, 2016). Apparently, with the foreseen increase in frequency and severity of salinity stress, more research efforts should be given, not only for rice but also for vegetable and fruit plants.

CONCLUSION

This review demonstrated complex responses that the plants employ to cope with salinity stress. This also means that there are various potential target pathways or genes for a researcher to manipulate in developing crop varieties with improved salinity stress resistance. Clearly, in-depth understanding of mechanisms and performance of plants under salinity stress conditions requires a combined data set, which is derived from phenotypic, physiological, biochemical and molecular analyses. In terms of economic and agricultural perspectives, productivity ability of a studied genotype should be examined along with its salinity stress resistance potential. In the future, investigation on how salt-resistant plants (i.e. halophytes) can withstand high salinity conditions might beneficially provide new strategies for development of crop cultivars with better salt resistance.

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CÁC CHỈ SỐ PHÂN TÍCH QUAN TRỌNG DÙNG TRONG NGHIÊN CỨU ĐÁNH GIÁ KHẢ NĂNG CHỊU MẶN Ở THỰC VẬT

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TÓM TẮT

Tiềm năng sản lượng tối đa của cây trồng và diện tích đất phù hợp cho trồng trọt thường bị hạn chế bởi các yếu tố bất lợi từ môi trường. Trong số các nhân tố stress phi sinh học, stress mặn là một trong những mối đe dọa chính, gây ra độc ion nội bào, stress mất nước và stress ôxy hóa. Tác động

của stress mặn được dự báo là ngày càng nghiêm trọng hơn do biến đổi khí hậu. Vì vậy, phát triển các giống cây trồng mới có khả năng chịu mặn tốt hơn bằng phương pháp lai tạo truyền thống hay bằng kỹ thuật di truyền luôn là mối quan tâm của các nhà khoa học. Trong bài viết này, chúng tôi thảo luận những chỉ số quan trọng dùng trong việc đánh giá về khả năng chịu mặn của cây để thu thập bộ dữ liệu đầy đủ liên quan đến thay đổi hình thái và điều chỉnh sinh lý, sinh hóa và phân tử; hoặc từ các phân tích ở quy mô -omics để có cái nhìn tổng quan về mạng lưới các con đường tham gia đáp ứng mặn. Các nghiên cứu cũng cho thấy rằng việc thiết lập điều kiện stress mặn phù hợp về mặt nồng độ và thời gian là rất cần thiết trong thí nghiệm. Hơn nữa, các nghiên cứu gần đây cũng chứng minh rằng số lượng gen trong genome, hoạt động từ các phân tử không mã hóa protein và điều hòa ngoài gen cũng ảnh hưởng đến khả năng chống chịu của cây. Tập hợp các thông tin này không chỉ mở rộng mức độ hiểu biết khoa học về các cơ chế đáp ứng thích nghi của thực vật mà còn giúp tìm ra các gen quan trọng trong đáp ứng stress mặn. Do đó, bài viết này có thể dùng để tham khảo trong các nghiên cứu về stress mặn phục vụ công tác cải tạo giống và phân tích chức năng gen.

Từ khóa: *các chỉ số phân tích, khả năng chống chịu stress của thực vật, phân tích chức năng gen, stress mặn, stress thẩm thấu*