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Review Article

Functional Screening and Genetic Engineering of Mangrove Salt Responsive Genes: A Review

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Abstract: Day by day increase in soil salinity has a negative impact on global food production. Salt stress leads to dehydration and osmotic stress resulting in stomatal closure and increased production of reactive oxygen species. This causes irreversible cellular damage and photo inhibition leading to serious damage to the plant cellular processes. Major crop plants are categorized under Glycophytes, which can't grow in the presence of high salt concentrations. Hence, the necessity for developing salt stress tolerant plants deserves much attention, though it is a herculean task. In the recent past a large number of plants are being engineered with salt stress tolerant genes in all the possible ways. However, a meaningful approach towards bio engineering for salinity tolerance could be the tuning of halophyte genes. Halophytes are plants, capable of growing under high salt concentrations. Mangroves are woody halophytes which possess an efficient ion influx and efflux regulatory mechanism by means of which they regulate their cellular ionic conditions. The present review depicts genetic engineering studies and genetically modified plant varieties using mangrove genes thus far and suggests possible gene candidates for upcoming transgenic research.

Keywords: Mangrove, Functional screening, Genetic engineering, Salt tolerance

Introduction

Global population is constantly increasing and will reach more than 9 billion in 2050 (Godfray *et al.,* 2010; Tester and Langridge 2010). So meeting an ever increasing demand in food production is a major challenge for current agricultural biotechnology. Environmental stresses including soil salinity cause over 50% crop loss. Soil salinity has an adverse effect on approximately 7% of total land area and 20% of the irrigated agriculture land. Excess salt causes ion imbalance and ion toxicity induced imbalances in metabolism of salt sensitive plants. Hyper osmotic stress that results in water deficit is also a consequence of salinity. Accordingly, soil salinity becomes increasingly an agricultural problem due to extensive spreading of agricultural practices like irrigation and so urgent care should be taken to breed crops with better salt tolerance and increased water use efficiency (Flowers 2004).

Plants respond to salt and drought stress in a closely related manner and the mechanisms overlap. Every aspect of plant physiology and metabolism is affected by salt and drought stresses. These represent suitable targets for genetic manipulation to improve salt and drought stress tolerance.

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Salt and drought stress signaling falls under three functional categories: ionic and osmotic stress signaling for the reestablishment of cellular homeostasis under stress conditions, detoxification signaling to control and repair stress damages, and signaling to coordinate cell division and expansion to levels suitable for the particular stress condition (Zhu 2002).

Various genes induced by salt stress are of two categories, namely, single-function genes and regulatory genes. The first category of genes generally facilitates production of protective metabolites, which include osmolytes, transporters/channel proteins, antioxidative enzymes, lipid biosynthesis genes, polyamines, etc. The second category of genes consists of regulatory proteins like basic leucine zipper (bZIP), drought responsive element binding protein(DREB),myelocytomatosis/myeloblastoma (MYC/MYB), and no apical meristem, ATAF 1, 2 and cup shaped cotyledon (NAC), which control the expression of many downstream salt stress tolerant genes (Shinozaki and Yamaguchi Shinozaki 2007; Agarwal and Jha 2010). These two categories of genes interact in above mentioned

signaling pathways to give abiotic stress tolerance.

Salt tolerance was induced in many plants by transformation and over expression of several genes related to abiotic stress tolerance in all possible ways (Singla Pareek *et al.,* 2001; Vinocur and Altman 2005; Bhatnagar *et al.,* 2008; Ashraf and Akram 2009). Recently, many reviews have been published on various aspects of salt stress tolerance (Zhu 2003; Agarwal *et al.,* 2006; Umezawa *et al.,* 2006; Apse and Blumwald 2007; Gaxiola *et al.,* 2007; Shinozaki and Yamaguchi Shinozaki 2007; Century *et al.,* 2008; Shao *et al.,* 2008; Rodriguez *et al.,* 2009; Agarwal and Jha 2010). Enhancing salt tolerance by manipulating salt loving halophyte genes are least discussed as compared to those by salt sensitive glycophyte genes. Even among halophytes, mangroves represent a group of plants adapted to highly saline environments. So it is more relevant to study salt tolerance mechanisms in mangroves, which are facultative halophytes and potential stress adaptors. Recent approaches in developing salt tolerant plants by employing genes from mangroves and screening of mangrove specific salt responsive genes are depicted in detail in the present review.

Mangroves and their adaptation to salinity:

Salt tolerance is the ability of plants to counteract the negative effects of high salt concentrations by activation of biochemical responses and thus grow and complete their life cycle. Plants that can survive on high concentrations of salt in the rhizosphere are called halophytes. Halophytes are further classified based on their capacity to tolerate salt concentrations. Obligate halophytes are characterized by low morphological and taxonomical diversity with optimal growth rates in highly saline habitats. On the other hand facultative halophytes are found in less saline habitats along the border between saline and non saline upland and characterized by broader physiological diversity which enables them to cope with saline and non saline conditions. Mangroves are facultative halophytes tolerant to both high and fluctuating salinity. Some authors have also categorized mangroves under obligate halophytes (Downton 1982; Clough 1984). At salinities of 5–25% of standard seawater, several mangrove species reach an optimum growth (Downton 1982; Clough 1984; Ball 1988; Burchett *et al.,* 1989; Ball and Pidsley 1995).

However, the range of salinity in which the plant is able to survive varies from species to species (Ball 1988). Either absence or excess of NaCl in the substrate, affects growth rate in several mangrove species (Downton 1982; Clough 1984; Burchett *et al.,* 1989; Pezeshki *et al.,* 1990; Ball and Pidsley 1995). As mangroves successfully live in highly saline environment, it is advantageous to use them to study the mechanisms by which plants respond and adapt to these environments. Mangrove research has advanced considerably in the last few years. A review on mechanisms of salt tolerance in mangroves is already published in detail (Parida and Jha 2010). A great number of works are available on salt tolerance mechanisms using *Arabidopsis thaliana* (Apse *et al.,* 1999; Nanjo *et al.,* 1999; Liu *et al.,* 2000; Quesada *et al.,* 2000; Shi *et al.,* 2000; Zhu 2000; Elphick *et al.,* 2001) and the facultative halophyte *Mesembryanthemum crystallinum* (Ratajczak *et al.,* 1994; Low *et al.,* 1996; Golldack and Deitz 2001; Su *et al.,* 2001; Agarie *et al.,* 2007) as models. Knowledge of salt tolerance mechanisms in mangroves which are potential stress adaptors (Downton 1982; Clough 1984) is essential to add on salt stress research. Understanding the mechanisms of salt tolerance in mangroves, identification of salt tolerant genes from mangroves and reviewing the successes will lead to effective means of breeding or genetically engineering salt tolerant crops.

Mangrove genes in transgenic studies:

Nowadays mangrove genes are widely used in transgenic studies to enhance the capacity of salt tolerance of model plants. The candidate genes used so far are discussed here forth. Monodehydroascorbate reductase (MDHAR), an important enzyme of the ascorbate-glutathione cycle, is involved in salt tolerance of plants through scavenging of reactive oxygen species (ROS). A cDNA encoding MDHAR from the mangrove plant *Acanthus ebracteatus* was introduced into rice to examine its role in salt tolerance. The transgenic rice lines over expressing AeMDHAR showed a significant increase in MDHAR enzyme activity and better salt tolerance compared to untransformed plants under salt stress (Sultana *et al.,* 2012).

Another component of salt stress signaling pathway, the MYB transcription factor play an important role in developmental and various other processes in plants. Transgenic tobacco plants constitutively expressing the AmMYB1 transcription factor isolated from the salt-tolerant mangrove tree *Avicennia marina* showed better tolerance to NaCl stress (Ganeshan *et al.,* 2013)

Antioxidant enzymes also play an important role in conferring abiotic stress tolerance. Superoxide dismutase (SOD) is the first enzyme in the enzymatic antioxidative pathway. Halophytic plants like mangroves have been reported to have a high level of SOD activity, which plays a major role in defending the mangrove species against severe abiotic stresses. A cDNA encoding a cytosolic copper zinc superoxide dismutase from the mangrove plant *Avicennia marina* was isolated and used to transform rice plant and it showed more tolerance to methyl viologen mediated oxidative stress and salt stress (Prashanth *et al.,* 2008). Another salt-tolerant gene, *CSRG1* (a gene which encodes a protein containing 197 amino acids, of which hydrophobic amino acids take about 42%. There is no homologous sequence in the Gene Bank), which was isolated from a kind of salt-tolerant mangroves, *Avicennia marina*, was transferred into tobacco genome. It is supposed that the special physiologic metabolic pathway formed by the products of *CSRG1* can really endow the tobacco plants with the high salt-tolerant ability, not only to Na^+ stress, but also to the comprehensive stress of various ions (Hantao *et al.,* 2004). A salt-inducible chloroplastic monodehydroascorbate reductase (MDAR) from mangrove *Avicennia marina* conferred salt stress tolerance on transgenic tobacco plants is also reported (Kavitha *et al.,* 2010). Clearly, transgenic studies on mangrove genes are a latest trend and so are less in number (Summarized in table I). Future line of work in this area include studies of different antioxidant pathways, homeostasis pathways, metabolic pathways, signaling pathways, regulatory proteins, and membrane transporters (Shinozaki and Yamaguchi Shinozaki 2007; Agarwal and Jha 2010). We are trying to give a clear picture of all possible targets for future transgenic works by reviewing functional screening studies of salt responsive mangrove genes, in the next section.

Table 1: Overexpression of mangrove genes for salt tolerance

Gene	Mangrove source	Transgenic plant	References
AcMDHAR	*Acanthus ebracteatus*	Rice	Sultana *et al.,*2012
AmMYB	*Avicennia marina*	Tobacco	Ganesan *et al.,*2013
Cu/ZnSOD	*Avicennia marina*	Rice	Prashanth *et al.,*2008
CSRG1	*Avicennia marina*	Tobacco	Hantao *et al.,*2004
Am MDAR	*Avicennia marina*	Tobacco	Kavitha *et al.,*2010

Functional screening for salinity tolerant genes from mangroves:

The discovery of genes in salt tolerant plants will provide the basis for effective genetic engineering strategies, leading to greater stress tolerance in economically important crops. 107 salinity tolerant candidate genes were identified and isolated from a mangrove plant, *Acanthus ebracteatus Vahl* and verified in *E. coli* host (Nguyen *et al.,* 2007). Huang et al (2003) isolated 10 cDNAs of genes from *Kandelia candel*. Of five genes expressed preferentially under salt condition, two were unknown; three were two kinds of low molecular mass heat-shock proteins (sHSPs) and ADP-ribosylation factor, respectively. The expressions of other five genes were repressed under NaCI stress, two encoded cyclophilins, three were tonoplast intrinsic proteins, early light-induced protein and 60S ribosomal protein, respectively.

In another experiment, a cDNA library was constructed from the leaves of *A. marina* and screened for betaine aldehyde dehydrogenase genes (BADH) which efficiently catalyze the oxidation of betainealdehyde. Two kinds of BADH cDNAs were isolated and expressed in *Escherichia coli* and purified. One among them showed higher expression under salinity (Hibino *et al.,* 2001). Later, as an effort to isolate anti-stress genes from mangrove plants, a cDNA library of *Avicennia marina* was constructed and screened for anti-stress genes by a functional expression screening with *Escherichia coli* cells. Several stress-related gene homologues, such as chaperonin-60, clpP protease of the clp/Hsp100 family of chaperones, ubiquitin, eukaryotic elongation factor 1 A (eEF1A), drought-induced AtDi19 gene of *Arabidopsis thaliana*, and secretory peroxidase, were successfully isolated (Tanaka *et al.,* 2002).

Functional characterization of AmMYB1, a single-repeat MYB transcription factor isolated from the salt tolerant mangrove tree *Avicennia marina* is also reported (Ganesan *et al.,* 2013). A fructose-1, 6-bisphosphate aldolase gene, designated

SpFBA, was isolated and characterized from *Sesuvium portulacastrum* roots in response to seawater and transferred to *Escherichia coli*. The study suggest that the SpFBA plays very important roles in responding to salt stress and related abiotic stimuli, and in improving the survival ability of *S. portulacastrum* under high salinity and drought (Fan *et al.,* 2009). Functional screening for cDNAs in the mangrove plant *Brugiera sexangula* using *Escherichia coli* as the host organism revealed the role of mangrove specific allene oxide cyclase (mangrin) in the salt tolerance mechanism (Yamada *et al.,* 2002). List of all the reported salt responsive mangrove genes are summarized in table II. In addition to these, some of the genes that are yet to be studied in mangroves, but reported to induce salt / drought tolerance include Na^+ H^+ antiporter (Apse *et al.,* 1999; Apse *et al.,* 2003; Jha *et al.,* 2010), Dehydrin (Brini *et al.,* 2007), Late embryogenesis abundant protein (LEA)- bZip (Qu *et al.,* 2012), Phytoene synthase (Han *et al.,* 2008), DREB (Bhatnagar *et al.,* 2007), Glyoxalase system(Espartero *et al.,* 1995; Veena *et al.,* 1999; Skipsey *et al.,* 2000; Jain *et al.,* 2002; Singla Pareek *et al.,* 2003; Saxena *et al.,* 2005; Yadav *et al.,* 2005; Singla Pareek *et al.,* 2008; Hossain and Fujita. 2009; Lin *et al.,* 2010; Mustafiz *et al.,* 2011; Tuomainen *et al.,* 2011; Wu *et al.,* 2013), Aquaporin (Peng *et al.,* 2007), Glutathione S Transferase (Chen *et al.,* 2012), Fatty acid desaturase (Zhang *et al.,* 2012), trihelix transcription factor genes GmGT-2A and GmGT-2B (Xie *et al.,* 2009) and mannose-1-phosphate guanyl transferase (Kumar *et al.,* 2012).

Table 2: List of salt responsive mangrove genes suggested to be used in future transgenic works.

Gene	Mangrove source	References
Glutathione S- transferase Z1	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Glutathione transferase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Manganese superoxide dismutase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Myo-insitol 1-phosphate synthase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Homogentisate phytylprenyltransferase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Carotenoid cleavage dioxygenase1–1	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Glutamate synthase (ferredoxin)	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Glutamine synthetase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Glutamine synthetase GS58	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Glycine dehydrogenase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Putative alanine aminotransferase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Putative quinone reductase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
NAD malate dehydrogenase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
NADP-malic enzyme	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Plastidic aldolase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Plastidic aldolase NPALDP1	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Latex plastidic aldolase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Phospholipid/ glycerol acyltransferase	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Chloroplast protease	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Amino acid permease-like protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Plasma membrane intrinsic protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Ubiquitin-conjugating enzyme family protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
E3 ubiquitin ligase SCF	*Acanthus ebracteatus*	Nguyen *et al.,*2007
33 kDa polypeptide of water oxidizing	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Germin like protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Proline rich protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Putative salt-tolerance protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Universal stress protein (USP)	*Acanthus ebracteatus*	Nguyen *et al.,*2007
14-3-3 protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
GTP binding protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Small GTP binding protein Sar1BNt	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Zinc finger (DNL type) family protein	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Calcium binding EF hand family	*Acanthus ebracteatus*	Nguyen *et al.,*2007
Cyclic nucleotide and calmodulin regulated	*Acanthus ebracteatus*	Nguyen *et al.,*2007
DNAJ Heat shock protein	*Kandelia candel*	Huang *et al.,*2003
cytosolic class I loss molecular mass HSP	*Kandelia candel*	Huang *et al.,*2003
cytosolic class II low molecular mass HSP	*Kandelia candel*	Huang *et al.,*2003
ADP-ribosylation factor (ARF)	*Avicennia marina*	Hibino *et al.,*2001
Betaine aldehyde dehydrogenase(BADH)	*Avicennia marina*	Tanaka *et al.,*2002
Chloroplast chaperonin-60	*Avicennia marina*	Tanaka *et al.,*2002
Clpp rotease (clpP)	*Avicennia marina*	Tanaka *et al.,*2002
Ubiquitin	*Avicennia marina*	Tanaka *et al.,*2002
Translation elongation factor-1 a	*Avicennia marina*	Tanaka *et al.,*2002
Drought-induced 19 (AtDi119)	*Avicennia marina*	Tanaka *et al.,*2002
Secretory peroxidase	*Sesuvium portulacastrum*	Fan *et al.,*2009
fructose-1,6-bisphosphate aldolase	*Brugiera sexangula*	Yamada *et al.,*2002
Mangrin(Allene oxide cyclase)		

Conclusion

Salinity is one of the major abiotic stresses decreasing agricultural crop production. Bio engineering for developing salt tolerant crops is a challenging area of research for future crop improvement programs. Development of plant molecular biology and understanding of the stress signaling pathways help to generate plants with least damaging effect on environmental conditions and concurrently promising an increase in productivity. With the availability of functional screening data, it now seems easier to identify unique stress responsive genes. The usage of specific salt responsible genes from various mangrove sources, listed in the present review could be a good choice for developing diverse stress tolerant crop varieties. We also suggest that it is important to study the salt tolerance mechanism of individual genera or species because mangrove trees have evolved their own specific and effective methods to adapt to specific environment and shows complexity and variation between species. Exploring the mechanisms of individual genera or species can lead to development of future crops, which can survive better under adverse environmental conditions and in turn lead to increased productivity.

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