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REVIEW

Signal transduction and biotechnology in response to environmental stresses

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Abstract

Providing sufficient food to burgeoning population from the steadily shrinking arable land seems to be very difficult in near future and is one of the foremost challenges for plant scientists. In addition, there are several biotic and abiotic stresses which frequently encounter crop plants during various stages of life cycle, resulting in considerable yield losses. Environmental stresses, including drought, flooding, salinity, temperature (both low and high), high radiation, and xenobiotics induce toxicity, membrane damage, excessive reactive oxygen species (ROS) production, reduced photosynthesis, and altered nutrient acquisition. Several indigenous defence mechanisms (physiological and molecular) are triggered in plants on exposure to environmental cues. Enhancement of resistance of crop plants to environmental stresses has been the topic of prime interest for agriculturalists and plant scientists since long. Development of water and salinity stress-tolerant crops through genetic engineering provides an avenue towards the reclamation of farmlands that have been lost due to salinity and lack of irrigation water/rainfall. Understanding the complexity of stress tolerance mechanisms in orthodox or model plants at the genetic and molecular levels improves feasibility of enhancing tolerance of sensitive crop plants.

Additional key words: cold, drought, flooding, gene expression, heat, salinity, reactive oxygen species, transcription factors, transgenic plants.

Introduction

Several genes and their products are responsive to a variety of environmental factors. Identification of these genes is significantly helpful to overcome stress-induced adverse effects at transcriptional and translational levels (Yamaguchi-Shinozaki and Shinozaki 2005, Umezawa *et al*. 2006, Floris *et al*. 2009, Yang *et al*. 2014). Most important gene products include chaperones, osmotin, heat shock proteins, antifreeze proteins, late embryogenesis abundant (LEA) proteins, mRNA binding proteins, enzymes of osmolyte (like proline, glycine betaine, polyamines, sugar alcohols) biosynthetic pathways, antioxidant enzymes, water channel proteins, kinases, transcription factors, phosphatases, hormone-related genes, *etc*. (Giri 2011, Choudhary *et al*. 2012, Fan *et al*. 2012, Ha *et al*. 2012, Osakabe *et al*. 2013, 2014 a,b).

The 20th century has witnessed a significant increase in quality, yield potential, and disease resistance in crops using breeding techniques including simple selection, cross pollination, hybridization, and natural/induced mutation (Ashraf and Akram 2009). Classical plant breeders have released different resistant crop lines/cultivars using conventional breeding techniques

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Abbreviations: ABA - abscisic acid; AOX - alternative oxidase; CDK - cyclin dependent kinase; CDPK - calcium-dependent protein kinase; DRE/CRT - dehydration-responsive element/C-repeat; DREB - DRE binding; EST - expressed sequence tags; GM - genetically modified; LEA - late embryogenesis abundant; MAPK - mitogen activated protein kinase; MYB - myeloblastosis; NAC - NAM-ATAF1, 2-CUC2 family; ROS - reactive oxygen species; SOS - salt overly sensitive.

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(*e.g.*, Johnson *et al.* 1991, Al-Doss and Smith 1998, Ashraf and O'Leary 1996, Hollington 2000, Johnson 2013). However, the advocates of genetic engineering argue that compared to conventional breeding this new approach is efficient, and requiring less labour and less time consuming. Futhermore, through genetic engineering only descried/targeted genes can be incorporated into the lines/cultivars of interest (Ashraf and Akram 2009, Johnson 2013).

Employing techniques like production of expressed sequence tags (EST) or expression profiling by microarrays or RNA sequence analysis, mutagenesis (random and targeted), complementation, and promoter trapping can be very helpful in identifying the key stress responsive genes, thereby providing important clues for the functional characterization of these stress-responsive genes, which lead to understanding the mechanisms of stress tolerance.

Contribution from molecular breeding and genetic engineering towards the understanding of stress response processes is of great importance. Complete examination of tolerance mechanisms, starting from signal perception and transduction to downstream regulation, is essential. Understanding of related cellular pathways linked with stress responses provides valuable insight for future studies. Genomic, transcriptomic, proteomic, and metabolomic assisted procedures have helped to reveal the complex regulatory networks involved in controlling abiotic stress tolerance mechanisms (Tran and Mochida 2010, Mochida and Shinozaki 2011, Jogaiah *et al.* 2013).

Functional genomics has an imperative role in identification of stress-responsive genes involved in stress tolerance which are later transferred into stress-sensitive species so as to confer their tolerance (Sreenivasulu *et al.* 2007, Varshney*et al.* 2013). In connection to this, biotechnology has a pivotal role in unravelling and improving the hidden tolerance mechanism pathways. However, biotechnological approaches need thorough information on the basic techniques involved in production of crop plants showing improved yield production. Implementation of integrative genomic and breeding approach seems vital so as to achieve enhanced and quality yield in response to varying environments (Sreenivasulu *et al.* 2007, Tran and Mochida 2010, Thao and Tran 2012, Jogaiah *et al.* 2013).

The highly complex nature of stress-triggered plant responses is depicted through the studies carried out at cellular, transcriptome, and physiological levels. However, responses elicited to multiple stresses are more complex, as compared to the individual one, bringing specific induction of gene expression programme that is actively implemented in counteracting the multiple stress-induced changes. Exposure of plants to multiple abiotic stresses can simultaneously increase the chance of biotic stress outbreaks like pest attack. Various signalling pathways mediated by different molecules specific to particular pathway, acting either independently or in close association, and showing a complex cross talk that together act for eliciting a series of genetically controlled molecular protective/tolerance responses/mechanisms (Atkinson and Urwin 2012).

An increasing understanding of which genes/alleles are important in stress resistance and a national and international regulatory system to oversee trade in genetically modified (GM) crops is necessary (Ha *et al.* 2012, Choudhary *et al.* 2012, Thao and Tran 2012).

Distinctive stress-induced responses in plants

Stresses triggers changes at physiological, biochemical and molecular levels (Tuteja *et al.* 2009, Ahmad *et al.* 2012a, Osakabe *et al.* 2014a). Model plants, such as *Arabidopsis thaliana* and *Oryza sativa*, have been preferably used to examine the stress-induced changes because of the availability of genomic sequences, mutant resources, and reference databases (Kosova *et al.* 2011, Mochida and Shinozaki 2011).

Every physiological and biochemical pathway is sensitive to environmental variations. Several adaptive mechanisms like avoidance and tolerance are employed by the plants to mitigate the stress effects. Tolerance mechanisms employing selective and efficient utility of ion transporters, proteins, osmoprotectants, antioxidants (enzymatic and non-enzymatic), and other cues/ molecules implemented in signalling cascades and transcriptional level control are activated so that the alterations triggered in biochemical and physiological pathways could be made to offset the stress-induced adverse effects. Stress identification, perception, and transduction of signals as well as elicitation and initiation of proper physiological and biochemical mechanisms determine the survival and potential of coping with stresses (Hasanuzzaman *et al.* 2013). However, studying responses of plants to stresses through genomics provides an overlapping picture between different biotic and abiotic stresses (Chen *et al.* 2002, Buchanan *et al.* 2005).

Environmental stresses induce numerous changes like metabolic toxicity, membrane disorganization and hence dysfunction, excessive reactive oxygen species (ROS) production, reduced photosynthesis, and altered nutrient acquisition and hence altered metabolism (Hasegawa *et al.* 2000, Sreenivasulu *et al.* 2007, Hasanuzzaman *et al.* 2013, Uzilday *et al.* 2014). Through molecular techniques, abiotic stress tolerance can be improved by genetic engineering/trangenic approach of various genes like synthesis/accumulation of osmoprotectants, chaperone production, ROS scavenging mechanism pathways, transporter system involved in efficient exclusion or compartmentation of ions (Cushman and Bohnert 2000, Hasegawa *et al.* 2000, Apse and Blumwald 2002, Zhu 2002, Viswanathan and Zhu 2004, Sangam *et al.* 2005, Valliyodan and Nguyen 2006, Ahmad *et al.* 2010, 2012a, Uzilday *et al.* 2014).

Diverse physiological and biochemical processes, altered ionic equilibrium, and genes and their products play important roles (Cushman and Bohnert 2000, Sreenivasulu *et al.* 2004, Yamaguchi-Shinozaki and Shinozaki 2005, Umezawa *et al.* 2006) and understandings related to these responses can help in further tracing the tolerance mechanisms. Contributions from functional genomics are gaining pace through continuously adding/discovering new genes by utilizing techniques like high throughput gene expression, alteration in expression of specific genes by transformation, characterizing genes of interest, *etc.* (Sreenivasulu *et al.* 2007). Expression profiling using microarrays, mutagenesis (random and targeted), complementation and promoter-trapping aid in the identifying the key stress responsive genes providing prelude towards functional characterization of these stress responsive genes and hence adding to the better understanding of the stress tolerance mechanisms. In connection to this, already sequenced genomes (*Arabidopsis* and rice) and expressed sequence tags (prepared from cDNA libraries of different crops exposed to stress) serve as precious and valuable source for gene discovery. However, this information is mostly limited to laboratory, but this needs to be proved in field studies to get better results in terms of enhanced agricultural productivity.

In order to improve plant traits that confer tolerance to stresses, contributions from molecular and genetic engineering studies add a substantial knowledge in understanding of the complexity of stress responses. Mechanisms and pathways which serve to carry and link whole regulatory/tolerance strategies starting from signal perception, its transduction all along up to activation of downstream regulatory transcription factors have been now characterized so that a complete understanding about various protective cellular pathways involved in stress responses/tolerance can be achieved.

Signal transduction in plants exposed to different stresses

Under stress conditions, understanding of the physiology and genetics of plant species is a pre-requisite before adopting the transgenic approach (Bhat and Srinivasan 2002, Jewell *et al.* 2010, Pérez-Clemente *et al.* 2013). Retrograde signalling, *i.e.*, from perception organelle to nucleus, has a key role in bringing coordination between signal receptors and nucleus so that expression of specific host genes vital for survival under adverse conditions is increased. Protein phosphorylation, dephosphorylation, phospholipid metabolism, Ca^{2+} sensing, *etc.*, are the fundamental events that are generally triggered by stressful cues.

Specific retrograde signalling molecules (ROS, nitric oxide, unsaturated fatty acids, *etc.*) as well as their understanding continuously provide key insights into the interactively coordinated network in response to prevailing environmental conditions (Trewavas and Malho 1997, Atkinson and Urwin 2012, Huang *et al.* 2012, Rahal *et al.* 2014). Thus, we can safely infer that signalling is instigated by several signal molecules and each molecule regulates a distinct set of genes (Fig. 1 Suppl.). In addition, any change in these molecules is highly regulated so a highly complex and specific stress response regulated by a specific set of genes is delivered. Some signalling cascades are specific while some show crosstalk at some steps (Xiong and Yang 2003, Kaur and Gupta 2005, Gadjev *et al.* 2006, Huang *et al.* 2012, Kim *et al.* 2013, Ma *et al.* 2013) so as to bring controlled and coordinated physiological and biochemical responses important for adaptation (Trewavas and Malho 1997, Zhu 2002, Jewell *et al.* 2010, Pérez-Clemente *et al.* 2013).

Some researchers have the opinion that oxidized products of proteolytic breakdown are the key players in mediating specific signalling pathways, *e.g.*, oxidized peptides and β-cyclocitral (an oxidative product of carotenoids) mediate mitochondrial and chloroplast (Ramel *et al.* 2012) ROS specific signalling responses (Moller and Sweetlove 2010).This area of research is a major focus for applied and fundamental studies these days. Most of the signalling molecules triggered under stress conditions have been explained below:

Calcium has been acknowledged as one of the important secondary messengers. It is ubiquitous and plays a crucial role in signal transduction under stress conditions (Tuteja and Mahajan 2007, Yi *et al.* 2012). Content of calcium initiate Ca-dependent signalling processes (Knight *et al.* 1991, 1998, Pandey *et al.* 2002), *e.g.*, under salinity stress Ca is believed to lead to ion homeostasis thereby enhancing stress tolerance (Urao *et al.* 1994, Saijo *et al.* 2000, Reddy and Reddy 2004, Cheong *et al.* 2010, Huda *et al.* 2013).

Calcium bound to different organic molecules including proteins plays an important role in signalling. For example, calcineurin B-like proteins cloned from *Arabidopsis* (Liu and Zhu 1998) sense the Ca signal and participate in salt stress signal transduction particularly to control compartmentation of Na^+ (Das and Pandey 2010, Ahmad *et al.* 2012b, Sarwat *et al.* 2013). Calcinuerin B like protein also initiates the activity of salt overly sensitive (SOS) pathway and its related genes, *e.g.*, *Zea mays* calcineurin B-like gene (*ZmCBL4*), encoding a CBL protein in maize, can increase salt stress tolerance in *Arabidopsis SOS3* mutant (Wang *et al.* 2007).

Calcium-dependent protein kinases (CDPKs) have been considered potential candidates for calcium-mediated signal transductions in response to abiotic stresses in plants (Franz *et al.* 2011, Jiang *et al.* 2013). It has been shown that a CDPK, CPK21, is involved in abiotic stress signalling (Franz *et al.* 2011). For example, a CDPK gene, *ZmCPK4*, overexpressed in maize plants under different abiotic stresses show its role as a stress-induced signalling molecule. Furthermore, *ZmCPK4* introgressed *Arabidopsis* plants show improved drought tolerance which triggered abscisic acid (ABA) metabolism to regulate stomatal movement, seed germination, or growth. This suggests the role of *ZmCPK4* in ABA-mediated regulation of stomatal closure under drought (Jiang *et al.* 2013).

In another study, Manzoor *et al.* (2012) observed that Ca^{2+} fluxes at the plasma membrane confer chloroplast energy dissipation mechanisms as well as increase in mitochondrial respiration. Ca-signalling molecules or transporters in mitochondria or chloroplasts are believed to have a role in controlling intra-/extra-organellar functions (Nomura and Shiina 2014). Recently, Edel and Kudla (2014) attempted to link evolutionary tendencies to functional predictions and concluded that calcium dependent regulation of Na^{+} homeostasis is most ancient function of this signalling cascade. Therefore, there is a need to use high-throughput technologies for identification of signalling networks in the Ca^{2+} signalling cascade, roles in cellular processes, their known functions or components as well as unravelling of complex Ca^{2+} proteomics and genomic technologies.

Reactive oxygen species play a central role in plant responses to environmental extremes (Breusegem *et al.* 2001, Mittler *et al.* 2004, Baxter *et al.* 2014). A significant amount of ROS is generated during electron transport and several other metabolic processes in mitochondria and chloroplasts while antioxidant systems (both enzymatic as well as non-enzymatic) maintain ROS levels and redox homeostasis. ROS-induced oxidative burst or elevated ROS content as a result of stress triggers signalling pathways so as to initiate reprogramming of expression of genes coding for chloroplast and mitochondrion localized proteins. ROS have a dual role, *i.e.*, they can either exacerbate damage to cellular molecules/organelles or can initiate signalling to activate multiple defence responses, which is attained only when production and scavenging are precisely controlled (Breusegem *et al.* 2001, Mittler *et al.* 2011, Suzuki *et al.* 2012, Foyer and Noctor 2013). In *Arabidopsis*, a network of at least 152 genes coding for both ROS-scavenging and ROS-producing proteins is involved in maintaining ROS content (Mittler *et al.* 2004).

Reduced plant growth under stress conditions is ascribed to reduction in cell division, hence reducing cell number (Burssens *et al.* 2000, Granier *et al.* 2000) thereby allowing energy conservations and providing a prelude to appropriate defence response (May *et al.* 1998, Vernoux *et al.* 2000). Cell cycle progression and plant stress responses are linked through active oxygen species and oxidative stress induced cell cycle arrest and checkpoints have been reported (Paulovich *et al.* 1997, Tuteja *et al.* 2009). For example, in tobacco cell suspensions and tobacco plants oxidative stress induced by menadione has been reported to restrict transition of G1 to S phase and to restrict resultantly entry into mitosis, which leads to impairment in DNA replication. Cell cycle arrest induced by oxidative stress is initiated by inhibition of activity of cyclin dependent kinases (CDK) and cell cycle gene expression with a concomitant activation of stress genes (Reichheld *et al.* 1999). Cell cycle progression is under the negative control of ROS (Cui *et al.* 1999). Nevertheless, the exact role of ROS in plant growth and development is still poorly understood. ROS are believed to have an important role in bringing an adequate response through their decisive roles at cell cycle check points.

Nitric oxide is another potential ubiquitous retrograde signalling molecule. Its content is altered considerably under biotic as well as abiotic stresses (Wimalasekera *et al.* 2011, Gupta *et al.* 2012, Habib and Ashraf 2014). Its function is determined by the site of production and stage of plant growth (Villanueva and Giulivi 2010). In animals the function and location of three isozyme forms of a key enzyme (nitric oxide synthase) involved in NO biosynthesis has been well documented (Bogdan 2001). However in plants, its biosynthetic pathway is not clear yet (Gas *et al.* 2009, Popova *et al.* 2010, Hancock *et al.* 2012, Qiao *et al.* 2014). Some believe that it is produced in cytoplasm (Gupta *et al.* 2011) while the others are of the opinion that chloroplast is the actual site of its production (Jasid *et al.* 2006). Generation of NO can be either of oxidative or reductive nature.

Polyamine, nitric oxide synthase, and hydroxylamine mediate pathways where nitrogen compounds such as arginine and hydroxylamine produce NO for signalling purposes under stress conditions (Igamberdiev and Hill 2004, Tun *et al.* 2006, Rumer *et al.* 2009, Corpas *et al.* 2006, 2009, Gupta and Igamberdiev 2011, John *et al.* 2016). Nitrate reductase, electron transport chain (ETC), and nitrite-nitric acid (operating at plasmalemma) are reductive pathways and contribute maximally to the NO pool (Stohr *et al.* 2001, Sakihama *et al.* 2002, Planchet *et al.* 2005, Gupta and Igamberdiev 2011, Corpas and Barroso 2013, Qiao *et al.* 2014).

An evidence from genetic studies has revealed the role of NO in regulation of nuclear gene expression (Grun *et al.* 2006, Palmieri *et al.* 2008, Qiao *et al.* 2014), in the expression of stress responsive genes by modifying transcription factors (TFs) and enzymes (Feng *et al.* 2013), and in the interaction with biomolecules like fatty acids or hormones (Liu *et al.* 2013, Sanchez-Calvo *et al.* 2013). An example is oligomerisation of non-expressor pathogenesis related (*NPR1*) gene by *S*-nitrosoglutathione, a NO donor, which is brought by *S*-nitrosylation of cysteine (Tada *et al.* 2008, Mukhtar *et al.* 2009, Lindermayr *et al.* 2010). Induction of oligomer-monomer switching of *NPR1* gene for nuclear translocation results in systemic acquired resistance (Fu and Dong 2013). Moreover, *S*-nitrosylation can also bring about alteration in expression of nuclear genes coding for pathogen resistance by modulating the DNA binding efficiency of transcription factors (Lindermayr *et al.* 2010, Fu and Dong 2013). Many reports pertain the role of NO in increasing expression of genes involved in antioxidants (Neill *et al.* 2008), nuclear defence (Mandal *et al.* 2012), and stress induced signalling molecules (Qiao *et al.* 2014).

Besides being involved in leaf expansion, seed germination and de-etiolation (Leshem and Haramaty 1996, Beligni and Lamattina 2000, Xu *et al.* 2011, Piterkova *et al.* 2012), NO induces defence genes and phytoalexin production and potentiates the induction of apoptosis (Delledonne *et al.* 1998, Durner *et al.* 1998, Beligni and Lamattina 2000, Beligni *et al.* 2002, Grun *et al.* 2006, Zhao *et al.* 2007) and floral transition (He *et al.* 2004). The provocation of the roles (stimulatory or inhibitory) is dependent on its content and interaction with ROS. By reaction with superoxide anion, NO can form peroxynitrite, which can potentially damage nucleic acids, proteins, and can result in perturbed enzyme activity. On the other hand, reacting with lipid peroxyl radicals, NO cleaves the self-perpetuating lipid peroxidation reaction (Beligni and Lamattina 1999). Inhibition of certain enzymes may provide safeguard for plant cellular functioning, *e.g.*, inhibition of enzyme aconitase reduces oxidative stress by restricting the flow of electrons through electron transport system and also the induction of alternate oxidase (AOX) activity which concomitantly results in enhanced synthesis of amino acids like glycine, serine, leucine, lysine, *etc.* (Gupta *et al.* 2012). But the actual mechanism of NO in addition to a potent signalling molecule and stress responsive element remains yet to be established.

MAPK: Other important molecules activated in response to water/salinity stress and regulating numerous cellular activities by phosphorylating threonine and serine residues of substrate proteins are mitogen activated protein kinases (MAPKs) (Kyriakis and Avruch 1996, Shou *et al.* 2004, Teige *et al.* 2004, Danquah *et al.* 2014, John *et al.* 2015). This phosphorylating activity of MAPK system links receptors (that are upstream) with their respective and specific downstream located targets. Protein polypeptide sequences encoded by *MAPK* genes are highly and precisely conserved and so is their function.

Functionally interconnected three protein kinases, *i.e.*, MAPK, MAPKK, and MAPKKK are involved in MAPK mediated signalling cascade during stress. In addition, they are involved in other processes like cell wall biosynthesis and cell growth and differentiation (Ichimura 2002, Shou *et al.* 2004, Antonsson *et al.* 2006, Colcombet and Hirt 2008, Danquah *et al.* 2014). By stimulus perception induced activation of MAPKKK triggers phosphorylation and activation of specific MAPKK, which subsequently activates MAPK. After being transported to nucleus, the activated MAPK activates particular downstream signalling agents like transcription factors and elicit a specific response (Xiong and Yang 2003). Individual *MAPK* gene encodes different protein kinases, which play a unique role in stress tolerance, *e.g.*, in rice nine such genes coding for specific protein kinase important for drought tolerance have been identified. It is widely accepted that plants quickly activate MAPK when confronted by abiotic stress. Different kinase cascade systems are involved/activated in signal perception and its subsequent transduction up to the elicitation of response and recovery (Mikolajczyk *et al.* 2000). For example, in alfalfa MAPK module MAPK kinase-stress induced MAPK (SIMKK-SIMK55) and in tobacco *Nicotiana tobaccum* MAPK kinase-salicylic acid-induced protein kinase/wounding-induced protein kinase (Nt MEK2-SIPK/WIPK) have been reported to be involved in osmotic stress signalling (Yang *et al.* 2001, Zhang and Klessig 2001). In addition, a two-component sensor receptor regulatory system involving histidine kinase for perception of various environmental stresses has been found. It either couples with downstream MAPK or directly phosphorylates specific targets so as to initiate cellular responses, *e.g.*, yeast selender 1 **(**SLN1) osmosensor is the best example of two component histidine kinase characterized, which in association with *Xenopus* protein disulfide isomerase-supressor of sensor kinase 1 **(**XPDI–SSK1) response regulator, regulates the high osmolarity glycerol (HOG) MAPK cascade, thereby enhancing the synthesis of glycerol to mitigate osmotic stress.

Variations in the specificity of MAPKs from functional viewpoint determine their multidimensional role in response to stresses. This knowledge can provide insights for enhanced crop tolerance to multiple stresses. Besides specificity in the individual pathways, existence of crosstalk between different MAPK modules during osmotic stress and ROS mediated signalling has been reported (Ulm *et al.* 2001, Danquah *et al.* 2013, Golldack *et al.* 2014). Kovtun *et al.* (2000) demonstrated in tobacco that expression of tobacco protein kinase (NPK1), an active orthologue of *Arabidopsis* NPK1-related protein kinase 1 (ANP1), increases tolerance to multiple stresses and expression of *Nicotiana* protein kinase (MAPKKK NPK1) in transgenic maize, which causes improved drought tolerance through protected and maintained photosynthetic rates as well as enhanced kernel mass (Shou *et al.* 2004).

There are several other reports which depict the role of MAPKs in stress tolerance (Ichimura *et al.* 2000, Xiong and Yang 2003, Alzwiy and Morris 2007, Xu *et al.* 2008, Yu *et al.* 2010). Expression of *OsMAPK5* and *OsMAPK44* genes enhances salt, cold, and drought tolerance in transgenic rice (Xiong and Yang 2003, Jeong *et al.* 2006). *Arabidopsis* plants overexpressing *Zea mays ZMKK4* gene show improved salt tolerance with a concomitant increase in free proline as well as soluble sugars and enhanced activities of antioxidant enzymes (POD and CAT) because of the upregulation of transcription factors leading to increased expression of other genes like Δ^1-pyrroline-5-carboxylate synthase 1 (*P5CS)* and cold regulated 47 (*COR47*), which directly or indirectly contribute to better growth performance under changing environment (Kong *et al.* 2011).

Enhanced activities of antioxidant enzymes and TFs induced by MAPK, which further controls expression of several downstream genes, provide an avenue towards enhanced stress tolerance. Kong *et al.* (2011) demonstrated that transgenic crops showing up-regulation of transcription factors like DRE binding protein 2A (DREB2A) also show enhanced expression of *P5SC* and *COR47* genes, hence resulting in cross tolerance developed through interaction of signalling molecules (Wurzinger *et al.* 2011). For example, *Lycopersicum esculentum CDPK1* gene brings interrelation between wounding and salinity, a good example of cross-tolerance imparting salt tolerance, through enhanced production of jasmonic acid and systemin (signal peptide) induced by wounding (Capiati *et al.* 2006).

Despite all these discoveries on the role of MAPK in signal transduction involved in stress tolerance, there is still a huge gap in knowledge of regulation of genes, involvement of MAPKs and differential stress tolerance capacity of different plant species.

Transcription factors are regulatory proteins that initiate stress tolerance by modulating the expression of various downstream genes through interaction with their promoter regions. Large number of TFs exist in plants, *e.g.*, *Arabidopsis* genome has 5.9 % of them. They are categorized according to the presence of DNA binding domains (Reichmann *et al.* 2000). Nevertheless, a number of stress response TFs have been demonstrated in transgenic plants, but the information about the function of transcriptional coactivators associated with abiotic stresses is still lacking.

Plant specific TFs which impart stress tolerance through induction and regulation of several stress related genes through their involvement in binding to dehydration-responsive element/C-repeat (DRE/CRT), *cis*-acting elements in gene promoters and active transcription of downstream genes have been revealed through molecular studies (Wang and He 2007, Andeani *et al.* 2009, Mizoi *et al.* 2012, Sazegari and Niazi 2012, Sun *et al.* 2012, Nasreen *et al.* 2013, Zhao *et al.* 2013, Keita *et al.* 2014, Li *et al.* 2014, Ma *et al.* 2014, Zhang *et al.* 2014). DREB transcription factors belong to the APETLA2/ethylene responsive element binding protein (AP2/EREBP) family having highly conserved binding factor domains, AP2/ERF, for APETLA2/EREBP. AP2/ERF differ from ERF in their amino acid sequences at the 14th and 19th position with the former having valine and glutamic acid, while the latter alanine and aspartic acid, respectively (Liu *et al.* 1998, Sakuma *et al.* 2002, Latini *et al.* 2007). DREB transcription factors exist as two major subclasses, *i.e.*, DREB1 and DREB2 differ in their role in response to stress with the former being employed in freezing, while the latter in drought and salinity stress tolerance (Liu *et al.* 1998, Fowler and Thomashow 2002, Xiong and Fei 2006, Nayak *et al.* 2009).

Transgenic plants overexpressing DREB TFs have been reported to show better growth under stress. For example, *Arabidopsis* plants overexpressing *DREB1A* gene show tolerance to cold (Liu *et al.* 1998). Overexpression of MsDREB2C induces better growth through enhanced proline content and transcription of genes functioning downstream of DREs with a subsequent reduction in water loss in transgenic *Arabidopsis*. Furthermore, it represses the expression of pathogen-related genes (Zhao *et al.* 2013). Microarray analysis of transgenic DREB reveals the increased expression of downstream located genes coding for various proteins and enzymes of immense use in metabolism including proteins such as late embryogenesis abundance (LEA) or heat shock and antioxidant and other enzymes (Agarwal and Jha 2010).

In *Arabidopsis*, DREB1s/CBFs transcription factor showing specific interaction with DRE/CRT *cis*-acting element controls expression of several stress responsive genes. Qin *et al.* (2004) isolated the homologue of DREB1/CBF from maize (ZmDREB1A) which remains specifically bound with DRE because of the presence of highly conserved valine at the 14th position in the ERF/AP2 DNA binding domain. Cold, salinity, and transient pathogen attack induce expression of *ZmDREB1A* gene (Qin *et al.* 2014). Overexpression of *ZmDREB1A* in transgenic *Arabidopsis* enhances tolerance to drought and freezing by inducing the expression of DREB1 stress responsive genes.

Transgenic *Arabidopsis* overexpressing stress responsive *OsDREB1* accumulate higher content of proline and free sugars and are tolerant to cold, drought, and salinity (Ito *et al.* 2006). Exposure to cold temperatures triggers expression of CBF transcription factor, which further mediates expression of cold responsive downstream genes (Thomashow 1999, Chinnusamy *et al.* 2003, Agarwal *et al.* 2006), while upstream located TF and inducer of CBF expression (ICE) are involved in regulating CBF expression (Chinnusamy *et al.* 2003). Overexpression of a novel *bZIP*TF gene, GmbZIP1 (isolated from salt tolerant soybean plants) into Chinese wheat cv. BS93 enhances its tolerance against drought stress without growth reduction, which suggests that *GmbZIP1* may be an important for introducing stress tolerance (Gao *et al.* 2011). In addition, expression of *Triticum aestivum* ABA insensitive (ABI)-like transcription factor gene 1 (*TaABL1*) increases stomatal closure under drought stress in transgenic wheat plants (Xu *et al.* 2014). Induction of *AtDREB1A* in rice plants improves chlorophyll and relative water content, and reduces ion leakage under drought stress (Ravikumar *et al.* 2014). Although a number of TFs have been tested for improving tolerance in different plants usually under a single stress, new crop cultivars containing multiple improved traits including nutritional profiles and yield with safety assessment under several stresses yet need to be explored.

Members of NAC (NAM-ATAF1, 2-CUC2) family are another plant specific TFs and have important role in a wide variety of developmental processes including stress responses (Fujita *et al.* 2004, Olsen *et al.* 2005, Nakashima *et al.* 2007, 2012, Tran *et al.* 2007, Ma *et al.* 2013, Jiang *et al.* 2014). Phylogenetic studies reveal that at least six major groups of *NAC* genes in ancient moss lineage and to-date more than 100 *NAC* genes have been identified in *Arabidopsis* and *Oryza sativa* (Nakashima *et al*. 2012).

Exposure to stressful environment triggers expression of NAC TFs. Apart from having the potential to function as homo- as well as hetero-dimer forms, several NAC TFs can share the same or different core recognition sequence and function *via* auto- or cross-regulation (Nuruzzaman *et al*. 2013). Though the role of NAC in stress tolerance is well established, the mechanism needs extensive research (Nakashima *et al*. 2012). For example, transgenic *Arabidopsis* and *Oryza sativa* overexpressing stress responsive NAC (*SNAC*) genes exhibite enhanced salinity (Hu *et al*. 2006) and drought resistance (Hu *et al*. 2006, Nakashima *et al*. 2012).

Similarly, expression of *NAC* gene from *Solanum lycopersicum*, *SlNAC1*, is enhanced by stresses like temperature (both low as well as high), salinity, drought, and wounding (Huang *et al*. 2013, Ma *et al*. 2013). Overexpression of *SlNAC1* in tomato increases freezing tolerance through maintenance of the photosystem II efficiency and oxygen evolving activities (Ma *et al*. 2013). Transcription of *SlNAC1* is also increased by application of phytohormones like ABA, JA, salicylic acid, gibberellin, ethylene, *etc*., and plants overexpressing *SlNAC1* have higher number of leaves and higher antioxidant enzyme activities as compared to wild counterparts (Ma *et al*. 2013). Similarly, transgenic plants with *SNAC2* gene have higher stress tolerance due to upregulation of genes coding for enzymes like peroxidase, ornithine aminotransferase, Na^+/H^+ antiporter and heat shock proteins (HSPs; Hu *et al*. 2008).

Oncogene *v-MYB* was the first member of myeloblastosis (MYB) TF family identified in avian myeloblastosis virus (Klempnauer *et al*. 1982), and *MYB* gene *C1* is the first plant MYB TF which was isolated from maize (Paz-Ares *et al*. 1987). Its different sub-classes are grouped on the basis of number of MYB repeats, *e.g*., 1R, 2R, 3R, 4R MYBs (Rosinski and Atchley 1998, Jin and Martin 1999, Dubos *et al*. 2010, Chen *et al*. 2014).

Usually, at N terminus, MYB TFs contain highly conserved domain of 1 to 4 imperfect MYB tandem repeats. Each repeat is at least 50 amino acids in length with tryptophan at regular intervals. Furthermore, their structure has 2 to 3 helix-turn-helix repeats (Stracke *et al*. 2001, Feller *et al*. 2011) and a highly conserved MYB DNA binding domain conferring the specificity (Katiyar *et al*. 2012, Chen *et al*. 2014). Role of MYB TFs in plant developmental processes like cell shape determination and cell differentiation, secondary metabolism, signal transduction, and stress tolerance is well documented (Lippold *et al*. 2009, Dubos *et al*. 2010, Feller *et al*. 2011; Du *et al*. 2012, Katiyar *et al*. 2012, Zhang *et al*. 2012, Chen *et al*. 2014, Wang *et al*. 2014).

More than 100 MYB proteins have been identified in *Arabidopsis* and majority of them have a putative role in transcriptional regulation of various biological processes including responses to biotic and abiotic stresses. Moreover, they have the ability to function through cross-talk mechanisms, *e.g*., *Arabidopsis thaliana* MYB2, (AtMYB2) enhances salt tolerance through interaction with calmodulin (Yoo *et al*. 2005), while overexpression of *AtMYB44* enhances stress tolerance by triggering ABA induced stomatal closure (Jung *et al*. 2008). Increased ABA content induces tolerance to environmental extremes resulting from overexpression of *MYB15* (Ding *et al*. 2009).

Transgenic plants overexpressing MYB TFs show higher stress tolerance through arbitrating down-regulation of 2C serine/threonine protein phosphatases (PP2Cs). For example, transgenic plants overexpressing AtMYB20 show improved salt tolerance as compared to that in which AtMYB20 is down-regulated and are found vulnerable to salinity (Cui *et al*. 2013), because salinity induces the expression of PP2Cs, which regulate ABA induced signalling negatively. However, AtMYB20 reverts this effect by binding to the promoter sites of various PP2Cs and lowers their expression and enhances tolerance by maintaining expression of ABA coding genes (Schweighofer *et al*. 2004, Jung *et al*. 2008, Kline *et al*. 2010, Cui *et al*. 2013). Hence, suppression of the genes bring negative regulation in stress tolerance (Jung *et al*. 2008, Cui *et al*. 2013).

The degree and specificity of transgene expression depends on the pedigree of host genome, *e.g*., Vannini *et al*. (2007) developed transgenic plants (*Arabidopsis* and tomato) overexpressing cold responsive *Osmyb4* gene, which shows improved tolerance to drought and viral outbreaks, but not to cold. In *Arabidopsis*, Agarwal *et al*. (2006) demonstrated the role of MYB15 in regulation of cold binding factor (*CBF*) gene and its role in cold tolerance. They reported that MYB15 overexpressing seedlings shows a decline in *CBF* gene expression and hence reduced cold tolerance as compared to wild type. In addition, they also reported that its loss-of-function enhanced expression of *CBF* gene thus suggesting a possible role of MYB15 in controlling complex and coordinated framework of TFs. Overexpression of *OsMYB4* imparts cold and drought tolerance in *Arabidopsis* and apple (*Malus pumila*) through the active induction of several physiological and biochemical pathways like accumulation of compatible solutes (Pasquali *et al*. 2008).

In transgenic rice, overexpression of *OsMYB3R-2* shows increased tolerance to cold. *OsMYB3R-2* encoding a TF binds specifically to a highly conserved mitosis specific *cis*-activator element, a sequence which is also reported in cyclin genes, *e.g*., OsCycB1;1 and/or *Oryza sativa* MSA *cis*-acting element (OsKNOLLE2). OsMYB3R-2 overexpression also enhances the transcript levels of G2/M specific genes, suggesting a putative role of this TF in mediating mechanisms through regulation of cell cycle (Ma *et al*. 2009).

Advantages and disadvantages of transgenic crops

Plant genetic engineering has made a promising progress during the last few decades as far as stable gene transformation and regulation of transgene optimization are concerned. Availability of target genes is a major constraint in its widespread applicability and in spite of this, genetic engineering is witnessing significant achievements reflected in upsurge in generation of transgenic crops with enhanced combating potential to stress. For example, rice genome sequencing provides a prelude towards better improvement of cereals. One of the prime bases towards the successful genome sequencing is the conserved organization of genes within a large section of chromosomes despite the diversity of plant genomes (Ku *et al.* 2000, Michael and Jackson 2013, Wendel *et al.* 2016). Nevertheless, recent advancement in plant molecular biology together with genomics has provided the possibility of revealing the blueprint and tailoring as well as modifying genomes. After *Arabidopsis thaliana* genome sequencing, plant genomics has started using new approaches and technologies to generate transcriptome, genome, and epigenome datasets of model crop plant species. However, ploidy, heterozygosity, and paralogy do create hardships in easy sequencing. However, generating *de novo* transcriptome assemblies assist in bypassing the genome complexes. Technologically driven by new software and algorithm facilities, the field of genomics anticipates sequencing, which will continue so as to improve the genome length and quality as well (Batley and Edwards 2009, Hamilton and Buell 2012, Edwards *et al.* 2013).

Genome editing technologies depends on molecular tools used to generate DNA double-strand breaks at a desired site within genome and sequence-specific nucleases (Cardi 2016). Recently, many sequence-specific nucleases, including zinc finger nucleases and TAL effector nucleases have been used into targeted cultivars in order to improve conventional plant breeding and genetic modification technologies (Voytas and Gao 2014). In addition to other organism, clustered regularly interspaced short palindromic repeats/ CRISPR-associated protein-9 (CRISPR/Cas9), a rapidly developing genome editing technology has been successfully used for improving crop plants. CRISPR/Cas9 is a relatively cheap and easy to implement technology has the potential to revolutionize plant breeding (Fichtner *et al.* 2014, Belhaj *et al.* 2015).

In plants, numerous stress responsive genes, characteristic to a particular stress tolerance have been isolated and characterized so far (Knight *et al.* 1999, Tamminen *et al.* 2001, Hsieh *et al.* 2002). Genetic engineering, a challenging field for enhancing tolerance, depends on some key fundamentals like identification of stress responsive/regulatory genes and precise isolation as well as insertion of isolated genes involved in different defence strategies. The past decade has witnessed the increasing roles of single function genes, transcription factors and other stress associated characters. Though the establishment of multigenic nature of stress response and tolerance has shifted genetic engineering to multiple gene function, TFs, and subsequent cross-talks between them (Agarwal *et al.* 2013). The increase in crop productivity, especially in stress-prone environments through increasing tolerance to ever-increasing threats of biotic and abiotic stresses, is the need of current scenario.

Further increasing efficiency of physiological attributes like water-use efficiency through development of markers for efficient water uptake and whole plant water status also seems a plausible approach for enhancing plant stress tolerance (Martinez-Ballesta and Carvajal 2014). Application of synthetic biological techniques not only for food production, but also for renewable industrial feed stocks are amongst various open challenges for plant biotechnologists. Besides this, overexpression of the selected elite genes in order to get more tolerant physiological and biochemical pathways as well as developing strategies towards secured global food supply is also vital keeping in mind the global climate change causing continuous increase in CO_2 concentration and soil degradation. In addition to all challenges pointed out earlier, several anthropogenically induced disturbances and fighting malnutrition, a prevalent and endemic problem in developing countries, through production of nutrient rich food producing crops or crops showing efficient nutrient accumulation is a matter of great concern, and it needs to gain attention from both plant biotechnologists and geneticists together with agriculturalists. Besides utilizing biotechnology for developing saccharide, protein, and fat rich crop products for combating malnutrition (Perez-Massot *et al.* 2013), stress tolerance enhancement to multiple stresses and transgenic safety risks should be taken into consideration.

Identification of genes and gene products involved in protecting structural and functional components of various cellular components and subsequent engineering of these genes can be very handy. Our limited information/knowledge about stress responsive/associated genes remains one of the major gaps in their comprehensive profiling and in unravelling key stress responsive genes from stress tolerant model plants, which can open new avenues in dissecting the complete mechanisms involved at molecular and gene level (Grover *et al.* 1999, Vinocur and Altman 2005, Hong *et al.* 2016).

The genetically modified organisms (GMO) have received a major objection all over the globe and now many countries have raised safety concerns about these foods. The rising pressure from various agencies has made government bodies to impose moratorium on certain GM plants. For example, in India restriction has been imposed on the use of GM egg plant on the pretext that this causes severe malnutrition. Reports from ecologists, environmentalists, health agencies, and non-governmental organizations (NGOs) are continuously adding to the safety risks of GM foods not only human-related but also to biodiversity. A list of a few cultivars/varieties of GM crops withdrawn due to allergies/toxins/political issues have been presented in Table 1 Suppl.

Safety assessments are mainly keeping in mind: *1*) presence as well as characteristics of over-expressed proteins, genes, and gene products and their probable bearing on the normal range of naturally occurring constituents, and *2*) unexpected adverse effects of GM foods. The Organization for Economic Co-operation and Development (OECD) has formulated stringent rules for assessing the GM foods for any possible toxicity like single and repeated dose toxicity, reproductive and developmental toxicity, and immunotoxicity. Trial studies are being carried out using sheep, pigs, broilers, lactating dairy cows, and fish for comparing the bioavailability of nutrients from the GM plants with their near-isogenic cultivars as well as commercial cultivars (GMO Panel report 2008). Inexplicable and inevitable potential toxicity/allergy induced by some GM foods has prompted every nation to go for extensive trials before making any of the foods available for commercial use. Overall, although production of transgenic plants is a tedious process, their acceptance and wide comercialization in several countries have motivated the researchers. Transgenic plants with higher yield production with minimum health or allergic problems are one of the primary goals of most plant scientists these days.

Conclusion and future challenges

Transgenic approach is preferred over the conventional one with some control measures for the biofortification of important crops because of it being convenient and time and labour saving approach of overcoming environmental problems. For example, rice plants overexpressing iron storage protein ferritin have been reported to have increased seed iron content (Lucca *et al.* 2001). But, adoption of GM crops is a time-taking process as a number of policies and laws need to be adopted before the commercial release of such cultivars/varieties. A transgene for one of the trait could involve regulation of a cascade of genes involved therein. That can cause human health problems. So, keeping in mind this problem, a number of government agencies are working mostly in the developed countries, but this issue is not being contemplated well in developing countries. The World Health Organization (WHO) and the Consultative Group on International Agricultural Research (CGIAR) have taken concrete steps against micronutrient deficiencies on priority so that malnutrition induced barriers in potential human socioeconomic development can be addressed. The CGIAR emphasizes on biofortification through the improvement in nutrient content of rice, maize, beans, *etc.* utilizing both breeding as well as biotechnological means (Perez-Massot *et al.* 2013). So, before using transgenic crops, it is crucial that transgenic crops (seeds and fruits) must be subjected to a rigorous risk assessment, and assessment of potential allergenicity/toxicity along with nutritional examination. So far, transgenic approach is considered as an extremely useful tool in basic plant science research, but understanding of the gene networks and molecular physiology of plant responses to environmental stresses should be a prerequisite.

Identifying and manipulating the expression of various tolerance pathways like biosynthetic pathways of osmolytes (proline and glycine betaine), and antioxidants (enzymatic as well as non-enzymatic), efficient transporters, transcription factors, *etc.*, in stress tolerant plant species and subsequent introgression of respective genes into the commercially important crops has been achieved. For example, several studies have been performed where scientists have developed transgenic crops by introducing genes from halophytic grasses for enhancing salinity tolerance through introduction of transporter genes that mediate efficient compartmentation and sequestration of ions into vacuole or apoplast. On the other hand, some of the genetically modified crops have been reported to be harmful for humans, environment, as well as biodiversity.

Furthermore, a major hurdle for commercializing a genetically engineered crop is securing approvals from multiple regulatory authorities all over the world. Multigenic nature of environmental stresses and their induced changes create several hardships and seem to be one of the major limitations in transgenic prospects. Genomes of some crop plants that have been sequenced to date under the internationally sponsored projects have provided considerable help in unravelling the key genes involved in various important pathways.

References

Agarwal, M., Hao, Y., Kapoor, A., Dong, C.H., Fujii, H., Zheng, X., Zhu, J.K.: A R2R3 type of MYB transcription factor is involved in the cold regulation of *cbf* genes and in acquired freezing tolerance. - J. biol. Chem. **281**: 37636-37676, 2006.

Agarwal, P.K., Jha, B.: Transcription factors in plants and ABA dependent and independent abiotic stress signaling. - Biol. Plant. **54**: 201-212, 2010.

Agarwal, P.K., Shukla, P.S., Gupta, K, Jha, B.: Bioengineering for salinity tolerance in plants: state of the art. - Mol. Biotechnol. **54**: 102-123, 2013.

Ahmad, P., Ashraf, M., Younis, M., Hu, X., Kumar, A., Akram, N.A., Al-Qurainy, F.: Role of transgenic plants in agriculture and biopharming. - Biotechnol. Adv. **30**: 524-540, 2012a.

Ahmad, P., Bhardwaj, R., Tuteja, T.: Plant signaling under abiotic stress environment. - In: Ahmad. P., Prasad, M.N.V. (ed.): Environmental adaptations and Stress Tolerance of Plants in the Era of Climate Change. Pp. 297-323. Springer Science + Business Media, New York 2012b.

Ahmad, P., Jaleel, C.A., Sharma, S.: Antioxidant defense system, lipid peroxidation, proline metabolizing enzymes, and biochemical activities in two *Morus alba* genotypes subjected to NaCl stress. - Russian J. Plant Physiol. **57**: 509-517, 2010.

Al-Doss, A.A., Smith, S.E.: Registration of AZ-97MEC and AZ-97MEC-ST very non-dormant alfalfa germplasm pools with increased shoot weight and differential response to saline irrigation. - Crop Sci. **38**: 568-568, 1998.

Alzwiy, I.A., Morris, P.C.: A mutation in the *Arabidopsis* MAP kinase kinase 9 gene results in enhanced seedling stress tolerance. - Plant Sci. **173**: 302-308, 2007.

Andeani, J.K., Mohsenzadeh, S., Mohabatkar, H.: Isolation and characterization of partial *DREB* gene from four Iranian *Triticum aestivum* cultivars. - World J. agr. Sci. **5**: 561-566, 2009.

Antonsson, B., Kassel, D.B., Di Paolo, G., Lutjens, R., Riederer, B.M., Grenningloh, G.: Signaling through MAP kinase networks in plants. - Arch. Biochem. Biophys. **452**: 55-68, 2006.

Apse, M.P., Blumwald, E.: Engineering salt tolerance in plants. - Curr. Opin. Biotechnol. **13**: 146-150, 2002.

Ashraf, M., Akram, N.A.: Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. - Biotechnol. Adv. **27**: 744-752, 2009.

Ashraf, M., O'Leary, O.J.: Effect of drought stress on growth, water relations and gas exchange of two lines of sunflower differing in degree of salt tolerance. . Int. J. Plant Sci. **157**: 729-732, 1996.

Atkinson, N.J, Urwin, P.E.: The interaction of plant biotic and abiotic stresses; from gene to the field. - J. exp. Bot. **63**: 695-709, 2012.

Batley, J., Edwards, D.: Genome sequence data: management, storage, and visualization. - Biotechniques **46**: 333-336, 2009.

Baxter, A., Mittler, R., Suzuki. N.: ROS as key players in plant stress signalling. - J. exp. Bot. **65**: 1229-1240, 2014.

Belhaj, K., Chaparro-Garcia, A., Kamoun, S., Patron, N.J., Nekrasov, V.: Editing plant genomes with CRISPR/Cas9. - Curr. Opin. Biotechnol. **32**: 76-84, 2015.

Beligni, M.V., Fath, A., Bethke, P.C., Lamattina, L., Jones, R.L.: Nitric oxide acts as an antioxidant and delays programmed cell death in barley aleurone layers. - Plant Physiol. **129**: 1642-1645, 2002.

Beligni, M.V., Lamattina, L.: Is nitric oxide toxic or protective? - Trends Plant Sci. **4**: 299-300, 1999.

Beligni, M.V., Lamattina, L.: Nitric oxide stimulates seed germination and de-etiolation and inhibits hypocotyl elongation, three light-inducible responses in plants. - Planta **210**: 215-221, 2000.

Bhat, S.R., Srinivasan, S.: Molecular and genetic analyses of transgenic plants: considerations and approaches. - Plant Sci. **163**: 573-581, 2002.

Breusegem, F.V., Vranova, E., Dat, J.F, Inze, D.: The role of active oxygen species in plant signal transduction. - Plant Sci. **161**: 405-414, 2001.

Bogdan, C.: Nitric oxide and the regulation of gene expression. - Trends cell. Biol. **11**: 66-75, 2001.

Buchanan, C.D., Lim, S., Salzman, R.A., Kagiampakis, I., Morishiqe, D.T., Weers, B.D., Klein, R.R., Pratt, L.H., Cordonnier-Pratt, M.M., Klein, P.E., Mullet, J.E.: *Sorghum bicolor*'s transcriptome response to dehydration, high salinity and ABA. - Plant mol. Biol. **58**: 699-720, 2005.

Burssens, S., Himanen, K., Van de Cotte, B., Beeckman, T., Van, M.M., Inze, D., Verbruggen, N.: Expression of cell cycle regulatory genes and morphological alterations in response to salt stress in *Arabidopsis thaliana*. - Planta **211**: 632-640, 2000.

Capiati, D.A., Pais, S.M., Tellez-Inon, M.T.: Wounding increases salt tolerance in tomato plants: Evidence on the participation of calmodulin-like activities in cross tolerance signalling. - J. exp. Bot. **57**: 2391-2400, 2006.

Cardi, T.: Cisgenesis and genome editing: combining concepts and efforts for a smarter use of genetic resources in crop breeding. - Plant Breed. **135**: 139-147, 2016.

Chen, N., Yang, Q., Pan, L., Chi, X., Chen, M., Hu, D., Yang, Z., Wang, T., Wang, M., Yu, S.: Identification of 30 MYB transcription factor genes and analysis of their expression during abiotic stress in peanut (*Arachis hypogaea* L.). - Gene **533**: 332-345, 2014.

Chen, W., Provart, N.J., Glazebrook, J., Katagiri, F., Chang, H.S., Eulgem, T., Mauch, F., Laun, S., Zou, G., Whitham, S.A., Budworth, P.R., Tao, Y., Xie, Z., Chen, X., Lam, S., Kreps, J.A., Harper, J.F., Si-Ammour, A., Mauch-Mani, B., Heinlein, M., Kobayashi, K., Hohn, T., Dangl, J.L., Wang, X., Zhu, T.: Expression profile matrix of *Arabidopsis* transcription factor genes suggests their putative functions in response to environmental stresses. - Plant Cell **14**: 559-574, 2002.

Cheong, Y.H., Sung, S.J., Kim, B.G., Pandey, G.K., Cho, J.S., Kim, K.N., Luan, S.: Constitutive overexpression of the calcium sensor CBL5 confers osmotic or drought stress tolerance in *Arabidopsis*. - Mol. Cells **29**: 159-165, 2010.

Chinnusamy, V., Ohta, M., Kanrar, S., Lee, B., Hong, X., Agarwal, M., Zhu, J.K.: ICE1: a regulator of cold-induced transcriptome and freezing tolerance in *Arabidopsis*. - Genes Dev. **17**: 1043-1054, 2003.

Choudhary, S.P., Yu, J.Q., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.S.: Benefits of brassinosteroid crosstalk. - Trends Plant Sci. **17**: 594-605, 2012.

Colcombet, J., Hirt, H.: *Arabidopsis* MAPKs: a complex signalling network involved in multiple biological processes. - Biochem. J. **413**: 217-226, 2008.

Corpas, F., Hayashi, M., Mano, S., Nishimura, M., Barroso, J.B.: Peroxisomes are required for *in vivo* nitric oxide accumulation in the cytosol following salinity stress of *Arabidopsis* plants. - Plant Physiol. **151**: 2083-2094, 2009.

Corpas, F.J., Barroso, J.B.: Nitro-oxidative stress *vs* oxidative or nitrosative stress in higher plants. - New Phytol. **199**: 633-635, 2013.

Corpas, F.J., Barroso, J.B., Carreras, A., Valderrama, R., Palma, J.M., Leon, A.M., Sandalio, L.M., Del Rio, L.A.: Constitutive arginine dependent nitric oxide synthase activity in different organs of pea seedlings during plant development. - Planta **224**: 246-254, 2006.

Cui, K., Xing, G., Liu, X., Xing, G., Wang, Y.: Effect of hydrogen peroxide on somatic embryogenesis of *Lycium barbarum* L. - Plant Sci. **146**: 9-16, 1999.

Cui, M.H., Yoo, K.S., Hyoung, S., Nguyen, H.T.K., Kim, Y.Y., Kim, H.J., Ok, S.H., Yoo, S.D., Shin, J.S.: An *Arabidopsis* R2R3-MYB transcription factor, AtMYB20, negatively regulates type 2C serine/threonine protein phosphatases to enhance salt tolerance. - FEBS Lett. **587**: 1773-1778, 2013.

Cushman, J.C., Bohnert, H.J.: Genomic approaches to plant stress tolerance. - Curr. Opin. Plant Biol. **3**: 117-122, 2000.

Danquah, A., De Zelicourt, A., Colcombet, J., Hirt, H.: The role of ABA and MAPK signaling pathways in plant abiotic stress responses. - Biotechnol. Adv. **32**: 40-52, 2014.

Das, R., Pandey, G.K.: Expressional analysis and role of calcium regulated kinases in abiotic stress signaling. - Curr. Genom. **11**: 2-13, 2010.

Delledonne, M., Xia, Y., Dixon, R.A., Lamb, C.: Nitric oxide functions as a signal in plant disease resistance. - Nature **394**: 585-588 1998.

Ding, Z., Li, S., An, X., Liu, X., Qin, H., Wang, D.: Transgenic expression of MYB15 confers enhanced sensitivity to abscisic acid and improved drought tolerance in *Arabidopsis thaliana*. - J. Genet. Genomics **36**: 17-29, 2009.

Du, H., Yang, S.S., Liang, Z., Feng, B.R., Liu, L., Huang, Y.B., Tang, Y.X.: Genome-wide analysis of the MYB transcription factor superfamily in soybean. - BMC Plant Biol. **12**: 106, 2012.

Dubos, C., Stracke, R., Grotewol, E., Weisshaar, B., Martin, C., Lepiniec, L.: MYB transcription factors in *Arabidopsis*. - Trends Plant Sci. **15**: 573-581, 2010.

Durner, J., Wendehenne, D., Klessig, D.F.: Defense gene induction in tobacco by nitric oxide, cyclic GMP and cyclic ADP-ribose. - Proc. nat. Acad. Sci. USA **95**: 10328-10333, 1998.

Edel, K.H., Kudla, J. Increasing complexity and versatility: How the calcium signaling toolkit was shaped during plant land colonization. - Cell Calcium **57**: 231-246, 2014.

Edwards, D., Batley, J., Snowdon, R.J.: Accessing complex crop genomes with next-generation sequencing. - Theor. appl. Genet. **126**: 1-11, 2013.

Fan, W., Zhang, M., Zhang, H., Zhang, P.: Improved tolerance to various abiotic stresses in transgenic sweet potato (*Ipomoea batatas*) expressing spinach betaine aldehyde dehydrogenase. - Plos ONE **7**: e37344, 2012.

Feller, A., Machemer, K., Braun, E.L, Grotewold, E.: Evolutionary and comparative analysis of MYB and bHLH plant transcription factors. - Plant J. **66**: 94-116, 2011.

Feng, J., Wang, C., Chen, Q., Chen, H., Ren, B., Li. X., Zuo, J.: S-nitrosylation of phosphotransfer proteins represses cytokinin signaling. - Nat. Commun. **4**: 1529, 2013.

Fichtner, F., Urrea Castellanos, R., Ulker, B.: Precision genetic modifications: a new era in molecular biology and crop improvement. - Planta **239**: 921-939, 2014.

Floris, M., Hany, M., Elodie, L., Christophe, R., Benoit, M.: Post-transcriptional regulation of gene expression in plants during abiotic stress. - Int. J. mol. Sci. **10**: 3168-3185, 2009.

Fowler, S., Thomashow, M.F.: *Arabidopsis* transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. - Plant Cell **14**: 1675-1690, 2002.

Foyer, C.H, Noctor, G.: Redox signaling in plants. - Antioxidants Redox Signal **18**: 2087-2090, 2013.

Franz, S., Ehlert, B., Liese, A., Kurth, J., Cazalé, A., Romeis, T.: Calcium-dependent protein kinase CPK21 functions in abiotic stress response in *Arabidopsis thaliana*. - Mol. Plant **4**: 83-96, 2011.

Fu, Z.Q, Dong, X.: Systemic acquired resistance: turning local infection into global defense. - Annu. Rev. Plant Biol. **64**: 839-863, 2013.

Fujita, M., Fujita, Y., Maruyama, K., Seki, M., Hiratsu, K., Ohme-Takagi, M., Tran, L.S., Yamaguchi-Shinozaki, K., Shinozaki, K.: A dehydration-induced NAC protein, RD26, is involved in a novel ABA-dependent stress signaling pathway. - Plant J. **39**: 863-876, 2004.

Gadjev, I., Vanderauwera, S., Gechev, T.S., Laloi, C., Minkov, I.N., Shulaev, V., Apel, K., Inze, D., Mittler, R., Van, B.F.: Transcriptomic footprints disclose specificity of reactive oxygen species signaling in *Arabidopsis*. - Plant Physiol. **141**: 436-445, 2006.

Gao, Q., Ren, Q., Liou, L.C., Bao, X., Zhang, Z.: Mitochondrial DNA protects against salt stress-induced cytochrome *c*-mediated apoptosis in yeast. - FEBS Lett. **585**: 2507-2512, 2011.

Gas, E., Flores-Perez, U., Sauret-Gueto, S., Rodriguez-Concepcion, M.: Hunting for plant nitric oxide synthase provides new evidence of a central role for plastids in nitric oxide metabolism. - Plant Cell **21**: 18-23, 2009.

Giri, J.: Glycine betaine and abiotic stress tolerance in plants. - Plant Signal Behav. **4**: 1746-1751, 2011.

Golldack, D., Li, C., Mohan, H., Probst, N.: Tolerance to drought and salt stress in plants: unraveling the signaling networks. - Front. Plant Sci. **5**: 151, 2014.

Granier, C., Inze, D., Tardieu, F.: Spatial distribution of cell division rate can be deduced from that of p34cdc2 kinase activity in maize leaves grown at contrasting temperatures and soil water conditions. - Plant Physiol. **124**: 1393-1402, 2000.

Grover, A., Sahi, C., Sanan, N., Grover, A.: Taming abiotic stresses in plants through genetic engineering: current strategies and perspective. - Plant Sci. **143**: 101-111, 1999.

Grun, S., Lindermayr, C., Sell, S., Durner, J.: Nitric oxide and gene regulation in plants. - J. exp. Bot. **57**: 507-516, 2006.

Gupta, K.J., Igamberdiev, A.U.: The anoxic plant mitochondrion as a nitrite: NO reductase. - Mitochondrion **11**: 537-543. 2011.

Gupta, K.J., Shah, J.K., Brotman, Y., Jahnke, Y., Willmitzer, L., Kaiser, W.M., Bauwe, H., Igamberdiev, A.U.: Inhibition of aconitase by nitric oxide leads to induction of the alternative oxidase and to a shift of metabolism towards biosynthesis of amino acids. - J. exp. Bot. **63**: 1773-1784, 2012.

Ha, S., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.S.: Cytokinins: metabolism and function in plant adaptation to environmental stresses. - Trends Plant Sci. **17**: 172-179, 2012.

Habib, N., Ashraf, M.: Effect of exogenously applied nitric oxide on water relations and ionic composition of rice (*Oryza sativa* L.) plants under salt stress. - Pak. J. Bot. **46**: 111-116, 2014.

Hamilton, J.P., Buell, C.R.: Advances in plant genome sequencing. - Plant J. **70**: 177-190, 2012.

Hancock, J.T., Neill, S.J., Wilson, I.D.: Nitric oxide and ABA in the control of plant function. - Plant Sci. **181**: 555-559, 2012.

Hasanuzzaman, M., Nahar, K., Alam, M.M., Roychowdhury, F., Fujita, M.: Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. - Int. J. mol. Sci. **14**: 9643-9684, 2013.

Hasegawa, P.M., Bressan, R.A., Zhu, J.K., Bohnert, H.J.: Plant cellular and molecular responses to high salinity. - Ann. Rev. Plant Physiol. Plant mol. Biol. **51**: 463-499, 2000.

He, Y., Tang, R.H., Hao, Y., Stevens, R.D., Cook, C.W., Ahn, S.M., Jing, L., Yang, Z., Chen, L., Guo, F., Fiorani, F., Jackson, R.B., Crawford, N.M., Pei, Z.M.: Nitric oxide represses the *Arabidopsis* floral transition. - Science **305**: 1968-1971, 2004.

Hollington, P.A.: Technological breakthroughs in screening/breeding wheat varieties for salt tolerance. - In: Gupta, S.K., Sharma, S.K., Tyagi, N.K. (Ed.): Proceedings of the National Conference "Salinity Management in Agriculture". Pp. 273-289, Central Soil Salinity Research Institute, Karnal 2000.

Hong, Y., Zhang, H., Huang, L., Li, D., Song, F.: Overexpression of a stress-responsive NAC transcription factor gene *ONAC022* improves drought and salt tolerance in rice. - Front. Plant Sci. in press, 2016.

Hsieh, T.H., Lee, J.T., Yang, P.T., Chiu, L.H., Charng, Y., Wang, Y.C., Chan, M.T.: Heterology expression of the *Arabidopsis* C repeat/ dehydration response element binding factor 1 gene confers elevated tolerance to chilling and oxidative stresses in transgenic tomato. - Plant Physiol. **129**: 1086-1094, 2002.

Hu, H., Dai, M., Yao, J., Xiao, B., Li, X., Zhang, Q., Xiong, L.: Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. - Proc. nat. Acad. Sci. USA **103**: 12987-12992, 2006.

Hu, H., You, J., Fang, Y., Zhu, X., Qi, Z., Xiong, L.: Characterization of a transcription factor gene *SNAC2* conferring cold and salt tolerance in rice. - Plant mol. Biol. **67**: 169-181. 2008.

Huang, G.T., Ma, S.L., Bai, L.P., Zhang, L., Ma, H., Jia, P., Liu, J., Zhong, M., Guo, Z.F.: Signal transduction during cold, salt, and drought stresses in plants. - Mol. Biol. Rep. **39**: 969-987, 2012.

Huang, W., Miao, M., Kud, J., Niu, X., Ouyang, B., Zhang, J., Ye, Z., Kuhl, J.C., Liu, Y., Xiao, F.: SlNAC1, a stress-related transcription factor, is fine-tuned on both the transcriptional and the post-translational level. - New Phytol. **197**: 1214-1224, 2013.

Huda, K.M.K., Banu, M.S.A., Tuteja, R., Tuteja, N.: Global calcium transducer P-type Ca^{2+}-ATPases open new avenues for agriculture by regulating stress signalling. - J. exp. Bot. **64**: 3099-3109, 2013.

Ichimura, K., Mizoguchi, T., Yoshida, R., Yuasa, T., Shinozaki, K.: Various abiotic stresses rapidly activate *Arabidopsis* MAP kinases ATMPK4 and ATMPK6. - Plant J. **24**: 655-665, 2000.

Ichimura, K.: Mitogen-activated protein k inase cascades in plants, a new nomenclature. - Trends Plant Sci. **7**: 301-308, 2002.

Igamberdiev, A.U., Hill, R.D.: Nitrate, NO and haemoglobin in plant adaptation to hypoxia: an alternative to classic fermentation pathways. - J. exp. Bot. **55**: 2473-2482, 2004.

Ito, Y., Katsura, K., Maruyama, K., Taji, T., Kobayashi, M., Seki, M., Shinozaki, K., Yamaguchi-Shinozaki, K.: Functional analysis of rice REB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. - Plant Cell Physiol. **47**: 141-153, 2006.

Jasid, S., Simontacchi, M., Bartoli, C.G., Puntarulo, S.: Chloroplasts as a nitric oxide cellular source. Effect of reactive nitrogen species on chloroplastic lipids and proteins. - Plant Physiol. **142**: 1246-1255, 2006.

Jeong, M.J., Lee, S.K., Kim, B.G., Kwon, T.R., Cho, W.S., Park, Y.T., Lee, J.O., Kwon, H.B., Byun, M.O., Park, S.C.: A rice (*Oryza sativa* L.) MAP kinase gene, *OsMAPK44*, is involved in response to abiotic stresses. - Plant Cell Tissue Organ Cult. **85**: 151-160, 2006.

Jewell, M.C., Campbell, B.C., Godwin, I.D.: Transgenic plants for abiotic stress resistance. - In: Kole, C., Michler, C.H., Abbott, A.G., Hall, T.C. (ed.): Transgenic Crop Plants. Pp. 67-132. Springer, Heidelberg 2010.

Jiang, S., Zhang, D., Wang, L., Pan, J., Liu, Y., Kong, X., Zhou, Y., Li, D.: A maize calcium-dependent protein kinase gene, *ZmCPK4*, positively regulated abscisic acid signaling and enhanced drought stress tolerance in transgenic *Arabidopsis*. - Plant Physiol. Biochem. **71:** 112-120, 2013.

Jiang, X., Zhang, C., Lu, P., Jiang, G., Liu, X., Dai, F., Gao, J.: RhNAC3, a stress-associated NAC transcription factor, has a role in dehydration tolerance through regulating osmotic stress-related genes in rose petals. - Plant Biotechnol. J. **12**: 38-48, 2014.

Jin, H., Martin, C.: Multifunctionality and diversity within the plant MYB-gene family. - Plant mol. Biol. **41**: 577-585, 1999.

Jogaiah, S., Govind, S.R., Tran, L.S.: Systems biology-based approaches toward understanding drought tolerance in food crops. - Crit. Rev. Biotechnol. **33**: 23-39, 2013.

John, R., Anjum, N.A., Sopory, S.K., Akram, N.A., Ashraf, M.: Some key physiological and molecular processes for cold acclimation: an overview. - Biol. Plant. **60**: 603-618, 2016.

Johnson, J.W., Box, J.E., Manandhar, J.B., Ramseur, E.L., Cunfer, B.M.: Breeding for Rooting Potential under Stress Conditions. - Colloques de l'INRA, France 1991.

Johnson, N.: Genetic engineering vs. Natural breeding: What's the difference? http://grist.org/food/genetic-engineering-vs-natural-breeding-whats-the-difference/, 2013.

Jung, C., Seo, J.S., Han, S.W., Koo, Y.J., Kim, C.H., Song, S.I.K., Nahm, B.H., Do Choi, Y., Cheong, J.J.: Over-expression of *AtMYB44* enhances stomatal closure to confer abiotic stress tolerance in transgenic *Arabidopsis*. - Plant Physiol. **146**: 623-635, 2008.

Katiyar, A., Smita, S., Lenka, S.K., Rajwanshi, R., Chinnusamy, V., Bansal, K.C.: Genome-wide classification and expression analysis of MYB transcription factor families in rice and *Arabidopsis*. - BMC Genomics **13**: 544, 2012.

Kaur, N., Gupta, A.K.: Signal transduction pathways under abiotic stresses in plants. - Curr. Sci. **88**: 1771-1780, 2005.

Keita, K., Takeru, O., Yuichi, U.: Functional characterization and expression profiling of a DREB2-type gene from lettuce (*Lactuca sativa* L.). - Plant Cell Tissue Organ Cult. **116**: 97-109, 2014.

Kim, J.H., Nguyen, N.H., Jeong, C.Y., Nguyen, N.T., Hong, S.W., Lee, H.: Loss of the R2R3 MYB, AtMyb73, causes hyper-induction of the *SOS1* and *SOS3* genes in response to high salinity in *Arabidopsis*. - J. Plant Physiol. **170**: 1461-1465, 2013.

Kline, K.G., Sussman, M.R, Jones, A.M.: Abscisic acid receptors. - Plant Physiol. **154**: 479-482 2010.

Knight, H., Brandt, S., Knight M.R.: A history of stress alters drought calcium signalling pathways in *Arabidopsis*. - Plant J. **16**: 681-687, 1998.

Knight, H., Veale, E.L., Warren, G.J., Knight, M.R.: The *sfr6* mutation in *Arabidopsis* suppresses low temperature induction of genes dependent on the CRT/DRE sequence motif. - Plant Cell **11**: 875-1886, 1999.

Knight, M.R., Campbell, A.K., Smith, S.M., Trewavas, A.J.: Transgenic aequorin reports the effects of touch and cold shock and elicitors on cytosolic calcium. - Nature **352**: 524-526, 1991.

Kong, X., Pan, J., Zhang, M., Xing, X., Zhou, Y., Liu, Y., Liu, Y., Li, D., Li, D.: ZmMKK4, a novel group C mitogen-activated protein kinase kinase in maize (*Zea mays*), confers salt and cold tolerance in transgenic *Arabidopsis*. - Plant Cell Environ. **34**: 1291-1303, 2011.

Kosova, K., Vitamvas, P., Prasil, I.T., Renaut, J.: Plant proteome changes under abiotic stress-contribution of proteomics studies to understanding plant stress response. - J. Proteomics **7**: 1301-1322, 2011.

Kovtun, Y., Chiu, W.L, Tena, G., Sheen, J.: Functional analysis of oxidative stress activated mitogen-activated protein kinase cascade in plants. - Proc. nat. Acad. Sci. USA **97**: 2940-2945, 2000.

Ku, H.M., Vision, T., Liu, J., Tanksley, S.D.: Comparing sequenced segments of the tomato and *Arabidopsis* genomes: large-scale duplication followed by selective gene loss creates a network of synteny. - Proc. nat. Acad. Sci. USA **97**: 9121-9126, 2000.

Kyriakis, J.M., Avruch, J.: Sounding the alarm: protein kinase cascades activated by stress and inflammation. - J. biol. Chem. **271**: 24313-24316, 1996.

Latini, A., Rasi, C., Sperandei, M., Cantale, C., Iannetta, M., Dettori, M., Amar, K., Galeffi, P.: Identification of a DREB-related gene in *Triticum durum* and its expression under water stress conditions. - Ann. appl. Biol. **150**: 187-195, 2007.

Leshem, Y.Y., Haramaty, E.: The characterization and contrasting effects of the nitric oxide free radical in vegetative stress and senescence of *Pisum sativum* Linn. foliage. - J. Plant Physiol. **148**: 258-263, 1996.

Li, X., Zhang, D., Li, H., Wang, Y., Zhang, Y., Wood, A.J.: EsDREB2B, a novel truncated DREB2-type transcription factor in the desert legume *Eremosparton songoricum*, enhances tolerance to multiple abiotic stresses in yeast and transgenic tobacco. - BMC Plant Biol. **14**: 44, 2014.

Lindermayr, C., Sell, S., Muller, B., Leister, D., Durner, J.: Redox regulation of the NPR1-TGA1 system of *Arabidopsis thaliana* by nitric oxide. - Plant Cell **22**: 2894-2907, 2010.

Lippold, F., Sanchez, D.H., Musialak, M.,Schlereth, A., Scheible, W.R., Hincha, D.K., Udvardi, M.K.: AtMyb41 regulates transcriptional and metabolic responses to osmotic stress in *Arabidopsis*. - Plant Physiol. **149**: 1761-1772, 2009.

Liu, J., Zhu, K.: A calcium sensor homolog required for plant salt tolerance. - Science **280**: 1943-1945, 1998.

Liu, Q., Kasuga, M., Sakuma, Y., Abe, H., Miura, S., Yamaguchi-Shinozaki, K., Shinozaki, K.: Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought and low temperature responsive gene expression, respectively, in *Arabidopsis*. - Plant Cell **10**: 1391-1406, 1998.

Liu, W.Z., Kong, D.D., Gu, X.X., Gao, H.B., Wang, J.Z., Xia, M., Gao, Q., Tian, L.L., Xu, Z.H., Bao, F., Hu, Y., Ye, N.S., Pei, Z.M., He, Y.K.: Cytokinins can act as suppressors of nitric oxide in *Arabidopsis*. - Proc. nat. Acad. Sci. USA. **110**: 1548-1553, 2013.

Lucca, P., Hurrell, R., Potrykus, I.: Genetic engineering approaches to improve the bioavailability and the level of iron in rice grains. - Theor. appl. Genet. **102**: 392-397, 2001.

Ma, N.N., Zuo, Y.Q., Liang, X.Q., Yin, B., Wang, G.D., Meng, Q.W.: The multiple stress-responsive transcription factor SlNAC1 improves the chilling tolerance of tomato. - Physiol. Plant. **149**: 474-486, 2013.

Ma, Q., Dai, X., Xu, Y., Guo, J., Liu, Y., Chen, N. et al.: Enhanced tolerance to chilling stress in *OsMYB3R-2* transgenic rice is mediated by alteration in cell cycle and ectopic expression of stress genes. - Plant Physiol. **150**: 244-256, 2009.

Ma, N., Feng, H., Meng, X., Li, D., Yang, D., Wu, C., Meng, Q.: Overexpression of tomato *SlNAC1* transcription factor alters fruit pigmentation and softening. - BMC Plant Biol. **14**: 351, 2014.

Mandal, M.K., Chandra-Shekara, A.C., Jeong, R.D., Yu, K., Zhu, S., Chanda, B., Navarre, D., Kachroo, A., Kachroo, P.: Oleic acid-dependent modulation of nitric oxide associated protein levels regulates nitric oxide-mediated defense signaling in Arabidopsis. - Plant Cell **24**: 1654-1674, 2012.

Manzoor, H., Chiltz, A., Madani, S., Vatsa, P., Schoefs, B., Pugin, A., Garcia-Brugger, A.: Calcium signatures and signaling in cytosol and organelles of tobacco cells induced by plant defense elicitors. - Cell Calcium **51**: 434-444, 2012.

Martinez-Ballesta, M.C., Carvajal, M.: New challenges in plant aquaporin biotechnology. - Plant Sci. **217**: 71-77, 2014.

May, M.J, Vernoux, T., Leaver, C., Van Montagu, M., Inze, D.: Glutathione homeostasis in plants: implications for environmental sensing and plant development. - J. exp. Bot. **49**: 649-667, 1998.

Michael, T.P., Jackson, S.: The first 50 plant genomes. - Plant Genome **6**: 10.3835, 2013.

Mikolajczyk, M., Awotunde, O.S., Muszynska, G., Klessig, D.F., Dobrowolska, G.: Osmotic stress induces rapid activation of a salicylic acid induced protein kinase and homolog of protein kinase ASK1 in tobacco cells. - Plant Cell **12**: 165-178, 2000.

Mittler, R., Vanderauwera, S., Gollery, G, Breusegem, F.V.: Reactive oxygen gene network of plants. - Trends Plant Sci. *9*: 490-498. 2004.

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G., Tognetti, V.B., Vandepoele, K., Gollery, M., Shulaev, V., Breusegem, F.V.: ROS signaling: the new wave? - Trends Plant Sci. **16**: 300-309, 2011.

Mizoi, J., Shinozaki, K., Yamaguchi-Shinozaki, K.: AP2/ERF family transcription factors in plant abiotic stress responses. - Biochim. biophys. Acta. **1819**: 86-96, 2012.

Mochida, K., Shinozaki, K.: Advances in omics and bioinformatics tools for systems analyses of plant functions. - Plant Cell Physiol. **52**: 2017-2038, 2011.

Moller, I.M., Sweetlove, L.J.: ROS signalling - specificity is required. - Trends Plant Sci. **15**: 370-374, 2010.

Mukhtar, M.S., Nishimura, M.T., Dangl, J.: NPR1 in plant defense: it's not over 'til it's turned over. - Cell **137**: 804-806, 2009.

Nakashima, K., Takasaki, H., Mizoi, J., Shinozaki, K., Yamaguchi-Shinozaki, K.: NAC transcription factors in plant abiotic stress responses. - Biochim. biophys. Acta **1819**: 97-103, 2012.

Nakashima, K., Tran, L.S.P., Nguyen, D.V., Fujita, M., Maruyama, K., Todaka, D., Todaka, D., Ito, Y., Hayashi, N., Shinozaki, K., Yamaguchi-Shinozaki, K.: Functional analysis of a NAC-type transcription factor OsNAC6 involved in abiotic and biotic stress-responsive gene expression in rice. - Plant J. **51**: 617-630, 2007.

Nasreen, S.J., Amudha, J., Pandey, S.S.: Isolation and characterization of soybean DREB 3 transcriptional activator. - J. appl. Biol. Biotechnol. **1**: 9-12, 2013.

Nayak, S.N., Balaji, J., Upadhyaya, H.D., Hash, C.T., Kishor, P.B.K., Chattopadhyay, D., Rodriquez, L.M., Matthew W. Blair, M.W., Baum, M., McNally, K., This, D., Hoisington, D.A., Varshney, R.K.: Isolation and sequence analysis of DREB2A homologues in three cereal and two legume species. - Plant Sci. **177**: 460-467, 2009.

Neill, S., Barros, R., Bright, J., Desikan, R., Hancock, J., Harrison, J., Morris, P., Ribeiro, P., Wilson, I.: Nitric oxide, stomatal closure, and abiotic stress. - J. exp. Bot. **59**: 165-176, 2008.

Nomura, H., Shiina, T.: Calcium signaling in plant endosymbiotic organelles: mechanism and role in physiology. - Mol. Plant **7**: 1094-1104, 2014.

Nuruzzaman, M., Sharoni, A.M., Kikuchi, S.: Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants. - Front. Microbiol. **4**: 1-16, 2013.

Olsen, A.N., Ernst, H.A., Leggio, L.L., Skriver, K.: NAC transcription factors, structurally distinct, functionally diverse. - Trends Plant Sci. **10**: 79-87, 2005.

Osakabe, Y., Osakabe, K., Shinozaki, K., Tran, L.S.: Response of plants to water stress. - Front. Plant Sci. **5**: 86, 2014a.

Osakabe, Y., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.S.: Sensing the environment: key roles of membrane-localized kinases in plant perception and response to abiotic stress. - J. exp. Bot. **64**: 445-458, 2013.

Osakabe, Y., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.S.: ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. - New Phytol. **202**: 35-49, 2014b.

Palmieri, M.C., Sell, S., Huang, X., Scherf, M., Werner, T., Durner, J., Lindermayr, C.: Nitric oxide-responsive genes and promoters in *Arabidopsis thaliana*: a bioinformatics approach. - J. exp. Bot. **59**: 177-186, 2008.

Pandey, R., Muller, A., Napoli, C.A., Selinger, D.A., Pikaard, C.S., Richards, E.J., Bender, J., Mount, D.W., Jorgensen, R.A.: Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. - Nucl. Acids Res. **30**: 5036-5055, 2002.

Pasquali, G., Biricolti, S., Locatelli, F., Baldoni, E., Mattana, M.: *Osmyb4* expression improves adaptive responses to drought and cold stress in transgenic apples. - Plant Cell Rep. **27**: 1677-1686, 2008.

Paulovich, A.G., Toczyski, D.P., Hartwell, L.H.: When checkpoints fail. - Cell **88**: 315-321, 1997.

Paz-Ares, J., Ghosal, D., Wienand, U., Peterson, P.A., Saedler, H.: The regulatory c1 locus of *Zea mays* encodes a protein with homology to myb proto-oncogene products and with structural similarities to transcriptional activators. - EMBO J. **6**: 3553-3558, 1987.

Perez-Clemente, R.M., Vives, V., Zandalinas, S.I., Lopez-Climent, M.F., Munoz, V., Gomez-Cadenas, A.: Biotechnological approaches to study plant responses to stress. - Biomed. Res. Int. **10**: 1155, 2013.

Perez-Massot, E., Banakar, R., Gomez-Galera, S., Zorrilla-Lopez, U., Sanahuja, G., Arjo, G., Miralpeix, B., Vamvaka, E., Farre, G., Rivera, S.M., Dashevskaya, S., Berman, J., Sabalza, M., Yuan, D., Bai. C., Bassie, L., Twyman, R.M., Capell, T., Christou, P., Zhu, C.: The contribution of transgenic plants to better health through improved nutrition: opportunities and constraints. - Genes Nutr. **8**: 29-34, 2013.

Piterkova, J., Luhova, L., Hofman, J., Tureckova, V., Novak, O., Petrivalsky, M., Fellner, M.: Nitric oxide is involved in light-specific responses of tomato during germination under normal and osmotic stress conditions. - Ann. Bot. **110**: 767-776, 2012.

Planchet, E., Gupta, K.J., Sonoda, M., Kaiser, W.M.: Nitric oxide emission from tobacco leaves and cell suspensions: rate limiting factors and evidence for the involvement of mitochondrial electron transport. - Plant J. **41**: 732-743, 2005.

Popova, Y., Thayumanavan, P., Lonati, E., Agrochao, M., Thevelein, J.M.: Transport and signaling through the phosphate-binding site of the yeast Pho84 phosphate transceptor. - Proc. natl Acad. Sci. USA **107**: 2890-2895, 2010.

Qiao, L.X., Ding, X., Wang, H.C., Sui, J.M., Wang, J.S.: Characterization of the β-1,3-glucanase gene in peanut (*Arachis hypogaea* L.) by cloning and genetic transformation. - Genet. mol. Res. **13**: 1893-1904, 2014.

Qin, F., Sakuma, Y., Li, J., Liu, Q., Li, Y.Q., Shinozaki, K., Yamagucgi-Shinozaki, K.: Cloning and functional analysis of a novel DREB1/CBF transcription factor involved in cold-responsive gene expression in *Zea mays* L. - Plant Cell Physiol. **45**: 1042-1052, 2004.

Qin, Y., Zhao, L., Skaggs, M.I., Andreuzza, S., Tsukamoto, T., Panoli, A., Wallace, K.N., Smith, S., Siddiqi, I., Yang, Z., Yadegari, R.: Actin-related protein 6 regulates female meiosis by modulating meiotic gene expression in *Arabidopsis*. - Plant Cell **26**: 1612-1628, 2014.

Rahal, A., Kumar, A., Singh, V., Yadav, B., Tiwari, R., Chakraborty, S., Dhama, K.: Oxidative stress, prooxidants, and antioxidants: the interplay. - Biomed. Res. Int. **76**: 19, 2014.

Ramel, F., Birtic, S., Ginies, C., Soubigou-Taconnat, L., Triantaphylides, C., Havaux, M.: Carotenoid oxidation products are stress signals that mediate gene responses to singlet oxygen in plants. - Proc. nat. Acad. Sci. USA **109**: 5535-5540, 2012.

Ravikumar, G., Manimaran, P., Voleti, S.R., Subrahmanyam, D., Sundaram, R.M., Bansal, K.C., Viraktamath, B.C., Balachandran, S.M.: Stress-inducible expression of AtDREB1A transcription factor greatly improves drought stress tolerance in transgenic indica rice. -Transgenic Res. **23**: 421-439, 2014.

Reddy, V.S., Reddy, A.S.: Proteomics of calcium signaling components in plants. - Phytochemistry **65**: 1745-1776, 2004.

Reichheld, J.P., Vernoux, T., Lardon, F., Van Montagu, M., Inze, D.: Specific checkpoints regulate plant cell cycle progression in response to oxidative stress. - Plant J. **17**: 647-656, 1999.

Reichmann, J.L., Heard, J., Martin, G., Reuber, L., Jiang, C.Z., Keddie, J., Adam, L., Pineda, O., Ratcliffe, O.J., Samaha, R.R., Creelman, R., Pilgrim, M., Broun, P., Zhang, J.Z., Ghandehari, D., Sherman, B.K., Yu, J.L.: *Arabidopsis* transcription factors, genome-wide comparative analysis among eukaryotes. - Science **290**: 2105-2110, 2000.

Rosinski, J.A., Atchley, W.R.: Molecular evolution of the Myb family of transcription factors: evidence for polyphyletic origin. - J. Mol. Evol. **46**: 74-83, 1998.

Rumer, S., Gupta, K.J., Kaiser, W.M.: Oxidation of hydroxylamines to NO by plant cells. - Plant Signal Behav. 4: 853-855, 2009.

Saijo, Y., Hata, S., Kyozuka, J., Shimamoto, K., Izui, K.: Overexpression of single calcium dependent protein kinase confers both cold and salt/drought tolerance on rice plants. - Plant J. **28**: 319-327, 2000.

Sakihama, Y., Nakamura, S., Yamazaki, H.: Nitric oxide production mediated by nitrate reductase in the green alga *Chlamydomonas reinhardtii*: an alternative NO production pathway in photosynthetic organisms. - Plant Cell Physiol. **43**: 290-297, 2002.

Sakuma, Y., Liu, Q., Dubouzet, J.G., Abe, H., Shinozaki, K., Yamaguchi-Shinozaki, K.: DNA-binding specificity of the

ERF/AP2 domain of *Arabidopsis* DREBs, transcription factors involved in dehydration and cold-inducible gene expression. - Biochem. biophys. Res. Commun. **290**: 998-1009, 2002.

Sanchez-Calvo, B., Barroso, J.B., Corpas, F.J.: Hypothesis, nitro-fatty acids play a role in plant metabolism. - Plant Sci. **199-200**: 1-6, 2013.

Sangam, S., Jayasree, D., Reddy, K.J., Chari, P.V.B., Sreenivasulu, N., Kavi Kishor, P.B.: Salt tolerance in plants-transgenic approaches. - J. Plant Biotechnol. **7**: 1-15, 2005.

Sarwat, M., Ahmad, P., Nabi, G., Hu, X.: Ca^{2+} signals: The versatile decoders of environmental cues. - Crit. Rev. Biotechnol. **33**: 97-109, 2013.

Sazegari, S., Niazi, A.: Isolation and molecular characterization of wheat (*Triticum aestivum*) dehydration responsive element binding factor (DREB) isoforms. - Aust. J. Crop Sci. **6**: 1037-1044, 2012.

Schweighofer, A., Hirt, H., Meskiene, I.: Plant PP2C phosphatases: emerging functions in stress signaling. - Trends Plant Sci. **9**: 236-243, 2004.

Shou, H., Bordallo, P., Wang, K.: Expression of the *Nicotiana* protein kinase (NPK1) enhanced drought tolerance in transgenic maize. - J. exp. Bot. **55**: 1013-1019, 2004.

Sreenivasulu, N., Sopory, S.K., Kavi Kishor, P.B.: Deciphering the regulatory mechanisms of abiotic stress tolerance in plants by genomic approaches. - Gene **388**: 1-13, 2007.

Sreenivasulu, N., Varshney, R.K., Kavi Kishor, P.B., Weschke, W.: Tolerance to abiotic stress in cereals: a functional genomics approach. - In: Gupta, P.K., Varshney, R.K. (ed.): Cereal Genomics. Pp. 483-414. Kluwer Academic Publishers, Dordrecht 2004.

Stohr, C., Strube, F., Marx, G., Ullrich, W.R., Rockel, P.: A plasma membrane-bound enzyme of tobacco roots catalyses the formation of nitric oxide from nitrite. - Planta **212**: 835-841, 2001.

Stracke, R., Werber, M., Weisshaar, B.: The *R2R3-MYB* gene family in *Arabidopsis thaliana*. - Curr. Opin. Plant Biol. **4**: 447-456, 2001.

Sun, Y., Li, Y., Hu, X., Yang, Q., Kang, J., Zhang, T.: Molecular cloning and characterization of a novel gene encoding DREB protein from *Buchloe dactyloides* (Nutt.). - J. agr. Sci. **4**: 12-22, 2012.

Suzuki, N., Koussevitzky, S., Mittler, R., Miller, G.: ROS and redox signalling in the response of plants to abiotic stress. - Plant Cell Environ. **35**: 259-270, 2012.

Tada, Y., Spoel, S.H., Pajerowska-Mukhtar, K., Mou, Z., Song, J., Wang, C., Zuo, J., Dong, X.: Plant immunity requires conformational changes of NPR1 *via* S-nitrosylation and thioredoxins. - Science **321**: 952-956, 2008.

Tamminen, I., Makela, P., Heino, P., Palva, E.T.: Ectopic expression of ABI3 gene enhances freezing tolerance in response to abscisic acid and low temperature in *Arabidopsis thaliana*. - Plant J. **25**: 1-8, 2001.

Teige, M., Scheikl, E., Eulgem, T., Doczi, R., Ichimura, K., Shinozaki, K., Dangl, J.L., Hirt, H.: The MKK2 pathway mediates cold and salt stress signaling in *Arabidopsis*. - Mol. Cell **15**: 141-152, 2004.

Thao, N.P., Tran, L.S.: Potentials toward genetic engineering of drought-tolerant soybean. - Crit. Rev. Biotechnol. **32**: 349-362, 2012.

Thomashow, M.F.: Plant cold acclimation, freezing tolerance genes and regulatory mechanisms. - Annu. Rev. Plant Physiol. Plant mol. Biol. **50**: 571-599, 1999.

Tran, L.S., Mochida, K.: Functional genomics of soybean for improvement of productivity in adverse conditions. - Funct. Integr. Genomics **10**: 447-462, 2010.

Tran, L.S., Nakashima, K., Sakuma, Y., Osakabe, Y., Qin, F., Simpson, S.D., Maruyama, K., Fujita, Y., Shinozaki, K., Yamaguchi-Shinozaki, K.: Co-expression of the stress inducible zinc finger homeodomain ZFHD1 and NAC transcription factors enhances expression of the *ERD1* gene in *Arabidopsis*. - Plant J. **49**: 46-63, 2007.

Trewavas, A.J., Malho, R.J.: Signal perception and transduction: the origin of the phenotype. - Plant Cell **9**: 1181-1195, 1997.

Tun, N.N., Santa-Catarina, C., Begum, T., Silveira, V., Handro, W., Floh, E.I., Scherer, G.F.: Polyamines induce rapid biosynthesis of nitric oxide (NO) in *Arabidopsis thaliana* seedlings. - Plant Cell Physiol. **47**: 346-354, 2006.

Tuteja, N., Ahmad, P., Panda, B.B., Tuteja, R.: Genotoxic stress in plants: shedding light on DNA damage, repair and DNA repair helicases. - Mutation Res. **681**: 134-149, 2009.

Tuteja, N., Mahajan, S.: Further characterization of calcineurin B-like protein and its interacting partner CBL-interacting protein kinase from *Pisum sativum*. - Plant Signal Behav. **2**: 358-361, 2007.

Ulm, R., Revenkova, E., Sansebastiano, G.P., Bechtold, N., Paszkowski, J.: Mitogen-activated protein kinase phosphatase is required for genotoxic stress relief in *Arabidopsis*. - Genes Dev. **15**: 699-709, 2001.

Umezawa, T., Fujita, M., Fujita, Y., Yamaguchi-Shinozaki, K., Shinozaki, K.: Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. - Curr. Opin. Plant Biotechnol. **17**: 113-122, 2006.

Urao, T., Katagiri, T., Mizoguchi, T., Yamaguchi-Shinozaki, K., Hayashida, N., Shinozaki, K.: Two genes that encode Ca^{2+} dependent protein kinases are induced by drought and high-salt stresses in *Arabidopsis thaliana*. - Mol. gen. Genet. **244**: 331-340, 1994.

Uzilday, B., Turkan, I., Ozgur, R., Sekmen, A.H.: Strategies of ROS regulation and antioxidant defense during transition from C_3 to C_4 photosynthesis in the genus *Flaveria* under PEG-induced osmotic stress. - J. Plant Physiol. **171**: 65-75, 2014.

Valliyodan, B., Nguyen, H.T.: Understanding regulatory networks and engineering for enhanced drought tolerance in plants. - Curr. Opin. Plant Biotechnol. **9**: 189-195, 2006.

Vannini, C., Campa, M., Iriti, M., Genga, A., Faoro, F., Carravieri, S., Maruyama, K., Fujita, Y., Shinozaki, K., Yamaguchi-Shinozaki, K.: Evaluation of transgenic tomato plants ectopically expressing the rice *Osmyb4* gene. - Plant Sci. **173**: 231-239, 2007.

Varshney, R.K., Mohan, S.M., Gaur, P.M., Gangarao, N.V.P.R., Pandey, M.K., Bohra, A., Sawargaonkar, S.L., Chitikineni, A., Kimurto, P.K., Janila, P., Saxena, K.B., Fikre, A., Sharma, M., Rathore, A., Pratap, A., Tripathi, S., Datta, S., Chaturvedi, S.K., Mallikarjuna, N., Anuradha, G., Babbar, A., Choudhary, A.K., Mhase, M.B., Bharadwaj, C., Mannur, D.M., Harer, P.N., Guo, B., Liang, X., Nadarajan, N., Gowda, C.L.: Achievements and prospects of genomics-assisted breeding in three legume crops of the semi-arid tropics. - Biotechnol. Adv. **31**: 1120-1134, 2013.

Vernoux, T., Wilson, R.C., Seeley, K.A., Reichheld, J.P., Muroy, S., Brown, S., Maughand, S.C., Cobbettd, C.S., Montagua, M.V., Inzea, D., Maya, M.K., Sung, Z.R.: The root meristemless1/cadmium sensitive2 gene defines a glutathione-dependent pathway involved in initiation and maintenance of cell division during postembryonic root development. - Plant Cell **12**: 97-110, 2000.

Villanueva, C., Giulivi, C.: Subcellular and cellular locations of nitric oxide synthase isoforms as determinants of health and disease. - Free Radicals Biol. Med. **49**: 307-316, 2010.

Vinocur, B., Altman, A.: Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. - Curr. Opin. Biotechnol. **16**: 123-132, 2005.

Viswanathan, C., Zhu, J.K.: Molecular perspectives on cross-talk and specificity in abiotic stress signaling in plants. - J. exp. Bot. **55**: 225-236, 2004.

Voytas, D.F., Gao, C.: Precision genome engineering and agriculture: opportunities and regulatory challenges. PLoS Biol. **12**: e1001877, 2014.

Wang, J., Ding, B., Guo, Y., Li, M., Chen, S., Huang, G., Xie, X.: Overexpression of a wheat phospholipase D gene, *TaPLDα*, enhances tolerance to drought and osmotic stress in *Arabidopsis thaliana*. - Planta **240**: 103-115, 2014.

Wang, M., Gu, D., Liu, T., Wang, Z., Guo, X., Hou, W., Bai, Y., Chen, X., Wang, G.: Overexpression of a putative maize calcineurin B-like protein in Arabidopsis confers salt tolerance. - Plant Mol. Biol. **65**: 733-746, 2007.

Wang, Y.M., He, C.F.: Isolation and characterization of a cold-induced DREB gene from *Aloe vera* L. - Plant mol. Biol. Rep. **25**: 121-132, 2007.

Wendel, J.F., Jackson S.A., Meyers, B.C., Wing, R.A.: Evolution of plant genome architecture. - Genome Biol. in press, 2016.

Wimalasekera, R., Tebartz, F., Scherer, G.F.: Polyamines polyamine oxidases and nitric oxide in development, abiotic and biotic stresses. - Plant Sci. **181**: 593-603, 2011.

Wurzinger, B., Mair, A., Pfister, B., Teige, M.: Crosstalk of calcium dependent protein kinase and MAP kinase signaling. - Plant Signal Behav. **6**: 8-12, 2011.

Xiong, L., Yang, Y.: Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid-inducible mitogen-activated protein kinase. - Plant Cell **5**:745-59. 2003.

Xiong, Y.W., Fei, S.Z.: Functional and phylogenetic analysis of a DREB/CBF-like gene in perennial ryegrass (*Lolium perenne* L.). - Planta **224**: 878-888, 2006.

Xu, D.B., Gao, S.Q., Ma, Y.Z., Xu, Z.S., Zhao, C.P., Tang, Y.M., Li, X.Y., Li, L.C., Chen, Y.F., Chen, M.: ABI-like transcription factor gene *TaABL1* from wheat improves multiple abiotic stress tolerances in transgenic plants. Funct. Integr. Genomics **14**: 717-30, 2014.

Xu, J., Li, Y., Wang, Y., Liu, H., Lei, L., Yang, H., Liu, G., Ren, D.: Activation of MAPK kinase 9 induces ethylene and camalexin biosynthesis and enhances sensitivity to salt stress in *Arabidopsis*. - J. biol. Chem. **283**: 26996-26106, 2008.

Xu, Y., Hu, W., Liu, J., Zhang, J., Jia, C., Miao, H., Xu, B., Jin, Z.: A banana aquaporin gene, MaPIP1, is involved in tolerance to drought and salt stresses. - BMC Plant Biol. **14**: 59, 2014.

Xu, Y.Z., Arrieta-Montiel, M.P., Virdi, K.S., De Paula, W.B.M., Widhalm, J.R., Basset, G.J., Davila, J.I., Elthon, T.E., Elowsky, C.G., Sato, S.J., Clemente, T.E., Mackenzie, S.A.: MutS HOMOLOG1 is a nucleoid protein that alters mitochondrial and plastid properties and plant response to high light. - Plant Cell **23**: 3428-3441, 2011.

Yamaguchi-Shinozaki, K., Shinozaki, K.: Organization of cis-acting regulatory elements in osmotic-and cold-stress-responsive promoters. - Trends Plant Sci. **10**: 88-94, 2005.

Yang, K.Y., Liu, Y., Zhang, S.: Activation of a mitogen activated protein kinase pathway is involved in disease resistance in tobacco. - Proc. nat. Acad. Sci. USA **98**: 741-746, 2001.

Yang, Z., Nakabayashi, R., Okazaki, Y., Mori, T., Takamatsu, S., Kitanaka, S., Kikuchi, J., Saito, K.: Toward better annotation in plant metabolomics: isolation and structure elucidation of 36 specialized metabolites from *Oryza sativa* (rice) by using MS/MS and NMR analyses. - Metabolomics **10**: 543-555, 2014.

Yi, M., Weaver, D., Eisner, V., Várnai, P., Hunyady, L., Ma, J., Csordás, G., Hajnóczky, G.: Switch from ER-mitochondrial to SR-mitochondrial calcium coupling during muscle differentiation. - Cell Calcium **52**: 355-365, 2012.

Yoo, J.H., Park, C.Y., Kim, J.C., Heo, W.D., Cheong, M.S., Park, H.C., Kim, M.C., Moon, B.C., Choi, M.S., Kang, Y.H., Lee, J.H.: Direct interaction of a divergent CaM isoform and the transcription factor, MYB2, enhances salt tolerance in *Arabidopsis*. - J. biol. Chem. **280**: 3697-3706, 2005.

Yu, L., Nie, J., Cao, C., Jin, Y., Yan, M., Wang, F., Liu, J., Xiao, Y., Liang, Y., Zhang, W.: Phosphatidic acid mediates salt stress response by regulation of MPK6 in *Arabidopsis thaliana*. - New Phytol. **188**: 762-773, 2010.

Zhang, L., Zhao, G., Xia, C., Jia, J., Liu, X., Kong, X.: A wheat R2R3-MYB gene, *TaMYB30-B*, improves drought stress tolerance in transgenic *Arabidopsis*. - J. exp. Bot. **63**: 5873-5885, 2012.

Zhang, P., Yang, P., Zhang, Z., Han, B., Wang, W., Wang, Y., Cao, Y., Hu, T.: Isolation and characterization of a buffalo grass (*Buchloe dactyloides*) dehydration responsive element binding transcription factor, BdDREB2. - Gene **536**: 123-128, 2014.

Zhang, S., Klessig, D.F.: MAPK cascades in plant defense signaling. - Trends Plant Sci. **6**: 520-527, 2001.

Zhao, J., Fujita, K., Sakai,K.: Reactive oxygen species, nitric oxide, and their interactions play different roles in *Cupressus lusitanica* cell death and phytoalexin biosynthesis. - New Phytol. **175**: 215-229, 2007.

Zhao, K., Shen, X., Yuan, H., Liu, Y., Liao, X, Wang, Q., Liu, L., Li, F., Li, T.: Isolation and characterization of dehydration-responsive element-binding factor 2C (MsDREB2C) from *Malus sieversii* Roem. - Plant Cell Physiol. **54**: 1415-1430, 2013.

Zhu, J.K.: Salt and drought stress signal transduction in plants. - Annu. Rev. Plant Biol. **53**: 247-273, 2002.