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REVIEW

Multifunctional genes: the cross-talk among the regulation networks of abiotic stress responses

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Abstract

Unfavourable environment brings many kinds of stresses to plants. To survive such stresses, efficient resistance is required for the plants. Multifunctional genes enable the cross-talk among the various abiotic stress resistance systems. This paper reviews the action mechanisms of multifunctional genes. These genes can be classified into three groups: genes encoding diverse proteins through mRNA splicing (*e.g. AOX* in rice); genes like *BADH*, *P5CS* and *HAV* that control drought, salinity, osmotic and heat stress resistance; and a gene family, for example *AQP*, controlling transport of many compounds including water and nutrients. These genes participate in signal sensing and transduction, transcriptional regulation and functional gene activation during stress resistance induction. Furthermore, it should be noted that, under abiotic stresses, the regulation cascades are mutually interdependent and there also exists a close correlation between those cascades and normal plant growth and development.

Additional key words: abscisic acid, aquaporins, cuticular wax, detoxification, osmotic adjustment, reactive oxygen species, signal transduction, transcriptional regulation.

Introduction

The increasing deterioration of the world environment has great influence on the plant abiotic stress resistance and has becoming one of the most important causes for crop yield reduction (Bhatnagar-Mathur *et al.* 2008, Mazzucotelli *et al.* 2008). Initially, researchers mainly focused attention on the morphological and physiological traits in plants under stresses (Zhang and Shan 1998, Zhang *et al.* 2007b). For example, plant leaves curl and shrink and wax load increases under water or salt stress (Zhang and Shan 1998). The development of molecular biology, genetic mapping and transgenic techniques opens a new route to understanding the mechanism underlying the above mentioned morphological changes. For example, it was found that osmoregulatory and antioxidant genes play important roles in biotic or abiotic stress resistance (Zhang *et al.* 2002).

Different abiotic stresses such as drought, cold, salinity and heavy metal pollution have similar effects on plants (Mittler 2006, Shen *et al.* 2006, Quresh *et al.* 2007, Shao *et al.* 2007, Zhuang *et al.* 2008). Generally, they cause disruption of osmotic and ionic homeostasis, and damage of proteins and cell membrane structure (Xiong and Zhu

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Abbreviations: ABA - abscisic acid; AOX - alternative oxidase; APX - ascorbate peroxidase; AQP - aquaporins; BADH - betain aldehyde dehydrogenase; CAT - catalase; CDPK - calmodulin binding protein kinase; COR - cold regulated proteins; DREB - dehydration-responsive element binding; EREB - ethylene-responsive element binding; GB - glycine betaine; GR - glutathione reductase; HSP - heat-shock protein; LEA - late-embryogenesis-abundant; MAPK - mitogen-activated protein kinase; NUE - nutrition use efficiency; POX - peroxidase; ROS - reactive oxygen species; SOD - superoxide dismutase; WUE - water use efficiency.

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2002, Vinocur and Altman 2005, Rácz *et al.* 2008). Once these disorders appear, the plants produce stress signals, which can combine to relevant sensors and transduce stress information by protein kinase networks till the activation of functional genes (Xiong and Zhu 2001, Chinnusamy *et al.* 2004, Goodwin and Sutter 2009, Ying *et al.* 2009). Finally, cellular homeostasis, proteins and cell membranes will be rebuilt. In these processes, participation of multifunctional genes enables the cross-talk among the gene regulation networks. As the regulation cascades of various abiotic stresses are mutually interdependent, the plants often show different stress resistance (Cheong *et al.* 2002). Up to now, some genes have been found to be multifunctional genes. For example, *BADH* encodes betain aldehyde dehydrogenase, and it is involved in the biosynthesis of glycine betaine (GB). GB is an amphoteric quaternary amine, acting as a compatible solute in plants. Transgenic plants with *BADH* not only manifested osmoregulation ability but also increased salt and heat tolerance (Moghaieb *et al.* 2000, Kumar *et al.* 2004, Yang *et al.* 2005b, 2008, Wu *et al.* 2008).

For plants growing in increasingly deteriorated environment, studies of the genomics, proteomics, signal transport network, metabolic network, and multifunctional genes are important for the understanding of the stress resistance (Xiong and Zhu 2001, Chinnusamy *et al.* 2004). Although multifunctional genes have been widely studied, as far as we know, the recent research progress has not been reviewed. Therefore, in this review, we propose the definition and classification of multifunctional genes, and summarize the progress from three aspects including signal sensing and transduction, transcription regulation and functional gene activation.

Definition and classification of multifunctional genes

Multifunctional gene is a gene or a gene family that can regulate several kinds of traits and manifest several kinds of functions. According to the published papers, it can be classified into three groups as follows:

The first class are genes that encode diverse proteins through mRNA splicing. For example, *ASY*, a multifunctional gene that may suppress tumor development, produces three protein variants from the cognate mRNAs by alternative splicing (Watari and Yutsudo 2003). Alternative oxidase (*AOX*) gene in soybean manifests different isoforms during cotyledon development, and each of them correlates with the increase of capacity of the alternative pathway (McCabe *et al.* 1998, Ferreira *et al.* 2008). Liu *et al.* (2005) isolated a cDNA clone encoding two novel heat-shock factors *OsHSF6* and *OsHSF12* in rice, and found that *OsHSF6* can regulate the early expression of stress genes in response to heat shock, whereas *OsHSF12* can act as a synergistic factor to regulate the expression of the down-stream genes. The first group of multifunctional genes is mainly found in animals and microorganisms. The other two groups are often observed in plants under abiotic stress conditions.

The second class includes genes like *BADH*, *P5CS* and *HAV* that control drought, salt, osmotic and heat stress resistance. For example, *Apetala* is a multifunctional gene involved in inflorescence, flower, and ovule development regulation in *Arabidopsis* (Byzova *et al.* 1999). *DREB*, a gene encoding transcription factor in plant, can improve the drought, salt and cold tolerance of rice as confirmed by transgenic researches (Ito *et al.* 2006). Similar results were found in *Arabidopsis* (Kasuga *et al.* 1999, Sakuma *et al.* 2006), tobacco (Kasuga *et al.* 2004, Cong *et al.* 2008), wheat (Pellegrineschi *et al.* 2004) and other plants.

The third class are gene families. For example, the genes encoding membrane aquaporins (*AQP*), controlling transport of many compounds including water and nutrients, play an important role in plant abiotic stress resistance, including drought, cold and high salt stress resistance (Jang *et al.* 2004, 2007, Yu *et al.* 2005). In addition, *AQP* can modulate water use efficiency (WUE) and nutrition use efficiency (NUE), and thus play an important role in increasing crop yield under unfavourable conditions (Porcel *et al.* 2006, Jang *et al.* 2007).

Multifunctional genes involved in signal sensing and transduction

Hormones, Ca^{2+}, carbamide, NO, H_2O_2, phospholipase (PL), polyphosphatidylinositol phosphate (PIP_2), inositol triphosphate (IP_3), diacylglycerol (DAG), *etc.* are signals during plant development and stress resistance process (Bhattacharjee 2008, Caeiro *et al.* 2008, Chang *et al.* 2008, Courtois *et al.* 2008, Lopez-Carrion *et al.* 2008, Quan *et al.* 2008). Among them ABA is one of the best researched messengers. Transgenic researches on genes regulating ABA sensitivity, such as *ABA27, HAB1* group, *LLA23*, and *AtMYB44,* indicate that ABA is important in the cold, drought and salt resistance and stomata opening regulation (Kume *et al.* 2005, Larkindale *et al.* 2005, Lin *et al.* 2007, Yang *et al.* 2005a, Saez *et al.* 2006, Jung *et al.* 2008). 9-*cis*-epoxycarotenoid dioxygenase (NCED) is a pivotal enzyme in the biosynthesis of ABA. Over-expression of NCED leads to the accumulation of ABA under stress conditions (Qin *et al.* 1999). For example, in detached leaves, *NCED* mRNA responds rapidly to small reduction in water content (Thompson *et al.* 2000). Transpiration rate in transgenic *Arabidopsis* with *AtNECD3* was reduced and drought resistance improved (Lefebvre *et al.* 2006). Over-expression of *VuNCED* in transgenic creeping bent grass induced accumulation of ABA under drought and NaCl stresses (Aswath *et al.* 2005). Similar results were reported on *EIN2* (a gene related to ABA signalling pathway) (Wang *et al.* 2007c), and *Sp12* and *Sp5* in tomato (Thompson *et al.* 2007).

Sensors can perceive stress signals through the combination reactions of signals (Wang *et al.* 2007c, Luan *et al.* 2002). Genes encoding sensors have been extensively studied (Taylor *et al.* 2005, Hu *et al.* 2006). For example, over-expression of a calcium sensor calcineurin B-like protein 1 (CBL1) in *Arabidopsis*, induces the expression of early stress-responsive transcription factors and stress adaptation genes in non-stressed plants (Albrecht *et al.* 2003, Cheong *et al.* 2003). Calcium dependent protein kinases (*CDPKs*) are unique Ca^{2+} sensors in plants. When *CDPK2* under stress-inducible promoter was over-expressed in barley, the responses of transgenic plants to cold, salt and ABA were different from those of wild plants (Sheen 1996). Besides, transgenic rice with over-expression of *OsCDPK7* exhibited enhanced tolerance to cold, salt and drought (Saijo *et al.* 2000). Transgenic plants with gene encoding other kinds of sensors can also exhibit increased abiotic stress tolerance. These sensors include salt sensor (Shi *et al.* 2002, Qiu *et al.* 2004) and osmosensor (Urao *et al.* 1999, Langridge *et al.* 2006).

Protein kinases participate in the transduction of signals in the whole regulation network (Koornneef and Pieterse 2008, Mohanpuria *et al.* 2008, Pandey *et al.* 2008). Mitogen activated protein kinase (*MAPK*) is generally considered as an important multifunctional gene involved in the cascade consisting of MAPK, MAPKK, MAPKKK The corresponding genes are activated in sequence after plant cells received the signals (Chinnusamy *et al.* 2004, Ren *et al.* 2008). After *MAPK* is activated, it further activates transcription factors in nucleus, or phospholipid-cleaving enzymes in cytoplasm. At least, some kinds of physiological and biochemical reactions are activated to acclimatize the plant to environmental stresses (Cheong *et al.* 2002, Chinnusamy *et al.* 2004, Xu *et al.* 2003, Wu *et al.* 2004, Hu *et al.* 2006,). It should be noted that one environmental stress can activate various kinases, and in turn, a single kinase gene can affect various kinds of stress resistance. For example, when maize was transformed with the tobacco *MAPKKK/NPK1*, an oxidative signal cascade was activated, leading to the improvement of cold, heat, and salt tolerance (Shou *et al.* 2004).

Moreover, these genes can regulate not only stress resistance but also normal development. For example, kinase with extracellular leucine-rich repeats is known for its effects on inflorescence development, leaf pleiotropy. *ERECTA* can affect the resistance to bacterial wilt, or regulate transpiration under water stress through manipulating stomata density, epidermal cell expansion, mesophyll cell proliferation and cell-to-cell contact in *Arabidopsis* (Torii *et al.* 1996, Lease *et al.* 2001, Douglas *et al.* 2002, Godiard *et al.* 2003, Xu *et al.* 2003, Masle *et al.* 2005).

Multifunctional genes involved in regulation of transcription

Regulation of transcription often works through binding of transcription factors (TFs) and *cis*-elements in the upstream of functional genes. There are a lot of TFs and most of them fall into gene families like *AP2/EREBPs* (*APETALA2* and ethylene-responsive element binding proteins), *DREB/CBF* (dehydration-responsive element/C-repeat-binding), *bZIP* (basic-domain leucine zipper), *NAC*, *MYB/MYC*, *Cys2/His2* zinc-finger and *WRKY* (Umezawa *et al.* 2006, Tran *et al.* 2007). TFs are the members of multifunctional gene family (Shen *et al.* 2003, Shao *et al.* 2007). Under both cold and drought stresses, *DREB2*, *bZIP*, *CBFs*, Cys_2/His_2 zinc-finger, *MYB/MYC* and other TFs are induced (Chinnusamy *et al.* 2004, Shinozaki and Yamaguchi-Shinozaki 2007).

Over-expression of TFs can induce stress-responsive gene expression and increase the abiotic stress tolerance (Xiong and Zhu 2001). For example, over-expression of *HRD* gene (an *AP2/ERF*-like TF from *Arabidopsis*) in rice increased leaf biomass, photosynthesis and WUE (Karaba *et al.* 2007). Similarly, over-expression of *OsMYB3R-2*, a rice *R1R2R3 MYB* gene in transgenic *Arabidopsis*, can increase its tolerance to freezing, drought, and salt stresses (Dai *et al.* 2007). WRKY proteins are other important transcription factors responding to drought, cold, heat, hurt and ABA treatments (Ross *et al.* 2007). In our group, eight *TaWRKY* genes (1, 2, 13, 14, 16, 17, 19 and 27) were cloned from wheat, and the level of transcription increased under dehydration and other abiotic stresses but at different levels in different cultivars. Recently, *TaWRKY* genes have been cloned and their functions were studied (Niu *et al.* 2006).

Activation of multifunctional genes

Stress resistance can be achieved through functional gene activation (Xiong and Zhu 2001, Cheong *et al.* 2002, Chinnusamy *et al.* 2004). The induction of genes related to osmotic adjustment, ROS scavenging, chaperone production as well as water and ion transport channels participates in the rebuilding of cellular homeostasis, reestablishing proteins structure and membranes during stresses (Xiong and Zhu 2002, Bhatnagar-Mathur *et al.* 2008). In addition, the genes involved in changes in structure of epidermis can be important for abiotic stress tolerance (Zhang *et al.* 2005b). Only when all these genes are translated normally, the plants survive from unfavourable environmental conditions (Bhatnagar-Mathur *et al.* 2008).

Multifunctional genes involved in osmotic regulation: Proline, betaine, free amino acids, sugars, sugar alcohols, alkaloids, *etc.*, are osmotically active compounds (Sharma and Dietz 2006, Sokhansanj *et al.* 2006). Their physiological functions include keeping cell pressure potential, stabilizing proteins and cell structures and scavenging of reactive oxygen species (Wang *et al.* 2003). The increase of their accumulation is achieved by over-expression of enzymes involved in their biosynthesis or suppression of enzymes causing their degradation (Chen and Murata 2002). Strategies for the genetic manipulation require precise understanding of biosynthetic pathways including up and down regulations of key regulatory enzymes, feedback inhibition, *etc.* (Vendruscolo *et al.* 2007).

Over-expression of pyrroline-5-carboxylate synthetase (*P5CS*) gene results in the overproduction of this enzyme as well as proline accumulation (Zhu *et al.* 1998, Sharma and Dietz 2006). Transgenic rice plants over-expressing *P5CS* showed increased amount of proline and, at least in part, enhanced biomass production under water stress or salinity (Zhu *et al.* 1998, Hong *et al.* 2000, Su and Wu 2004, Sokhansanj *et al.* 2006). Similarly, transgenic soybean with *P5CS* showed improved drought and heat resistance (De Ronde *et al.* 2001, 2004), transgenic tobacco showed improved salt resistance (Parvanova *et al.* 2004a,b) and transgenic wheat showed improved drought resistance (Vendruscolo *et al.* 2007).

Mt1D encodes mannitol-1-phosphate dehydrogenase, which catalyzes the reversible conversion of fructose-6-phosphate to mannitol-1-phosphate and mannitol-1-phosphate is converted to mannitol *via* nonspecific phosphatases. Mannitol exists in numerous plant species, but not in wheat (Abebe *et al.* 2003). Transgenic wheat with *Mt1D* accumulates mannitol from 0.6 to 2.0 mol g^{-1}(f.m.) in the mature leaves and showed drought and salt resistance but some abnormalities (Abebe *et al.* 2003). Furthermore, transgenic *Petunia* expressing *Mt1D* showed improved cold tolerance (Chiang *et al.* 2005) and transgenic loblolly pine (Tang *et al.* 2005) and *Populus tomentosa* (Hu *et al.* 2005) improved salt tolerance.

Glycine betaine (GB) plays an important role in stabilization of oxygen-evolving complex of photosystem 2, Rubisco activity and membrane integrity (Chen and Murata 2002, Sakamoto and Murata 2002, Park *et al.* 2007). *CodA* encoding choline oxidase is an important multifunctional gene regulating the biosynthesis of GB. Transgenic rice over-expressing *CodA* showed better tolerance to salt and cold (Sakamoto and Murata 1998, Mohanty *et al.* 2002), transgenic tobacco showed reduced oxidative damage under freezing stress (Parvanova *et al.* 2004a,b) and transgenic tomato showed improved cold and oxidative stress tolerance (Park *et al.* 2004, 2007).

From the above-mentioned survey, it is obvious that the stress resistance can be improved in transgenic plants with increased accumulation of osmotically active compounds. These compounds can be also exogenously applied and they can affect gene expression. For example, the exogenous trehalose alters the expression of transcription factors and genes related to cell wall modification, nitrogen metabolism, and fatty acid biosynthesis (Bae *et al.* 2005).

Multifunctional genes involved in ROS scavenging: When plants are under stress conditions, reactive oxygen species are produced, which disturb oxidation-reduction balance and might damage proteins, lipids and nucleic acids (Xiong and Zhu 2001, Mittler *et al.* 2006, Shamsi *et al.* 2008, Silva *et al.* 2008). Plants protect themselves by increased activities of antioxidative enzymes, such as ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione reductase (GR) and production of low molecular mass antioxidants (Río *et al.* 2006, Wang *et al.* 2007b, Rana *et al.* 2008, Serrot *et al.* 2008).

When compared with wild type plants, the transgenic ones over-expressing genes encoding ROS-scavenging enzymes had higher cold, drought, and salinity resistance (Chen *et al.* 2005, Tarantino *et al.* 2005, Shen *et al.* 2006, Eltayeb *et al.* 2007, Lee *et al.* 2007). For example, transgenic alfalfa plants over-expressing *SOD* showed tolerance to cold and drought (Samis *et al.* 2002, Rubio *et al.* 2002), similarly, transgenic rice (Badawi *et al.* 2004, Gupta *et al.* 2005), *Arabidopsis* (Wang *et al.* 2004), and cabbage (Tseng *et al.* 2007) to drought and salinity. Transgenic tobacco plants over-expressing *APX*, *GST* (coding glutathione S-transferase) and *GPX* (coding glutathione peroxidase) were studied under oxidative stress induced by herbicides or ozone, and under chilling and salinity (Roxas *et al.* 2000, Kwon *et al.* 2002, Eltayeb *et al.* 2007, Lee *et al.* 2007). It is interesting that a ROS-scavenging genes suppressed in transgenic plant can be activated by abiotic stress (Tarantino *et al.* 2005). For instance, expression of Cu/Zn-*SOD* decreased in the transgenic tobacco under normal conditions and it increased under salt and PEG stresses (Chen *et al.* 2005).

Multifunctional genes involved in the protection of proteins: Multifunctional genes involved in stabilizing the structures of proteins and cell membranes play important roles for abiotic and biotic stress resistance (Cho and Hong 2006). Late embryogenesis abundant (LEA) proteins and molecular chaperones often have conservative sequence and polar amino acids, so they are stable (Fu *et al.* 2007, Jyothsnakumari *et al.* 2009). LEA proteins, molecular chaperones such as HAV1, heat shock proteins (HSP) and cold regulated proteins (COR) are also required during normal development of plants (Manfre *et al.* 2006). Under abiotic stresses, LEA and molecular chaperones are produced in a variety of plant organs to stabilize protein structures, cell membranes and ion homeostasis (Vij and Tyagi 2007).

Transgenic plants over-expressing genes encoding LEA proteins and molecular chaperone can increase the resistance to drought, salt, cold and other stresses (Cho and Hong 2006, Jyothsnakumari *et al.* 2009). For example, *HAV1* gene from barley over-expressed in transgenic rice, led to drought and salt resistance (Xu *et al.* 1996) due to the cell membrane protection and osmotic adjustment (Babu *et al.* 2004, Fu *et al.* 2007). Transgenic wheat and oat over-exressing *HAV1* also showed improved drought and salt stress resistance (Sivamani *et al.* 2000, Maqbool *et al.* 2002, Bahieldin *et al*. 2005, Oraby *et al.* 2005).

Transgenic tobacco with sense *NtHSP70-1* exhibited slower decrease in water content under progressive drought than the wild type or the transgenic anti-sense plants. Moreover, the expression of *CaERD15* (early responsive to dehydration) is considerably reduced in tobacco plants that over-expressed *NtHSP70-1* (Cho and Hong 2006, Vij and Tyagi 2007).

Multifunctional genes coding ion and water transporters: Aquaporins (AQP) are important membrane transporters of water and other small molecules and ions (Hachez *et al.* 2006). Ion channels transport ions more specifically than AQP. Both respond to different abiotic stresses (Galmés *et al.* 2007, Wang *et al.* 2007a). For example, the transcript level of plasma membrane intrinsic protein (*PIP*) gene decreased in olive plants submitted to drought stress (Secchi *et al.* 2007). On the other hand, expression of *TaTPC1* gene (coding Ca^{2+}-channel protein) increased under high salinity, polyethylene glycol, low temperature (4 °C), and ABA treatment (Wang *et al.* 2005). Over-expression of a *Panax ginseng* gene coding AQP alters the salt tolerance, drought tolerance and cold acclimation ability of transgenic *Arabidopsis* (Peng *et al.* 2007). Increased activity of vacuolar Na^+/H^+ antiporter in transgenic rice (Zhao *et al.* 2006), wheat (Xue *et al.* 2004) and cotton (Wu *et al.* 2004) increased their salt tolerance.

Multifunctional genes related to cuticular wax formation: Plant cuticle is the first protective barrier against many biotic and abiotic stresses (Leide *et al.* 2007). It is generally accepted that abiotic stresses induce the expression of genes related to the biosynthesis and accumulation of cuticular wax, which in turn affect the stress resistance (Shepherd and Griffiths 2006). For example, nonspecific lipid-transfer protein (nsLTP) can transport several classes of phospholipids and glycolipids. The expression of *nsLTP* was induced by cold (in barley), drought (in barley and sunflower), and salinity (in tomato) (Salcedo *et al.* 2007). Another case in point is that the transcript level of *Cer6* encoding β-ketoacyl-coenzyme A, an important synthase for cuticular wax production, which is increased in *Arabidopsis* under drought, salinity and ABA treatment (Hooker *et al.* 2002). In transgenic alfalfa or *Arabidopsis* with *Wxp1*, a putative *Medicago truncatula* AP2 domain-containing transcription factor gene, cuticular wax was accumulated and thus drought tolerance was increased (Zhang *et al.* 2005a, 2007a). Transgenic rice plants over-expressing *Shn2* and *Cer6* also showed increase in WUE and drought resistance (Karaba 2007).

In addition, the *Arabidopsis* mutants such as *Cer1* (Aarts *et al.* 1995) and *Cer6* (Hooker *et al.* 2002) were male-sterile. Aharoni (2004) identified an *Arabidopsis* mutant *shn* that displays a brilliant, shiny green leaf surface with increased cuticular wax compared with wild-type plants. In contrast, over-expression of the *Shn* genes increased cuticle permeability, alters leaf and petal epidermal cell structures, trichome number, branching, and the stomatal index. Recently, we focused on the functions of wheat cuticular wax and the relationships between the wax and stresses. We found that the wax content of wheat flag leaf during grain filing has positive correlation to photosynthetic rate, leaf temperature, leaf WUE and the yield (Zhang and Shan 1998, Huang *et al.* 2003). Currently, three complete sequences and some partial sequences of genes related to cuticular wax have been cloned and the expression patterns were analyzed under abiotic stresses. It is found that the genes related to wax biosynthesis can respond to different stresses. However, the reason of expression responses and the relationship between wax components and WUE under different stresses require further studies.

Summary and outlook

When a plant is under unfavourable conditions, ROS can be produced, the ion homeostasis disturbed, and the structures and functions of proteins and cell membranes damaged. Meanwhile, compatible solutes, ROS-scavenging enzymes, LEA proteins, molecular chaperones, and stress regulating factors are induced to rebuild the cell. It is clear that the signalling pathways of abiotic stresses have cross-talk. There is cross-talk among the signalling pathways of individual abiotic stresses and connections with normal metabolism and development (Kosová *et al.* 2008).

Plant abiotic stress resistance is a multidisciplinary area ranging from physiology to molecular biology. Take the drought resistance as an example. It depends on the water absorption, which depends on the root morphological characteristics (length, density, distribution, hair development) and physiological adaptations (osmotic adjustments, hydraulic conductance) (Yadav *et al.* 1997, Dubrovsky *et al.* 1998, Ma *et al.* 2001). On the other hand, water transport can be affected by AQP activity (Jang *et al.* 2004, 2007, Yu *et al.* 2005). No less important is regulation of transpiration by stomata and the relationship between photosynthesis and transpiration (WUE) (Buckley *et al.* 2005, Zhang *et al.* 2007b).

Previously, the research focused on plant abiotic stress resistance has been mainly concentrated on mono-functional genes or the specific function of multifunctional genes. To endow a plant with multiple stress resistance, co-transformation of several genes is possible, however, it is complicated and troublesome to design plasmid and transform plant (Komari *et al.* 1996). Moreover, most transgenic plants are model species such as *Arabidopsis thaliana* and tobacco. Nowadays, the production of transgenic plants in some crops such as rice, wheat, potato, and sugar beet, have gained various degrees of success. Transformation of multifunctional genes to crops might be useful. Some regulating factors, especially TFs, are transformed because the corresponding transgenic plants possess multiple ability of abiotic stress resistance.

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