

Changing Honda and Toyota: Innovative Molecular Paradigms For Drought Tolerance in Rice

Ajay Kohli

Plant Breeding, Genetics, and Biotechnology Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines. Email: a.kohli@cgiar.org

Abstract

With several decades of research on generating drought tolerant crop plants, especially rice, there is still no clear vision on the complexity that underlies this trait. Multiple pathways, networks and genes underlying the plants' response to drought, which are manifested in various physiological aspects, make it extremely difficult to generate rice genotypes that would exhibit drought tolerance in various genetic and environmental backgrounds. This is because of specific rice genotypes suited to various eco-physiological conditions are grown in various habits. While conventional and marker assisted breeding make progress towards generating some products that could serve as stop-gap solutions, it is only through a deeper understanding of the intricate molecular and physiological processes that more robust and stable varieties can be generated to withstand water deficit in multiple genetic and environmental backgrounds. With progress in high-throughput technologies and multidisciplinary methods providing rare insights into morpho-physiological aspects of plants, especially in the case of roots, the stage is set for novel paradigms to view and research for drought tolerant rice. Missing, orphan and under-appreciated links are appearing which must be integrated in our understanding of rice response to drought. Some such novel links have reached a point of leading to useful results. Certain others are being continually refined towards the ultimate goal of growing rice in the future, under limiting water, energy and labor conditions, while overcoming yield barriers and producing sufficient quantities of grains to address global hunger and poverty. This paper provides a cursory view on some approaches – with links to research results in the plant molecular biology laboratory of IRRI – that hold promise for more robust drought tolerance than we have yet seen.

Keywords: Rice, drought, root, nutrient, QTL, protein oligomerization, phytohormone

Introduction

In Japanese language Honda means 'main rice field' and Toyota means 'bountiful rice field'. Rice fields of the future are destined to change not just eco-geographically due to predicted climate-change and socio-economic-change scenarios but also due to technology-change scenarios. The converging of multiple disciplines from engineering and technology streams of knowledge, together with classical physics, chemistry and mathematics to address issues in biology is steadily revolutionizing biology. Such convergence of multidisciplinary tools and techniques to answer biological questions is starting to unravel predicted or unforeseen additional layers of complexity in biological systems. Attempts to underpin biological mechanisms through such an approach by considering the entire system of the biological entity/unit under consideration is generally recognized as 'systems biology'. Through this approach, an integrated understanding of the organism is attempted which is inclusive of several variables at multiple levels ranging from molecular and

cellular level to eco-physiological interaction of the phenotype, genotype and the environment.

In crop biology the main research emphasis at present is on increasing yield of major cereals to combat the present and predicted climate-change and demography-change-mediated problems of hunger and poverty. In 2007, the assessment (IPCC-AR4 2007) of the Intergovernmental Panel on Climate Change (IPCC) concluded that "there is a confidence level >90% that there will be more frequent warm spells, heat waves, and heavy rainfall and a confidence level >66% that there will be an increase in droughts, tropical cyclones, and extreme high tides" (IPCC 2007). Thus, unpredictable strength and frequency of abiotic stresses such as drought, heat, salinity and flooding are estimated to be the biggest factors for crop losses (FTF 2011). Combining that with evidence of land, water and labor shortage in agriculture, the need is to develop climate resilient, ecosystem friendly and natural resource conservative farming systems and crop

varieties. Within this purview the importance of rice as the most important cereal crop is now well accepted. Rice cultivation areas stand to be more severely and adversely affected by climato-demography changes.

The most pressing issue with rice cultivation to the desirable yield levels is the availability of fresh water. There is a large body of research on drought tolerance in crop plants. Research towards this goal has been progressing rapidly and in the last 4 years some long running projects have drawn closer to success in either the release of stress tolerant varieties or advanced agricultural-field testing. Plant breeding approaches, both conventional as well as marker assisted breeding (MAB) have shown some promise. For example, drought tolerant variety of soybean was released using improved nitrogen fixation under drought as a screen (Sinclair et al 2007) and a salt tolerant wheat variety was released in Pakistan after screening advanced filial generations of a cross between a salt tolerant but agronomically inferior genotype and a salt sensitive high yielding genotype (Ashraf 2010). Drought tolerant rice varieties developed at IRRI in collaboration with Central Rainfed and Upland Rice Research Station (CRURRS) in Hazaribagh, India, were also released and are being actively disseminated in India (Singh and Singh 2010). Meanwhile, transgenic approaches utilizing gene and regulatory network discovery through 'omics' technologies have also shown promise. For example, a bacterial cold shock protein (*cspA*) was used through its RNA chaperone activity, to improve drought stress tolerance in maize (Castiglioni et al 2008).

Due to the apparent urgency of the matter, numerous reviews have been published to take stock of research in generating abiotic stress tolerant plants. The reviews targeted a particular stress such as drought, salinity or heat or a particular crop such as rice, wheat, maize or barley to address food security issues under the predicted climate and demography change scenarios. Particular approaches such as conventional breeding, MAB, transgenic or 'omics' have been reviewed for their potential as avenues to generate abiotic stress tolerant plants. Similarly, mechanistic basis of particular genes or networks were reviewed for their role in conferring abiotic stress tolerance in plants. Some attempts at holistic reviews were made to bring the different elements together, suggesting a continuum of biology and agronomy in dealing with crop yield under stress. Such diversity in needs, approaches, opinions and indeed results has led to a preponderance of literature, which can be more confusing than informing. Indeed, this confusion was recently documented by Pinheiro and Chaves (2011) who reviewed 450 research papers on drought-mediated changes in photosynthesis. Under

drought, photosynthesis is affected by decreased intake and diffusion of CO₂ due to stomatal opening modulation by phytohormones. In response to altered carbon intake, the changed leaf sugar status acts as a metabolic signal. In concert with other phytohormones, it inhibits growth, which further alters the carbon:nitrogen ratio. The stress conditions generated by water deficit perception and nutrient and energy imbalances further loop in phytohormones, reactive oxygen species (ROS) and second messengers such as calcium to affect transcriptional regulation of numerous genes. Their meta-analysis indicated that variables on the time and severity of stress and plant species along with the process under investigation, made it difficult to find a general trend in relating molecular responses to the physiological status of the plant.

Due to the surge in research activity since the release of IPCC AR4 in April 2007, the number of reviews retrieved from ISI-WOS on abiotic stress tolerance in plants/crops in the last 4 years was double that in the previous 4 years, which in turn was only 1.2 times higher than the preceding 4 years. Advances in screening and phenotyping approaches for conventional breeding and MAB or those that include agronomy or resource management strategies have been extensively reviewed (Araus et al 2008; Goff 2011; Jena and Mackill 2008; Lefebvre et al 2009; McKenzie et al 2009; Newton et al 2010; Nevo and Chen 2010; Schubert et al 2009; Serraj et al 2009, 2011; Sinclair 2011; Tsonev et al 2009). Additionally, three recent reviews considered the molecular approaches towards abiotic stress tolerance and provided good background information. In the first, gene discovery targets were narrowed down to 3 main approaches that were reviewed, the transcription factors, osmoprotectants and protein post translation modification (Yang et al 2011). Although, much useful through directed focus, it left the need to fill the gap on alternate approaches. In the second drought responsive rice genes were reviewed by Hadiarto and Tran (2011). The third review was near exhaustive in presenting the information on different genes used/studied for abiotic stress tolerance in crops (Amudha and Balasubramani 2011).

The 'omics' facilitated gene discovery platforms have contributed substantially in providing a number of candidate genes closing in on the prospect of transgenic rice fields in future, which is an issue of anxiety in equal measure, to the proponents and opponents of genetically modified products and enabling technologies. Highly informed policy decisions based on rational, non-frenetic debates are the call of time because transgenic technologies can supplement the achievements of conventional or marker assisted breeding. Meanwhile however, drought of different kinds, intensities and

frequencies in all eco-geographies remains the most devastating factor for rice yield. Consequently, generating drought tolerant rice varieties remains one of the most desirable research outputs in crop biology. Bringing systems biology to bear on research towards generating drought tolerant rice is a requisite to expedite this output. This necessitates innovative approaches, novel paradigms and harnessing the multidisciplinary research to understand the complex and variable process of drought tolerance. Some such approaches and paradigms on the horizon are highlighted in this paper.

Large-effect QTLs

QTL mapping for desirable traits has been a major route to marker assisted breeding. However, most QTLs do not hold in different genotypes and under different environmental conditions. One reason for this is that the QTLs identified may be epistatic to another QTL only in a given genotype and under a particular environment. Also, most QTLs have a small effect on the trait and need to be operational in concert with other QTLs for the trait under consideration. In effect then there are a number of QTLs identified for various traits including drought tolerance, but few have been identified down to the gene level to see if the effect of the gene replicates by itself the effect of the QTL. Large effect QTLs may circumvent the QTL breakdown issue. This can be targeted only through rigorous phenotyping protocols. Such protocols have been standardized and adopted at IRRI for drought tolerance (Kumar et al 2008). The important change in phenotyping was to look for yield under drought instead of just monitoring survival of the plant. Drought tolerance and yield are both complex traits. The altered approach led to identification of a number of large-effect QTLs for rice drought tolerance (Venuprasad et al 2012a; 2012b; Ghimire et al 2012; Dixit et al (2012); Vikram et al 2011; Bernier et al 2007), which have been shown to work in different genotypes and under different eco-geographies.

Molecular dissection of one of these QTLs, DTY12.1 in our group led to the identification of multiple candidate genes affecting different traits towards drought tolerance. Earlier studies on the physiological basis of the function of DTY12.1 indicated that grain yield under drought was improved mainly through improvement in root water uptake (7%) under water-limited conditions (Bernier et al 2009). We found six candidate genes in DTY12.1, identified using a novel *in silico* approach (Oane et al 2010). Two of these genes are cellulose synthase, (*CesA10*) and transcription factor *no apical meristem* (NAM). Cellulose synthase was implicated in root hair proliferation as an explanation for the functionality of DTY12.1 (Narciso et al 2010). It was demonstrated that lines having the QTL possessed denser and longer root hair than the lines without the

QTL. *In silico* analysis of the promoter region of *CesA10* showed that its promoter contained a putative NAM/NAC binding site. Interestingly, a NAM gene was also one of the candidate genes. The function of NAC proteins in stress response was implicated in several studies. NACs are found to play a role in various processes such as organ formation (Aida et al 1997), abiotic/biotic stress responses, senescence and hormone signal transduction (Xie, 2000; Seki et al 2002; Oono et al 2003). Abiotic stresses such as heat shock, cold and drought induced expression of these proteins. For instance, over-expression of three different *Arabidopsis* NAC genes (*ANAC019*, *ANAC055* and *ANAC072*) showed upregulation of several stress-inducible genes and showed increased drought tolerance (Rabbani et al 2003; Tran et al 2004). In rice, over-expressing stress-responsive *NAC 1* (NAM, ATAF and CUC)/*OsNAC6/SNAC2* significantly increased drought and salt resistance at the vegetative stage (Hu et al 2006, 2008; Nakashima et al 2007; Zheng et al 2009). *NAC1* was reported to be induced by auxin and mediates auxin signaling which is involved in lateral root production (Malamy and Benfey 1997). An additional candidate gene, an auxin response factor (ARF) implicate a role of this NAM gene through regulating the ARF which in turn may regulate a number of auxin responsive stress inducible genes. An amidohydrolase whose promoter also contains NAM binding sequences was also found in this region. Amidohydrolases have a role in nitrogen metabolism which, as discussed later, is a critical factor under drought conditions for nutrient mobilization. We have shown that transgenic rice over-expressing the DTY12.1 NAM exhibit increased lateral roots. Additionally we were able to show up-regulation of *CesA10*, ARF and amidohydrolase in this transgenic plant, indicating that these genes acted in concert to affect multiple pathways to provide the robust tolerance characterized for DTY12.1. Such an orchestrated response through what may be seen as a local regulatory network of multiple genes that can be fractionated is what makes this particular region a large effect QTL. Fractionation of DTY12.1 was proved by a recombination event retrieved wherein 0.8 Mb of the original 1.2 Mb was recovered. These plants showed a reduced effect of the QTL indicating that absence of some important candidate genes may have caused the reduction in effect.

Fractionation of a large effect QTL in maize was also revealed when the well characterized QTL *teosinte branched1* (*tb1*) was assessed for its role in affecting plant architecture, ear morphology and yield. It was shown that for plant architecture the QTL operated through a single gene at *tb1* locus while for the ear morphology the gene at *tb1* was acting in concert with additional genes (Studer and Doebley 2011).

The innovative paradigm shift to screening for yield under drought has resulted in large and important steps taken towards generating drought tolerant rice and maize material for MAB. A number of such rice QTLs have been tested at IRRI and at multiple sites under different genetic backgrounds and the QTL effect is maintained.

Nutrient uptake and drought tolerance

The nitrogen status of plants under stress is a critical factor in stress tolerance. Under water-deficit conditions, for example, nitrogen content can decline drastically (Gonzalez-Dugo et al 2010). Maintenance of high biological nitrogen fixation under drought was used to select *Glycine max* genotypes, which led to the release of drought-tolerant varieties (Chen et al 2007). However, it is not only the symbiosis-dependent plants that cope better with drought under improved N content, but also the symbiosis-independent plants. For example, in rice, various physiological parameters such as photosynthesis, relative chlorophyll content, water use efficiency, transpiration and overall growth were significantly higher with the application of N during drought than under drought with no N application (Suralta 2010). Similarly, under drought stress applied to barley at three growth stages, tillering, shooting and earing, the negative effect on grain yield could be relatively relieved with N fertilizer application (Krcek et al 2008). Why does increased N help to relieve the effects of drought? Plants under stress tend to maintain the internal nutrient status of the C–N ratio either by modulating the partitioning of nutrients or by nutrient re-mobilization. Vegetative growth may be controlled to limit the tissues that require balanced nutrient status. For example, Norway spruce under drought but with an N source available exhibited less new shoot development than this species under drought, but with no N source available (Rosengren-Brinck and Nihlgard 1995). This suggested preferential allocation of available N to maintain the nutrient status of a limited body of the plant. In rice, reproductive tiller formation may be favored over new leaf development under drought with the limiting N availability. Under progressive drought, an imbalance in the internal nutrient status of aerial parts is more likely to occur before terminal water-deficit per se. This is because the perception of water-deficit initiates hydraulic and hormonal changes that restrict stomatal opening, in turn restricting transpiration pull and carbon dioxide entry, both of which initiate changes in C and N metabolism and assimilation. Hence, under drought, along with setting in motion the physiological and molecular machinery for efficient water uptake and use, the plant's effort is also toward activating mechanisms that ensure efficient nutrient uptake, re-mobilization and use. For nutrient uptake and mobilization by roots the activity of

exuded or internal root proteases may be critical. Proteases in the aerial parts may also be activated for the purpose of leaf N re-mobilization. However, root proteases are likely to play a more important role due to being at the site of N uptake. Our preliminary results demonstrate much higher protease activity in the roots of different rice genotypes under drought than in the shoots (Kohli et al 2012). Uptake of amino acids (AA) by plant roots as additional or alternate source of N through AA transporters is known (Nasholm et al 2009). Interestingly, it was shown by carbon and nitrogen isotope labeling that wheat roots took up AAs in the form of tripeptides in preference to nitrates and single AAs. Uptake of nitrates was inferior to that of ammonium, L-trialanine and even the biologically unutilized D-trialanine (Hill et al 2011).

These results suggest that more efforts should be directed in understanding the real physiological changes under drought. It is possible that by concentrating on water uptake or water use efficiency by plants under drought we have been missing some important nutrient related links to drought tolerance. Indeed severe drought conditions in the field are all about water deficit yet an appreciation of the role of nutrient status during drought may enable generating varieties which address optimal uptake and utilization of both water and nutrients to tide over the difficult period.

Roots to drought tolerance

For obvious reasons root traits have been an active area of research in drought tolerance. Characterization of diversity in root architecture in relation to drought response in rice established an early consensus on looking for long and thick roots. Such deeper root phenotype has been almost standard in rice drought tolerance research and rice varieties such as FR13A, Khao Dawk Mali 105 (KDML 105), Azucena, and Dular are still being used as standard drought resistant genotypes in most experiments.

Over the last few years however, root research is an exemplary area of multidisciplinary approaches being utilized to gain a much better understanding of the changes in root traits under stress, starting from gross architecture changes to real time physiological and molecular changes including hormonal and transport processes. It will not be an exaggeration to say that plant root research today is at the cutting edge utilizing advanced engineering and modeling techniques. The use of non-destructive positron emission tomography (PET), X-ray computed tomography (CT; Garbout et al 2012) and laser ablation tomography (Jonathan Lynch, personal communication) have overcome laborious and destructive root sampling, which limited our vision on root response to different environmental stimuli. PET

imaging systems have been earlier used to look at static water profile in the vicinity or plant roots in the soil (Nakanishi et al 2003). Advanced mathematical, modeling and imaging approaches were recently used to reveal that root gravitropism is affected by lateral movement of auxin in specific cells at particular times through a statolith-mediated tipping mechanism (Band et al 2012). The gene affecting gravitropism towards deeper roots leading to drought tolerance in rice was recently cloned (Yusaku Uga, personal communication) as the *Dro1* gene from a QTL of the same name identified earlier (Uga et al 2011).

It is becoming clear through such approaches that deep roots may not be the only morphological character to look for in the search for an ideal root architecture for drought tolerance in rice. Research at IRRI has shown that drought tolerant genotype has highly branched and increased short lateral roots arising under drought. Interestingly another change of paradigm observation was thinner xylem vessels under drought in the drought tolerant genotype. Such morpho-anatomical observations are redefining or complementing classical wisdom on root architecture necessary for drought tolerance.

Role of phytohormone cross-talk

Role for phytohormones has been elaborated during earlier research on drought tolerance. Although quite intuitive to physiologists, the interplay of phytohormones to affect different traits and phenotypes in response to stress has dawned on the horizons of molecular biologists only recently. Plant responses to the environment through regulation of gene expression and cellular processes come about by phytohormone-mediated signaling processes. Nutrient remobilization and source/sink transitions are also being increasingly realized to be under hormonal control. Abscisic acid (ABA) remains the best studied hormone for plant stress response. However, other hormones such as cytokinins, auxins, gibberellins, brassinosteroids, strigolactones, jasmonic acid, salicylic acid as well as the gaseous hormones, ethylene and nitric oxide (NO) are being studied for their role in abiotic stress response. Hence, manipulation of the phytohormone synthesis and action across the spatio-temporal continuum of the plant life-cycle is an attractive avenue to understand and/or engineer abiotic stress tolerance.

A modification of cytokinin expression, with the critical difference in the use of a stress and maturation-induced promoter in rice, resulted in water stress tolerance to produce higher yield under stress (Peleg et al 2011). Critical regulatory responses of cytokinins under drought and salinity were also highlighted by Nishiyama et al (2011). Peleg et al (2011) particularly

noted the differences in the content of other phytohormones in the cytokinin modulated transgenic rice lines, which suggested interplay between various phytohormones. They then reviewed such synergistic or antagonistic interactions between phytohormones and highlighted the interactions between auxins, ethylene and cytokinins and similar interactions between gibberellins and brassinosteroids, and gibberellins and salicylic acid (Peleg and Blumwald 2011). The fact that different hormones affect the same trait for example, stomatal opening, in a similar or opposite manner was also highlighted. Similarly, the effects of three different phytohormones auxin, ABA and cytokinins on the single trait of nitrogen acquisition were integrated in a recent review (Kiba et al 2011). Nitrogen acquisition and remobilization is an important trait to be considered in abiotic stress tolerance (Kohli et al 2012). Crosstalk at the hormonal as well as at the transcriptional, metabolomic and signaling level was highlighted in the *superroot2* (*SUR2*) auxin overproducing mutant (Morant et al 2010), which revealed complex interactions between positively and negatively acting transcription factors, while similar processes were shown earlier to be regulated by different hormones through mostly non-overlapping transcriptional responses (Nemhauser et al 2006).

Research on the role of ABA in abiotic stress, along with that in other plant processes, has recently received a boost due to the latest seminal discoveries. Impact of the identification of ABA receptors and its concomitant signaling pathway reinforcement and the discovery of ABA transport in tissues was recently reviewed in the context of opportunities for generating stress tolerant (Joshi-Saha et al 2011) and high yielding crops (Umezawa et al 2011). The discovery of the ABA receptors, their homology to the START domain proteins and comparison to other hormone:receptor combinations as well as additional putative ABA receptors have also been reviewed (Klingler et al 2010). Nearly 10% of the protein-coding genes are regulated by ABA, much more than by other plant hormones. One of the ABA regulated transcription factor (TF) in rice, ABI5-Like1 (ABL1), a basic region/leucine zipper motif TF is induced by salinity, drought, and osmotic pressure and by auxin. It binds ABA-responsive elements (ABREs; G-box) and transcriptionally activates a number of stress response genes including some ABRE-containing containing genes related to auxin metabolism thus providing another example of hormonal crosstalk (Yang et al 2011). ABA cross-talk with gibberellic acid (GA) orchestrated by DELLAs proteins for seedling development under salinity was demonstrated (Yuan et al 2011; Hirano et al 2008). Such cross talk between ABA and brassinosteroids was also reported, whereby the interaction was not based on

modification of similar traits through independent or parallel pathways but was due to the primary signaling outputs of the brassinosteroids that were modified by ABA (Zhang et al 2009). Similarly, the position of NO in relation to ABA in regulating *Arabidopsis* stomatal opening was recently clarified (Dubovskaya et al 2011) and the interaction of NO with auxins during heavy metal stress was also documented (Xu et al 2010, 2011a). NO is becoming a highly important phytohormone because a number of physiological processes are affected by NO (Siddiqui et al 2011). Affects of external application of sodium nitrosopruside, an NO donor, on alleviating different abiotic stresses on different plants were recently reviewed (Siddiqui et al 2011). The cellular sources of NO however, are still not perfectly clear. Equally, there is a gap in our understanding of how NO signaling works in terms of gene targets etc. and how the signal is translated into a physiological response. A recent review summarized the state-of-the-art in the role and mechanism of NO-mediated stress tolerance (Baudouin 2011). Importantly, apart from its interaction with ABA and brassinosteroids, NO interacts with other phytohormones. Regulation of iron acquisition genes implicates its interaction with ethylene (Garcia-Marquez et al 2011). In tomato, acclimation to high salinity involves cross-talk between NO and SA (salicylic acid) (Gemes et al 2011).

The role of cross-talk between auxins and ethylene for root development and architecture – much relevant to tolerance of drought, salinity, flooding or nutrient stress tolerance - is an increasingly researched area (Benkova and Hejatko 2009). For example, *Arabidopsis* root architecture response under low boron supply is mediated by auxin and ethylene (Martin-Rejano et al 2011). A negative role for ethylene in lateral root formation and a positive role in adventitious root formation through modulation of auxin transport was proposed (Negi et al 2010). However, the complex interactions between auxin and ethylene in terms of promoting or inhibiting lateral root growth were investigated in *Arabidopsis* to reveal that there were differences in how these hormones affected development of new lateral root primordia or development of existing lateral root primordia (Ivanchenko et al 2008) or root cell elongation (Strader et al 2010). Lateral root growth could also be dramatically increased by treating a transgenic *Arabidopsis* line overexpressing cytokinin oxidase/dehydrogenase with brassinolide, indicating alternate hormonal routes to similar morphologies (Vercruyssen et al 2011). This concept was illustrated in a review (Potters et al 2009) which brought together literature on stress induced morphogenic responses (SIMR) whereby similar morphological changes were

mediated by gradients of auxin and ethylene along with those of ROS and antioxidants under different stresses. Potters et al (2009) speculated that similar morphologies may not result just from conserved pathways but from conserved final metabolic state needed to achieve growth and development in the same direction even through alternate pathways. For example, it was shown that hormonal pathways of auxin and strigolactone, a new plant hormone, converge for regulation of root hair elongation and ethylene has an epistatic role to strigolactones (Kapulnik et al 2011). Yet, genetic details of root hair development revealed increased root hair under elevated CO₂ through auxin signaling and transport mechanisms affected by ethylene (Niu et al 2011).

Apart from classic plant hormones, the plant growth-regulating factors such as jasmonates, strigolactones, salicylates, triacontanol, polyamines, ascorbic acid, and tocopherols also play important roles in abiotic stress tolerance. The first three are seen to have more broad application although the latter three have also been implicated in processes regulating abiotic stress response (Alcazar et al 2010; Gill and Tuteja 2010). Triacontanol is a fatty alcohol also known as myricil alcohol. It is a relatively lesser known growth factor but was recently implicated in affecting stem morphology in a contrasting way to salinity treatments (Cavusoglu et al 2008) and it was effective in preventing damaging effects of drought on membrane leakage (Rajasekaran and Blake 1999).

It is obvious that our molecular understanding of phytohormone cross-talk under normal or stress conditions is in its infancy. Previous research concentrating on cause and/or effect of a single hormone under drought clearly justifies the importance of understanding the cross-talk patterns to better appreciate effects such as SIMR, which may hold the key to underpinning the complexity of drought response in rice and in other plants. Substantial progress in hormone metabolite analysis, which is still not possible at a high-throughput level, is urgently required. Hormones can be supplied externally and hence hold an important key to the solution, if our understanding of their in vivo levels and interactions is advanced.

Checking an overkill plant stress response

A stress induced Ca²⁺ binding protein, caleosin (AtCLO4) expressed in stomatal guard cells was shown to be a negative regulator of ABA responses in *Arabidopsis* (Kim et al 2011). The AtCLO4 overexpression lines were more tolerant to abiotic stresses but more importantly, when these were supplied with exogenous ABA they became susceptible to the stresses and key ABA-dependent regulatory genes, such

as *ABF3* and *ABF4* were down-regulated. This result makes it particularly interesting to hypothesize that *AtCLO4* may be needed to keep the ABA-mediated stress response under check from over-reacting to completely close the stomata and stop growth. This is similar to two latest reports suggesting that as a drought stress response plants may indeed stop growth and nutrient acquisition processes more than necessary, when water availability was still not an issue (Skirycz et al 2011a and b).

An important role was outlined for ABA in reproductive stage drought tolerance through looking at ABA content and homeostasis in the anthers. The tolerant wheat variety expressed an ABA catabolic enzyme sooner than the susceptible variety to decrease the early drought response accumulation of ABA in the anthers. Persistence of ABA may lead to pollen abortion through the repression of cell wall invertases needed to maintain sink strength. Transgenic rice expressing the wheat catabolic gene - ABA 8'-hydroxylase under the tapetum-specific promoter exhibited increased cold tolerance (Ji et al 2011). Additional ABA biosynthesis genes, ABA regulated genes and genes regulating ABA action used in different plants to understand or engineer abiotic stress tolerance are reviewed by Amudha and Balasubramanian (2011).

Preliminary results with silencing of a ROS scavenging enzyme gene in our laboratory also indicate the need to control an over-reaction of plant stress response pathways. Not surprisingly, silencing the gene with a constitutive promoter was not as effective in leading to an extended stay-green effect under drought as silencing it with its endogenous promoter which contained dehydration response motifs. This result suggested that silencing the gene only under drought conditions may be useful in checking an over-kill response, thus preventing the plant from setting in motion an unnecessarily strong response to, for example, closing the stomata.

High-throughput omics platform technologies can be used to compare transcript, protein and/or metabolite between tolerant and susceptible varieties to underpin factors that contribute to over-reaction. These factors can then be manipulated to engineer drought tolerance.

Conclusions

Through the use of multidisciplinary approach to research for drought tolerant rice a number of new avenues have arisen which complement or change certain paradigms and allow deeper understanding of the processes underlying drought response in rice. An integrated approach facilitated by such an understanding will allow stable genotypes with drought tolerance.

REFERENCES

- Aidar M, Ishida T, Fukaki H, Fujisawa H and Tasaka M.** 1997. Genes involved in organ separation in *Arabidopsis*: an analysis of the cup-shaped cotyledon mutant. *Plant Cell* 9(6): 841-57.
- Alcazar R, Altabella T, Marco F, Bortolotti C, Reymond M, Koncz C, Carrasco P and Tiburcio AF.** 2010. Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. *Planta* 231:1237-1249.
- Amudha J and Balasubramani G.** 2011. Recent molecular advances to combat abiotic stress tolerance in crop plants. *Biotechnol Mol Biol Rev* 6:31-58.
- Araus JL, Slafer GA, Royo C and Serret M.** 2008. Breeding for yield potential and stress adaptation in cereals. *Crit Rev Plant Sci* 27:377-412.
- Ashraf M.** 2010. Registration of 'S-24' Spring wheat with improved salt tolerance. *J Plant Regist* 4:34-37.
- Band LR, Wells DM, Larrieu A, Sun J, Middleton AM, French AP, Brunou G et al.** 2012. Root gravitropism is regulated by a transient lateral auxin gradient controlled by a tipping-point mechanism. www.pnas.org/lookup/suppl/doi:10.1073/pnas.1201498109/-/DCSupplemental.
- Baudouin E.** 2011. The language of nitric oxide signalling. *Plant Biology* 13:233-242.
- Benkova E and Hejatko J.** 2009. Hormone interactions at the root apical meristem. *Plant Mol Biol* 69:383-396.
- Bernier J, Kumar A, Venuprasad R, Spaner D and Atlin GN.** 2007. A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Sci* 47:507-516.
- Bernier, J, Serraj R, Kumar A, Venuprasad R, Impa S, Rp V, Oane R, Spaner D and Atlin GN.** 2009. The large-effect drought-resistance QTL *qt112.1* increases water uptake in upland rice. *Field Crops Res* 110(2): 139-146.
- Castiglioni P, Warner D, Bensen RJ, Anstrom DC, Harrison J, Stoecker M, Abad M, Kumar G, Salvador S, D'ordine R, Navarro S, Back S, Fernandes M, Targolli J, Dasgupta S, Bonin C, Luethy MH and Heard JE.** 2008. Bacterial RNA chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions. *Plant Physiol* 147:446-455.
- Cavusoglu K, Kilic S and Kabar K.** 2008. Effects of some plant growth regulators on stem anatomy of radish seedlings grown under saline (NaCl) conditions. *Plant Soil Environ* 54: 428-433.

- Chen P, Sneller CH, Purcell LC, TR, Sinclair TR, King CA and Ishibashi T.** 2007. Registration of soybean germplasm lines R01-416F and R01-581F for improved yield and nitrogen fixation under drought stress. *J Plant Regist* 1: 167-168.
- Dixit S, Mallikarjuna Swamy BP, Vikram P, Ahmed HU, Sta Cruz MT, Amante M, Atri D, Leung H and Kumar A.** 2012. Fine mapping of QTLs for rice grain yield under drought reveals sub-QTLs conferring a response to variable drought severities. *Theoret Appl Genet* 125, 155-169.
- Dubovskaya, LV, Bakakina, YS, Kolesneva, EV, Sodel, DL, McAinsh, MR, Hetherington, AM and Volotovskii, ID.** 2011. cGMP-dependent ABA-induced stomatal closure in the ABA-insensitive *Arabidopsis* mutant *abi1-1*. *New Phytologist* 191:57-69.
- FTF** 2011. Feed the future: global food security research strategy. *Feed the Future is the U.S. Government's global hunger and food security initiative*. <http://www.feedthefuture.gov/>
- Garbout A, Munkholm LJ, Hansen SB, Petersen BM, Munk OL and Pajor R.** 2012. The use of PET/CT scanning technique for 3D visualization and quantification of real-time soil/plant interactions. *Plant Soil* 352:113-127. <http://dx.doi.org/10.1007/s11104-011-0983-8>
- Garcia MJ, Suarez V, Romera FJ, Alcantara E and Perez-Vicente R.** 2011. A new model involving ethylene, nitric oxide and Fe to explain the regulation of Fe-acquisition genes in strategy I plants. *Plant Physiol Biochem* 49:537-544.
- Gemes K, Poor P, Horvath E, Kolbert Z, Szopko D, Szepesi A and Tari I.** 2011. Cross-talk between salicylic acid and NaCl-generated reactive oxygen species and nitric oxide in tomato during acclimation to high salinity. *Physiol Plant* 142:179-192.
- Ghimire KH, Quiatchon LA, Vikram P, Swamy BPM, Dixit S, Ahmed H, Hernandez JE, Borromeo TH and Kumar A.** 2012. Identification and mapping of a QTL (*qDTY1.1*) with a consistent effect on grain yield under drought. *Field Crops Res* 131: 88-96
- Gill SS and Tuteja N.** 2010. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol Biochem* 48:909-930.
- Goff SA.** 2011. A unifying theory for general multigenic heterosis: energy efficiency, protein metabolism, and implications for molecular breeding. *New Phytologist* 189:923-937.
- Gonzalez-Dugo V, Durand JL and Gastal F.** 2010. Water deficit and nitrogen nutrition of crops. *Agron Sustain Dev* 30: 529-544
- Hadiarto T and Tran L-SP.** 2011. Progress studies of drought-responsive genes in rice. *Plant Cell Reports* 30:297-310.
- Hill PW, Quilliam RS, DeLuca TH, Farrar J, Farrell M, et al.** 2011. Acquisition and assimilation of nitrogen as peptide-bound and D-enantiomers of amino acids by wheat. *PLoS ONE* 6(4): e19220. doi:10.1371/journal.pone.0019220
- Hirano K, Ueguchi-Tanaka M and Matsuoka M.** 2008. GID1-mediated gibberellin signaling in plants. *Trends Plant Sci* 13:192-199.
- Hu, H, You J, Fang Y, Zhu X, Qi Z and Xiong L.** 2008. Characterization of transcription factor gene *SNAC2* conferring cold and salt tolerance in rice. *Plant Mol Biol* 67:169-181.
- Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q and Xiong L.** 2006. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proc Natl Acad Sci* 103(35): 12987.
- IPCC-AR4.** 2007. *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Solomon SD, Qin M, Manning Z, Chen M, Marquis KB, Averyt MT and Miller HL, Cambridge, UK.
- IPCC.** 2007. Summary for Policymakers. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ and Hanson CE. 2007. *Climate Change: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, UK.
- Ivanchenko MG, Muday GK and Dubrovsky JG.** 2008. Ethylene-auxin interactions regulate lateral root initiation and emergence in *Arabidopsis thaliana*. *Plant J* 55:335-347.
- Jena KK and Mackill DJ.** 2008. Molecular markers and their use in marker-assisted selection in rice. *Crop Sci* 48:1266-1276.
- Ji X, Dong B, Shiran B, Talbot MJ, Edlington JE, Hughes T, White RG, Gubler F and Dolferus R.** 2011. Control of abscisic acid catabolism and abscisic acid homeostasis is important for reproductive stage stress tolerance in cereals. *Plant Physiol* 156:647-662.
- Joshi-Saha A, Valon C and Leung J.** 2011. Abscisic acid signal off the STARTing block. *Mole Plant* 4 (2011), pp. 562-580.
- Kapulnik Y, Resnick N, Mayzlish-Gati E, Kaplan Y, Wininger S, Hershenhorn J and Koltai H.** 2011. Strigolactones interact with ethylene and auxin in regulating root-hair elongation in *Arabidopsis*. *J Exp Bot* 62 (8): 2915-2924.

- Kiba T, Kudo T, Kojima M and Sakakibara H.** 2011. Hormonal control of nitrogen acquisition: roles of auxin, abscisic acid, and cytokinin. *J Exp Bot* 62:1399-1409.
- Kim YY, Jung KW, Yoo KS, Jeung JU and Shin JS.** 2011. A Stress-Responsive Caleosin-Like Protein, AtCLO4, Acts as a Negative Regulator of ABA Responses in *Arabidopsis*. *Plant Cell Physiol* 52:874-884.
- Klingler JP, Batelli G and Zhu J-K.** 2010. ABA receptors: the START of a new paradigm in phytohormone signalling. *J Exp Bot* 61:3199-3210.
- Kohli A, Narciso JO, Miro B and Raorane M.** 2012. Root proteases: reinforced links between nitrogen uptake and mobilization and drought tolerance. *Physiol Plant* 145: 165-79.
- Krcek M, Slamka P, Olsovska K, Brestic M and Bencikova M.** 2008. Reduction of drought stress effect in spring barley (*Hordeum vulgare* L) by nitrogen fertilization. *Plant Soil Environ* 54:7-13
- Kumar A, Bernier J, Verulkar S, Lafitte HR and Atlin GN.** 2008. Breeding for drought tolerance: direct selection for yield, response to selection and use of drought-tolerant donors in upland and lowland-adapted populations. *Field Crops Res* 107:221-231.
- Lefebvre V, Kiani SP and Durand-Tardif M.** 2009. A focus on natural variation for abiotic constraints response in the model species *Arabidopsis thaliana*. *Int J Mol Sci* 10:3547-3582.
- Malamy JE and Benfey PN.** 1997. Organization and cell differentiation in lateral roots of *Arabidopsis thaliana*. *Development (Cambridge, England)* 124(1): 33-44.
- Martin-Rejano EM, Camacho-Cristobal JJ, Begona Herrera-Rodriguez M, Rexach J, Teresa Navarro-Gochicoa M and Gonzalez-Fontes A.** 2011. Auxin and ethylene are involved in the responses of root system architecture to low boron supply in *Arabidopsis* seedlings. *Physiol Plant* 142:170-178.
- McKenzie BM, Bengough AG, Hallett PD, Thomas WTB, Forster B and McNico, JW.** 2009. Deep rooting and drought screening of cereal crops: A novel field-based method and its application. *Field Crops Res* 112:165-171.
- Morant M, Ekstrom C, Ulvskov P, Kristensen C, Rudemo M, Olsen CE, Hansen J, Jorgensen K, Jorgensen B, Moller BL and Bak S.** 2010. Metabolomic, transcriptional, hormonal, and signaling cross-talk in *Superroot2*. *Mol Plant* 3:192-211.
- Nakanishi TM, Okuni Y, Furukawa J, Tanoi K, Yokota H, Ikeue N, Matsubayashi K, Uchida H and Tsiji A.** 2003. Water movement in a plant sample by neutron beam analysis as well as positron emission tracer imaging system. *J Radio Anal Nuclear Chem* 255:149-153
- Nakashima K, TranL and Nguyen DV.** 2007. Functional analysis of a NAC-type transcription factor OsNAC6 involved in abiotic and biotic stress-responsive gene expression in rice. *Plant J* 51(4): 617-630.
- Narciso J, Oane RH, Kumar A and Kohli A.** 2010. Cellulose synthase as a major candidate gene in the large effect QTL for rice yield under drought stress. *Philippine J Crop Sci* 35:1.
- Nasholm T, Kielland K and Ganeteg U.** 2009. Uptake of organic nitrogen by plants. *New Phytol* 182: 31-48.
- Negi S, Sukumar P, Liu X, Cohen JD and Muday GK.** 2010. Genetic dissection of the role of ethylene in regulating auxin-dependent lateral and adventitious root formation in tomato. *Plant J* 61:3-15.
- Nemhauser JL, Hong F and Chory J.** 2006. Different plant hormones regulate similar processes through largely nonoverlapping transcriptional responses. *Cell* 126:467-475.
- Nevo E and Chen G.** 2010. Drought and salt tolerances in wild relatives for wheat and barley improvement. *Plant Cell Environ* 33:670-685.
- Newton AC, Akar T, Baresel JP, Bebeli PJ, Bettencourt E, Bladenopoulos KV, Czembor JH, Fasoula DA, Katsiotis A, Koutis K, Koutsika-Sotiriou M, Kovacs G, Larsson H, Pinheiro de Carvalho MAA, Rubiales D, Russell J, Dos Santos TMM and VazPatto MC.** 2010. Cereal landraces for sustainable agriculture. A review. *Agron Sustain Dev* 30:237-269.
- Nishiyama R, Watanabe Y, Fujita Y, Dung Tien L, Kojima M, Werner T, Vankova R, Yamaguchi-Shinozaki K, Shinozaki K, Kakimoto T, Sakakibara H, Schmuelling T and Lam-Son Phan T.** 2011. Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *Plant Cell* 23:2169-2183.
- Niu Y, Jin C, Jin G, Zhou Q, Lin X, Tang C and Zhang Y.** 2011. Auxin modulates the enhanced development of root hairs in *Arabidopsis thaliana* (L) Heynh. under elevated CO₂. *Plant Cell Environ* 34:1304-1317.
- Oane RH, VJ Ulat A Kumar and A Kohli.** 2010. Identification of candidate genes in DTY12.1 region through date mining. *Philippine J Crop Sci* v. 35: 101.

- Oono Y, M Seki, T Nanjo, M Narusaka, M Fujita, R Satoh, M Satou, T Sakurai, J Ishida, K Akiyama, and others.** 2003. Monitoring expression profiles of *Arabidopsis* gene expression during rehydration process after dehydration using ca. 7000 full-length cDNA microarray. *Plant J* 34(6): 868–887.
- Peleg Z and Blumwald E.** 2011. Hormone balance and abiotic stress tolerance in crop plants. *Cur Opin Plant Biol* 14: 290-295.
- Peleg Z, Reguera M, Tumimbang E, Walia H and Blumwald E.** 2011. Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. *Plant Biotechnol J* 9:747-758.
- Pinheiro C and Chaves MM.** 2011. Photosynthesis and drought: can we make metabolic connections from available data? *J Exp Bot* 62:869-882.
- Potters G, Pasternak TP, Guisez Y and Jansen MAK.** 2009. Different stresses, similar morphogenic responses: integrating a plethora of pathways. *Plant Cell Environ* 32:158-169.
- Rabbani MA, K Maruyama, H Abe and MA Khan.** 2003. Monitoring expression profiles of rice genes under cold, drought, and high-salinity stresses and abscisic acid application using cDNA microarray and RNA gel-blot analyses. *Plant Physiol* 133(4): 1755–1767.
- Rajasekaran LR and Blake TJ.** 1999. New plant growth regulators protect photosynthesis and enhance growth under drought of jack pine seedlings. *J Plant Growth Regul* 18:175-181.
- Rosengren-Brinck U and Nihlgard B.** 1995. Effects of nutritional status on the drought resistance in Norway spruce. *Water Air Soil Poll* 85: 1739-1744
- Schubert S, Neubert A, Schierholt A, Suemer A and Zoerb C.** 2009. Development of salt-resistant maize hybrids: The combination of physiological strategies using conventional breeding methods. *Plant Sci* 177:196-202.
- Seki M, Narusaka M, Ishida J and Nanjo T.** 2002. Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high salinity stresses using a full-length cDNA microarray. *Plant J* 31(3): 279-92.
- Serraj R, Kumar A, McNally KL, Slamet-Loedin I, Bruskiewich R, Mauleon R, Cairns J and Hijmans RJ.** 2009. Improvement of drought resistance in rice. *Adva Agron* 103: 41-99
- Serraj R, McNally KL, Slamet-Loedin I, Kohli A, Haefele SM, Atlin G and Kumar A.** 2011. Drought resistance improvement in rice: An integrated genetic and resource management strategy. *Plant Prod Sci* 14:1-14.
- Siddiqui MH, Al-Wahaibi MH and Basalah MO.** 2011. Role of nitric oxide in tolerance of plants to abiotic stress. *Protoplasma* 248:447-455.
- Sinclair TR, Purcell LC, King CA, Sneller CH, Chen P and Vadez V.** 2010. Drought tolerance and yield increase of soybean resulting from improved symbiotic N₂ fixation. *Field Crops Res* 101: 68–71
- Sinclair TR.** 2011. Challenges in breeding for yield increase for drought. *Trends Plant Sci* 16:289-293.
- Sinclair TR, Purcell LC, King CA, Sneller CH, Chen P and Vadez V.** 2007. Drought tolerance and yield increase of soybean resulting from improved symbiotic N-2 fixation. *Field Crops Res* 101:68-71.
- Singh AN and Singh US.** 2010. Targeted dissemination of stresstolerant rice varieties: propagating Swarna-Sub1, Sahbhagi Dhan, and CSR36 in Uttar Pradesh, India *STRASA News*, pp 1-2.
- Skirycz A, Claeys H, De Bodt S, Oikawa A, Shinoda S, Andriankaja M, Maleux K, Eloy NB, Coppens F, Yoo S-D, Saito K and Inze D.** 2011a. Pause-and-stop: The effects of osmotic stress on cell proliferation during early leaf development in *Arabidopsis* and a role for ethylene signaling in cell cycle arrest. *Plant Cell* 23:1876-1888.
- Skirycz A, Vandenbroucke K, Clauw P, Maleux K, De Meyer B, Dhondt S, Pucci A, Gonzalez N, Hoeberichts F, Tognetti VB, Galbiati M, Tonelli C, Van Breusegem F, Vuylsteke M and Inze D.** 2011b. Survival and growth of *Arabidopsis* plants given limited water are not equal. *Nat Biotech* 29:212-214.
- Strader LC, Chen GL and Bartel B.** 2010. Ethylene directs auxin to control root cell expansion. *Plant J* 64:874-884.
- Studer AJ and Doebley JF.** 2011. Do large effect QTL fractionate? A case study at the maize domestication QTL teosinte branched1. *Genetics* 188:673-81.
- Suralta RR.** 2010. Plastic root system development responses to drought-enhanced nitrogen uptake during progressive soil drying conditions in rice. *Philippine Agric Sci* 93: 458-462
- Tran L, Nakashima K, Sakuma Y, Simpson SD, Fujita Y, Maruyama K, Fujita M, Seki M, Shinozaki K and Yamaguchi-Shinozaki K.** 2004. Isolation and Functional analysis of *Arabidopsis* stress-inducible NAC transcription factors that bind to a drought-responsive cis-element in the early responsive to dehydration stress 1 promoter. *Plant Cell* 16:2481-2498.
- Tsonev S, Todorovska E, Avramova V, Kolev S, Abu-Mhadi N and Christov NK.** 2009. Genomics assisted improvement of drought tolerance in maize: qQTL approaches. *Biotechnol Biotech Eq*

- 23:1410-1413.
- Uga Y, Okumo K and Yano M.** 2011. *Dro1*, a major QTL involved in deep rooting of rice under upland field conditions. *J Exp Bot* 62: 2485-2494
- Umezawa T, Hirayama T, Kuromori T and Shinozaki K.** 2011. The regulatory networks of plant responses to abscisic acid. In: *Plant Responses to Drought and Salinity Stress: Developments in a Post-Genomic Era* 57: 201-248.
- Venuprasad R, Bool ME, Quiatchon L and Atlin GN.** 2012a. A QTL for rice grain yield in aerobic environments with large effects in three genetic backgrounds. *Theoret Appl Genet* 124: 323-332
- Venuprasad R, Bool ME, Quiatchon L, Sta Cruz MT, Amante M and Atlin GN.** 2012b. A large-effect QTL for rice grain yield under upland drought stress on chromosome 1. *Mol Breed* 30: 535-547
- Vercruyssen L, Gonzalez N, Werner T, Schmuelling T and Inze D.** 2011. Combining enhanced root and shoot growth reveals cross talk between pathways that control plant organ size in *Arabidopsis*. *Plant Physiol* 155:1339-1352.
- Vikram P, Swamy BPM, Dixit S, Ahmed HU, Sta Cruz MT, Singh AK and Kumar A.** 2011. *qDTY1.1*, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. *BMC Genet* 2011, 12:89 doi:10.1186/1471-2156-12-89
- Xie Q.** 2000. *Arabidopsis* NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. *Genes Dev* 14(23): 3024-3036.
- Xu J, Wang W, Sun J, Zhang Y, Ge Q, Du L, Yin H and Liu X.** 2011. Involvement of auxin and nitric oxide in plant Cd-stress responses. *Plant Soil* 346:107-119.
- Xu J, Wang W, Yin H, Liu X, Sun H and Mi, Q.** 2010. Exogenous nitric oxide improves antioxidative capacity and reduces auxin degradation in roots of *Medicago truncatula* seedlings under cadmium stress. *Plant Soil* 326:321-330.
- Yang X, Yang Y-N, Xue L-J, Zou M-J, Liu J-Y, Chen F and Xue H-W.** 2011. Rice ABI5-Like1 Regulates abscisic acid and auxin responses by affecting the expression of ABRE-containing genes. *Plant Physiol* 156:1397-1409.
- Yuan K, Rashotte AM and Wysocka-Diller JW.** 2011. ABA and GA signaling pathways interact and regulate seed germination and seedling development under salt stress. *Acta Physiol Plant* 33:261-271.
- Zhang S, Cai Z and Wang X.** 2009. The primary signaling outputs of brassinosteroids are regulated by abscisic acid signaling. *Proc Natl Acad Sci USA* 106:4543-4548.
- Zheng X, Chen B, Lu G and Han B.** 2009. Overexpression of a NAC transcription factor enhances rice drought and salt tolerance. *Biochem Biophys Res Co* 379(4): 985-989.
-
- Citation:** Kohli A. 2013. Changing Honda and Toyota: innovative molecular paradigms for drought tolerance in rice. In: Muralidharan K and Siddiq EA, eds. 2013. *International Dialogue on Perception and Prospects of Designer Rice*. Society for Advancement of Rice Research, Directorate of Rice Research, Hyderabad 500030, India, pp 202-212.