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Recent advances in molecular tool development for drought tolerance breeding in cereal crops: a review

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Abstract

Drought stress is one of the major yield constraints for cereal crops. Traditionally, for developing drought tolerant cultivars, selection either direct or indirect is practiced. Although this approach is effective, yet time consuming and labour intensive. Identification of drought related quantitative trait loci (QTLs) coupled with marker assisted selection has shown some positive results. Transgenic and “omics” technologies promise to make progress in breeding for drought tolerance through a more fundamental understanding of underlying mechanisms of drought tolerance and identifying potential candidate genes. These new approaches provide opportunities to direct the continued breeding of genotypes giving stable yields under drought stress.

Key words: drought tolerance, marker assisted selection, omics, quantitative trait loci, transgenics.

Introduction

Cereal crops have been predominantly used as staple food around the globe since the time immemorial. However, our efforts in meeting the food requirements on sustainable basis for ever increasing population are seriously being hampered due to biotic and abiotic stresses. Abiotic factors (like drought, salinity and temperature), are most important accounting for about 70% reductions in yield of our cereal crops (Boyer, 1982). Drought is a major yield limiting factor badly affecting the crop productivity worldwide (Hussain et al., 2011). The simplest definition of drought in the context of agriculture is a situation when the water availability to plant is less than what is required to sustain its growth and development (Deikman et al., 2011). Drought tolerance is the ability of the plant to survive in water limited conditions (Turner, 1979). However, inducing drought tolerance in crop plants is not a simple task rather one of the most difficult challenges currently the breeders face. This is due to its polygenic nature with low heritability and high $G \times E$ interactions (Fleury et al., 2010). This complex nature and also the lack of proper understanding of the underlying mechanisms of drought tolerance explain the slow progress in improving the yield of crops in drought prone environments (Tuberosa, Salvi, 2006; Cattivelli et al., 2008). Plants use different mechanisms to cope with the drought. Like they use the escape strategy through accelerating flowering before the onset of drought season (Deikman et al., 2011), or improve the water use efficiency (WUE) through closing stomata and increasing root development (Gowda et al., 2011) or can also use some tolerance mechanisms such as osmotic adjustment and production of antioxidants (Umezawa et al., 2006), yet there is no unified drought mechanism at the whole plant or gene level (Blum, 2004). This review encompasses an overview on the current work reported in

inducing drought tolerance in cereal crops mainly wheat, rice and maize, highlighting the role of conventional breeding in conjunction with marker assisted selection, transgenic approaches and modern genomic tools.

Conventional breeding for drought tolerance

In the last century, conventional plant breeding, especially the cereal breeding has played a very vital role in tackling the food productivity issues on sustainable level (Araus et al., 2008; Ashraf, 2010). The Green Revolution, occurring between the early 1940s and the late 1970s, was actually based on conventional breeding leading to development of high yielding cereal crops thus saving millions of people from starvation (Rajaram, 2005). The overall plant response to drought stress is quite complex involving the interaction of different component traits (primary and secondary) with the external environment. Most of the drought related cereal breeding programs concentrate on selection strategies of those cultivars that yield well under drought stress. This selection can be either empirical focusing on primary trait selection such as yield or physiological based on secondary parameters (Araus et al., 2008).

The selection based on yield potential has led to development of high yielding cultivars of wheat and maize performing well in drought prone environments (Araus et al., 2002). The role of International Maize and Wheat Improvement Center (CIMMYT), International Rice Research Institute (IRRI) and International Center for Tropical Agriculture (CIAT) has been phenomenal in this regard. Breeders from these institutes selected genotypes yielding in both stress and stress free environments. This resulted in maize yield increase from 59 to 233 kg ha⁻¹

cycle⁻¹ (Bänziger et al., 2004 as reviewed by Ashraf, 2010) and similarly under drought conditions, yield gains were also high (146 kg ha⁻¹ year⁻¹) (Campos et al., 2004). However, the progress through this empirical selection has been slow due to low heritability of yield (Ribaut et al., 1997).

Consequently the yield improvements in drought prone environments can be made through identifying secondary traits involved in drought tolerance. The effectiveness of selection of these secondary traits has been well documented in rice (Manickavelu et al., 2006), wheat (Richards et al., 2000) and in maize (Chapman, Edmeades, 1999). A number of such secondary parameters including anatomical traits (e.g., root characteristics), physiological attributes (e.g., gas exchange, osmotic adjustment), measures of plant water status (e.g., leaf water potential; relative water contents) and cell membrane stability are recognized as important components of drought tolerance in cereals (Jongdee et al., 2002; Toorchi et al., 2003; Steele et al., 2006). The prerequisite requirement for these secondary traits is their high genetic correlation with grain yield, high heritability with low G × E interaction. Secondary traits meeting these criteria will greatly enhance the selection efficiency (Araus et al., 2008). Some of the traits like leaf water potential, senescence (stay green) and osmotic adjustment (OA) have been extensively studied to have strong positive correlation with grain yield (Jongdee et al., 2006; Cattivelli et al., 2008). From the above discussion, it can be inferred that breeders have made excellent

strides by improving the crop phenology making it to sustain drought, even then there is a need to use some of the advanced methods of biotechnology for drought tolerance improvements in our cereal crops.

Mapping quantitative trait loci (QTLs) associated with drought tolerance

Traits which show continuous variation (polygenic) are called quantitative traits while genes behind those traits are simply referred to as QTLs. Mapping is putting genes or QTLs in order indicating relative distances among them assigning them to their linkage groups on the basis of their recombination values (Hussain, 2006). Generally the mapping population is derived from crosses between closely related species differing in the traits in question. There is long standing interest in QTL mapping due to the fact that it will ultimately help us to gain insight into very basic architecture of the trait concerned. Five types of populations are generally employed for QTL mapping. These are double haploids, recombinant inbred lines (RILs), backcross populations, near isogenic lines (NILs) and F2 populations. This QTL mapping allows assessing the locations, numbers, magnitude of phenotypic effects, and pattern of gene action (Vinh, Paterson, 2005). Different recent mapping populations used for QTL analysis for drought tolerance in cereals are described in Table 1.

Table 1. Summary of most recent quantitative trait loci (QTLs) associated with drought tolerance in cereals

Trait	Cross	Species	QTL mapping population	References
Physio-morphological traits	CT9993 × IR62266	rice	RILs	Subashri et al., 2009
Physio-morphological and yield traits	IR 20 × Nootripathu	rice	NILs	Gomez et al., 2010
Various morpho-physiological traits	Zhenshan 97 × IRAT 109	rice	NILs	Ding et al., 2011
Photosynthesis parameters	Low land rice cv. Shennong 265 × Upland rice cv. Haogelao	rice	backcross (ILs)	Gu et al., 2012
Various morpho-physiological traits	Durum × Wild emmer	wheat	RILs	Peleg et al., 2009
Various productivity and physiological traits	Seri M82 × Babax	wheat	RILs	McIntyre et al., 2010, Suzuky et al., 2010
Leaf growth and ASI	Ac7643 × Ac7729/TZSR W	maize	RILs	Welcker et al., 2007
Root traits	CML444 × SC-Malawi	maize	RILs	Trachsel et al., 2009
Root traits and yield	Lo964 × Lo1016	maize	NILs	Landi et al., 2010
Root traits	Ac7643 × Ac7729/TZSRW	maize	RILs	Ruta et al., 2010
Physiological traits associated with seedling water stress	Zong3 × 87-1	maize	RILs	Liu et al., 2011
Plant senescence, relative leaf chlorophyll contents and root capacitance	CML444 × SC-Malawi	maize	RILs	Messmer et al., 2011
Stay green	Q319 × Mo17	maize	F2	Zheng et al., 2009

ASI – anthesis-silking interval; RILs – recombinant inbred lines, NILs – near isogenic lines, ILs – introgression lines

Today unprecedented efforts are being made in dissecting complex traits into their single genetic determinants (QTLs) in order to increase the efficiency of marker assisted selection (MAS) (Gu et al., 2012). An increasing number of QTLs related to drought response have been reported, and these include QTLs for root morphology and other root traits such as root penetration ability (Price et al., 2002; Babu et al., 2003; Uga et al., 2011), osmotic adjustment (Robin et al., 2003), grain yield and yield components (Lafitte et al., 2004; Xu et al., 2005), stay green (Jiang et al., 2004), canopy temperature, leaf rolling and leaf drying (Yue et al., 2006).

Most QTLs for drought tolerance in wheat have been identified through yield and yield component measurements under water-limited conditions (as

reviewed by Fleury et al., 2010). However, QTL mapping related to drought stress can be applied to any growth stage from germination to grain filling stage. QTLs corresponding to different morphological and physiological traits in various mapping populations have been identified like growth of shoot and roots (Landjeva et al., 2008); osmotic adjustment (Morgan, Tan, 1996), grain yield (Kirigwi et al., 2007; Salem et al., 2007) and thousand grain weight (Nezhad et al., 2012).

The applications of QTL mapping in the genetic dissection of the drought tolerance in rice are certain to be difficult (Price et al., 2002). However, the current research is on identifying QTLs stable across variable environments and also be able to co-segregate with yield (Witcombe et al., 2008). Babu et al. (2003) used double

haploids derived from rice lines and subjected them to water stress. The experiment resulted in identification of 47 drought related QTLs. They also identified major QTLs on chromosome 4 with pleiotropic effects on yield under drought stress. Similarly Bernier et al. (2009) mapped a QTL qtl12.1 with a large effect on grain yield under drought stress. Sellamuthu et al. (2011) identified a total of 46 QTLs related to reproductive growth traits correlated with yield. The overall phenotypic effects ranged 9.5% to 35.6%. Recently Vikram et al. (2011) identified a major QTL (qDTY1.1) for grain yield under reproductive stage drought stress on chromosome 1. Roots play a critical role in water and nutrient absorption. Hence a deeper root system is desirable as it contribute to enhanced water uptake during drought stress. A number of root related QTLs have been identified in rice. Steele et al. (2006) mapped a QTL on chromosome 9 involved in root length and thickness. Similarly Obara et al. (2010) mapped a major QTL qRL6.1 for root length, on chromosome 6. Uga et al. (2011) identified a major QTL Dro 1 on chromosome 9 playing a crucial role in deep rooting.

During the last two decades, numerous QTLs related to morpho-physiological and secondary traits like anthesis-silking interval (ASI), leaf rolling, stay green and deeper rooting in maize have been identified showing a strong correlation with yield and displayed increased genetic variability in drought conditions (Nikolic et al., 2011). Lebreton et al. (1995) are given the credit to have first attempted to apply QTL analysis in maize to get genetic insights into the drought tolerance phenomenon. Later Ribaut et al. (1996) identified six putative QTLs for ASI under drought on chromosomes 1, 2, 5, 6, 8 and 10, together accounting for 47% of the phenotypic variance. Nikolic et al. (2011) identified and mapped 43 QTLs related to yield and other agronomic traits. Earlier Ruta et al. (2010) working on 208 RILs derived from a cross of maize parent varieties Ac7643 (drought tolerant) and Ac7729/TZSRW (drought susceptible), identified 13 root related QTLs. Similarly Jing et al. (2011) identified numerous QTLs related to ASI, plant height, grain yield, ear height and ear setting under drought stress conditions.

In summary, many drought related QTLs have been identified in our major cereal crops that can be effectively used in our breeding programs. This necessitates that more and more replicated yield tests are to be conducted in order to accurately characterize their effects and to evaluate their stability across different environments (Cattivelli et al., 2008). As lack of stability across different environments and QTL \times E interaction evaluation remains a major impediment towards the efficient use of marker assisted selection (MAS) (Bernier et al., 2008; Cattivelli et al., 2008).

Marker assisted selection (MAS) to improve drought tolerance

Since drought tolerance characters are quantitative in nature, the complete genetic dissection of these complex traits into component genetic factors is a preliminary task. Therefore molecular genetic markers offer a great opportunity of locating the QTLs controlling these traits (Manickavelu et al., 2006). These molecular markers are very powerful as these remain unaffected by the external environment. Once it is ensured that these markers are tightly linked and tagged with a QTL concerned, selection at early segregating generation can be pursued (Khan, 2012). Thus MAS saves time and valuable resources by eliminating undesirable

phenotypic evaluation. With the replacement of 1980s RFLP markers with more advanced polymerase chain reaction (PCR) based markers like simple sequence repeats (SSR) or microsatellites, amplified fragment length polymorphism (AFLP) and random amplified polymorphic DNA (RAPD), the cost effectiveness of MAS is greatly increased as very small amount of template DNA is required to screen large populations (Ghafoor, McPhee, 2012). Earlier Kirigwi et al. (2007) constructed a SSR/EST (expressed sequence tag) marker map to find a grain yield QTL on the proximal region of wheat chromosome 4AL having a significant impact on drought stress performance. Huseynova and Rustamova (2010) successfully used RAPD markers to screen 12 wheat genotypes against drought tolerance.

In maize, MAS was applied to introgress QTLs reducing ASI. Molecular markers were linked with five QTLs related to ASI. The selected lines were superior to the control ones under severe drought stress (Ribaut et al., 2004). Ribaut and Ragot (2007) used marker assisted backcrossing in maize to introgress the alleles at five QTLs for ASI trait. Similarly in rice, Courtois et al. (2003) used MAS to transfer a number of QTLs related to deep rooted character from the japonica upland cultivar 'Azucena' to the lowland indica variety IR64. Steele et al. (2006) used marker assisted backcrossing to transfer five root related QTLs from 'Azucena' to Indian cultivar 'Kalinga III'. Using the SSR markers, Yue et al. (2006) identified a number of QTLs related to yield and root parameters under drought. Bernier et al. (2007) screened 436 F3 rice lines by adopting the MAS approach and a QTL on chromosome 12 having a marked effect on the yield under drought stress conditions was identified.

Although molecular markers have been successfully associated with QTLs, yet this association has shown limited practicality in cereal breeding (Araus et al., 2008). One of the prerequisites of MAS is the close linkage of DNA marker with the target locus. However, this linkage can be broken by the genetic recombination. Furthermore, the effects of individual QTLs on the phenotype are relatively small. This implies the need to manipulate several (perhaps from three to five) QTLs in the breeding program for significant impact (Araus et al., 2008; Kamoshita et al., 2008). Moreover, there is a possibility that DNA markers developed for a certain genetic background may prove ineffective for others (Gupta et al., 2006). Apart from this there are some cost related issues, inadequate quality of markers and epistatic interactions that need to be addressed before the MAS can successfully be deployed in our breeding programs.

Transgenics

The identification of candidate genes is critical for our understanding of molecular and physiological mechanisms of drought tolerance in cereals, as it will enable us to use transgenic approaches in breeding for abiotic stress tolerance (Dolferus et al., 2011). A transgenic approach is one that involves some structural modifications in traits through gene transfers from one species to the other (Ashraf, 2010). As the regulatory networks underlying the abiotic stress responses are being fully understood, more and more candidate genes will be identified to be used in development of transgenic plants (Barnabás et al., 2008). A detailed description of drought tolerance genes can be found in the review of Hadiarto and Tran (2011). A number of such genes associated with drought tolerance have been identified. Like transcription factors that upregulate and downregulate the expression of other genes.

Some of the other identified stress-responsive genes are functional genes which encode metabolic components, such as late embryogenesis abundant (LEA) proteins and osmoprotectant-synthesizing enzymes. (Yang et al., 2010 as reviewed by Hadiarto and Tran, 2011). Most important and well studied class of transcription factors is drought responsive element binding (DREB) factors especially *DREB1A* and *DREB2A* identified in *Arabidopsis* as well as in cereal crops (Hussain et al., 2011). Initial studies with DREB started with *Arabidopsis*. Over-expression of *DREB1/CBF* in *Arabidopsis* resulted in the activation of expression of many stress-tolerance genes and the tolerance of the plant to abiotic stresses was greatly improved (as reviewed by Gosal et al., 2009). In most of the cases the overexpression of *DREB1A* is

obtained by using constitutive (CaMV 35S) promoter or the dehydration inducible (rd29A) promoter. In transgenic *Arabidopsis* plants Kasuga et al. (1999) found that overexpression of *CBF3/DREB1A* accompanied by constitutive promoter CaMV 35S greatly improved plant's tolerance to abiotic stresses including drought stress. Similarly, the use of the stress inducible promoter rd29A in conjunction with *DREB1* has been found to enhance drought tolerance in tobacco (Kasuga et al., 2004) and wheat (Pellegrineschi et al., 2004). RD29 genes are induced by desiccation, cold and salt stresses thus endowing plants to tolerate these stresses (Jia et al., 2012). A list of some of the recent transgenic lines produced in cereal crops is given in Table 2.

Table 2. List of transgenic lines produced in cereal crops for drought tolerance

Transgene	Crop	Trait improved	Reference
<i>HVA1</i>	rice	transgenic plants showed improved tolerance to drought conditions	Xiao et al., 2007
<i>HVA1</i>	wheat	transgenic plants showed improved tolerance to drought conditions	Sivamani et al., 2000
<i>CBF3/DREB1A</i>	rice	drought and salinity tolerance	Oh et al., 2005
<i>SNAC1</i>	rice	transgenic plants showed improved tolerance to drought conditions	Hu et al., 2006
<i>OsNAC10</i>	rice	transgenic plants showed improved grain yield and tolerance to drought	Jeong et al., 2010
<i>Os LEA-3-1</i>	rice	transgenic plants showed increased growth under drought conditions	Xiao et al., 2007
Tomato ethylene response factor (ERF) protein <i>TSRF1</i>	rice	<i>TSRF1</i> improved the osmotic and drought tolerance of rice seedlings without growth retardation	Quan et al., 2010
Tomato ethylene response factor (ERF) protein <i>JERF3</i>	rice	over expression of <i>JERF3</i> significantly enhanced drought tolerance of transgenic rice	Zhang et al., 2010
Sorghum <i>SbDREB2</i> gene with stress-induced promoter CaMV35S or rd29A	rice	over expression of <i>SbDREB2</i> significantly enhanced drought tolerance and yield improvement in transgenic rice	Bihani et al., 2011
Rice <i>OsDREB2A</i> gene with stress-inducible promoter rd29A	rice	over expression of <i>OsDREB2A</i> significantly enhanced drought and salt tolerance of transgenic rice	Mallikarjuna et al., 2011
Rice <i>OsSDIR1</i> gene	rice	over expression of <i>OsSDIR1</i> gene significantly enhanced drought and salt tolerance	Gao et al., 2011
<i>mtlD</i> (osmoprotectant)	wheat	improved fresh and dry weights, plant height, and flag leaf length in transgenic plants	Abebe et al., 2003
<i>Asr1</i> (A putative transcription factors)	maize	transgenic maize lines showed improved tolerance to drought	Jeanneau et al., 2002
<i>ZmNF-YB2</i> (an orthologous maize transcription factor from the nuclear factor <i>Y(NF-Y)</i> family)	maize	transgenic maize lines showed improved tolerance to drought	Castiglioni et al., 2008
<i>ZmNF-YB2</i>	maize	transgenic maize plants showed 50% increased yield under drought conditions	Nelson et al., 2007
<i>OsPFA-DSP1</i> (a rice protein tyrosine phosphatase)	rice	transgenic rice and <i>Tobacco</i> plants showed sensitivity to drought stress	Liu et al., 2012

Oh et al. (2005) successfully engineered the rice with transcription factor *CBF3/DREB1A* from *Arabidopsis thaliana*. Recently Cui et al. (2011) found the overexpression of *OsDREB2A* significantly enhanced drought and salt tolerance of transgenic rice plants. Overexpression of *ZmDREB2A* with CaMV 35S or rd29A promoters resulted in better tolerance to drought in maize (Qin et al., 2007). Wang et al. (2011) isolated the *ZmDBP4* gene, a member of the A-1 subgroup of the *CBF/DREB* subfamily, from maize seedlings. They found that overexpression of *ZmDBP4* in transgenic *Arabidopsis* leads to improved cold and drought tolerance.

In addition to DREB, another class of transcription factors involved in developmental regulation of plants conferring drought tolerance is stress

responsive NAC (NAM ATAF and CUC2) family. More than 100 members of this family have been identified but only few of them have been characterized (Hussain et al., 2011). Hu et al. (2006) found that overexpression of NAC encoding rice *SNAC1* gene in transgenic rice showed high yield and tolerance to drought. Ethylene responsive factors (ERFs) belong to the large *APETALA2 (AP2)/ERF* transcription factor superfamily involved in growth, development and both biotic and abiotic stress responses in plants (Hussain et al., 2011; Li et al., 2011). In a recent study, an overexpression of tomato ERF protein *JERF1* in transgenic rice plants resulted in improved tolerance to drought stress (Zhang et al., 2010).

LEA proteins found in the seeds and vegetative parts of plants have been tested to have some association

with increased stress tolerance in plants (Gosal et al., 2009). Several transgenic rice and wheat plants overexpressing barley LEA gene *HVA1* have shown increased tolerance to water deficit conditions (Sivamani et al., 2000; Xiao et al., 2007). Another important class of proteins, known as heat shock proteins (HSPs), generally remains undetectable in the vegetative tissues of plants under normal growth conditions and can be induced when environmental stresses ensue (Bartels, Sunkar, 2005). Sun et al. (2001) found that transgenic *Arabidopsis* plants overexpressing *AtHSP17.7* showed improved tolerance to drought and salinity. Similarly in rice small heat-shock protein encoding *sHSP17.7* gene was overexpressed in 'Hoshinoyume' rice variety that resulted in drought tolerant transgenic plants (Sato, Yokoya, 2008). Further strategies used to successfully improve drought tolerance in cereals include the overexpressions of osmoprotectants (Abebe et al., 2003), phosphatases (Xu et al., 2007), and other stress related genes (Shi et al., 2001).

Tremendous progress has been made in the past two decades in developing transgenic lines, helping us to understand and manipulate plant responses to stress. Most of these lines have been tested in the laboratory and many of these recent discoveries are in rice which serves as a model for other cereal crops. The effectiveness of these transgenic lines in enhancing drought tolerance without jeopardizing yield and other related traits under the field conditions needs to be fully assessed.

Use of "omics" technologies for drought tolerance

The applications of omics type technologies are beginning to have an impact in enhancing our understanding of plant's responses towards external environmental stimuli. The term "omics" is a blend of high throughput genomics, proteomics (analysis of protein complement) and metabolomics approaches. The generation of expressed sequence tags (ESTs) from cDNA libraries and complete genome sequence information in *Arabidopsis* and rice provide valuable information about gene discovery (Sreenivasulu et al., 2007). Houde et al. (2006) reported that the digital expression analysis of EST sequences combined with gene annotation, resulted in the identification of several pathways associated with abiotic stress tolerance in wheat. With the advancement of DNA microarray technology, several hundred stress induced genes have been identified in plants (Umezawa et al., 2006). cDNA and oligonucleotide microarrays have been widely used in plants, such as *Arabidopsis*, rice, maize (Vij, Tyagi, 2007). Seki et al. (2001) constructed *Arabidopsis* full-length cDNA microarrays using about 1300 full-length cDNAs. Forty-four genes were identified as drought inducible. Kawasaki et al. (2001) first reported the use of microarray to study global gene expression profiling in response to abiotic stress in rice. Later Gorantla et al. (2005) used functional genomics and generated a large number of ESTs from cDNA libraries and identified 589 genes involved in drought stress. Wang et al. (2007) compared gene expression between upland and lowland rice cultivars under drought stress using cDNA microarray. Compared with rice, the genomes of other cereals are large and complex (Paterson, 2006). Even then the projects to sequence the genomes of some cereals have been undertaken like in maize (<http://www.maizegenome.org/>), sorghum (<http://www.jgi.doe.gov/>) (Bedell et al., 2005) and wheat (<http://www.wheatgenome.org/>) (Varshney et al., 2006). Apart from ESTs, other techniques like

serial analysis of gene expression (SAGE), array-based transcript profiling technologies and quantitative real time PCR (qRT-PCR) allow us to assess the high throughput expression of thousands of genes involved in drought tolerance (Sreenivasulu et al., 2007).

Investigating the effects of drought on the protein composition may also provide a clue towards understanding a link between external environmental stress and plant development (Barnabás et al., 2008). Thus proteome analysis is applied to study the alterations in gene expression in relation to drought (Hu et al., 2010). Salekdeh et al. (2002) working on the proteome analysis identified more than 1000 proteins in rice. Out of these, 42 were differentially expressed in drought stress. Ali and Komatsu (2006) performed a proteomic analysis on rice leaf sheaths and identified a protein actin depolymerizing factor (ADF). The increased level of ADF in drought tolerant plants suggested that ADF is one of the target proteins induced in drought stress. Recently Yang et al. (2011) performed a proteome analysis of rice roots to identify water deficit responsive proteins among two cultivars IR64 and 'Azucena'. Out of 700 proteins detected, only 15 showed different responses to water stress between two ecotypes.

Similar proteome analysis has also been started in other cereal crops as well. Riccardi et al. (2004) identified 46 proteins in maize leaves. They found an increase in quantity of these proteins in leaves of plants subjected to water stress. Hu et al. (2011) found a differential expression of 22 proteins in maize roots in response to drought stress.

Metabolomics is one of the omics used to acquire comprehensive information about the metabolites in plants (Okazaki, Saito, 2012). The metabolite changes in plants in response to environmental stresses suggest that complete metabolite profiling may provide valuable insights into stress tolerant mechanisms of plants (Langridge et al., 2006). Metabolomics is a relatively new area of research and it is expected that when combined with genomics, transcriptomics and proteomics, it will help us to understand and interpret many complex biological processes (Langridge et al., 2006; Okazaki, Saito, 2012).

From the above discussion, it can be inferred that considerable progress has been made in the field of omics, providing valuable information on the structure and behaviour of crop genomes, with better understanding of plant responses to environmental stresses (Langridge, Fleury, 2011). However, there are challenges and issues that need to be tackled and considered for successful exploitation of the omics technologies. Some of these are regulatory variations, precise phenotyping, technical and cost related issues (Varshney et al., 2006).

Conclusion and future prospects

Considering the importance of cereal crops as a predominant source of food around the world, identification of traits and genotypes associated with drought tolerance is absolutely necessary. Concerted efforts are required to fully understand the physiological and genetic basis of drought tolerance. Focus should be on screening resistant germplasm and discovering potential candidate genes. Characterization and mapping of such genes at the physiological and molecular level will be key factors in the application of molecular marker technology to the development of more drought tolerant cultivars. Transgenic and omics based technologies have been shown to be powerful tools holding a tremendous promise for the future. However, these approaches need

to be fine-tuned and their significance at the controlled and field conditions need be fully assessed. Surely, the new genomic tools will enhance but not replace the conventional breeding and selection process (Varshney et al., 2005). An interdisciplinary approach combining the knowledge of plant breeders, crop physiologists and molecular biologists would be most appropriate to study and evaluate the complex plant responses to develop drought tolerant cereal crops.

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Nauji pasiekimai kuriant molekulinis įrankius sausrui atsparių javų selekcijai: apžvalga

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Santrauka

Sausros sukeltas stresas yra vienas iš javų derlių ribojančių veiksnių. Kuriant sausrui atsparias veisles, tradiciškai taikoma tiesioginė arba netiesioginė atranka. Nors tai veiksmingas metodas, tačiau jis yra imlus laikui ir darbiui. Kiekybinių požymių lokusų, susijusių su sausra, identifikavimas kartu su žymekliais pagrįsta atranka jau davė teigiamų rezultatų. Atsparumo sausrui selekcijoje taikomos pažangios transgeninės ir ominės technologijos, leidžiančios geriau suprasti pagrindinius atsparumo sausrui mechanizmus ir nustatyti potencialius genus kandidatus. Šie metodai suteikia galimybę selekciją nukreipti į genotipų, sausros sukulto streso sąlygomis duodančių stabilų derlių, kūrimą.

Reikšminiai žodžiai: atsparumas sausrui, kiekybinių požymių lokusai, omika, transgenika, žymekliais pagrįsta atranka.