Critical Reviews in Plant Sciences, 33:205–224, 2014

ISSN: 0735-2689 print / 1549-7836 online
DOI: 10.1080/07352689.2014.870417

Functional Genomics of Drought Tolerance in Bioenergy Crops

Hengfu Yin,[1,*] Chun Ju Chen,[1,*] Jun Yang,[1] David J. Weston,[1,2] Jin-Gui Chen,[1,2] Wellington Muchero,[1,2] Ning Ye,[1] Timothy J. Tschaplinski,[1,2] Stan D. Wullschleger,[3] Zong-Ming (Max) Cheng,[4] Gerald A. Tuskan,[1,2] and Xiaohan Yang[1,2]

[1]*Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831, USA*
[2]*BioEnergy Science Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831, USA*
[3]*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831, USA*
[4]*Department of Plant Sciences, University of Tennessee, Knoxville, Tennessee 37996, USA*

Table of Contents

[*]These authors contributed equally to this work.

Address correspondence to Xiaohan Yang, Biosciences Division, Oak Ridge National Laboratory, P.O. Box 2008 MS-6422, Oak Ridge, TN 37831-6422, USA. E-mail: yangx@ornl.gov

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With predicted global changes in temperature and precipitation, drought will increasingly impose a challenge to biomass production. Most of the bioenergy crops have some degree of drought susceptibility as revealed for example through measures of low water-use efficiency (WUE). It is imperative to improve drought tolerance and WUE in bioenergy crops for sustainable biomass production in arid and semi-arid regions. Genetics and functional genomics can play critical roles in generating knowledge to inform and aid genetic improvement for drought tolerance in bioenergy crops. The molecular aspects of drought response have been extensively investigated in model plants like *Arabidopsis*, yet our understanding of the molecular mechanisms underlying drought tolerance in bioenergy crops is limited. Plants in general exhibit various responses to drought stress depending on species and genotype. A rational strategy for studying drought tolerance in bioenergy crops is to translate the knowledge from model plants relative to the unique features associated with individual bioenergy species and genotypes. In this review, we summarize the general knowledge concerning drought responsive pathways, with a focus on the identification of commonality and specialty in drought responsive mechanisms among alternate species and genotypes. We describe the genomic resources developed for bioenergy crops and discuss genetic and epigenetic regulation of drought responses. We also examine comparative and evolutionary genomics as a means to leverage the ever-increasing genomics resources and provide new insights beyond what is known from studies on individual species. Finally, we outline future opportunities for studying drought tolerance using the emerging technologies.

Keywords drought, bioenergy crops, *Populus*, *Panicum*, genomics, epigenetics, proteomics, transcriptome

I. INTRODUCTION

With the ever-increasing need for alternative transportation fuels, more and more plant species are being used to produce biofuels such as biodiesel and bioalcohol (El Bassam, 2010; Kole *et al.*, 2012). The development and deployment of bioenergy crops are limited in part by the availability of economically viable, agronomic-quality land for biomass production. One of the most limiting factors on marginal agricultural land is water availability. Drought stress on such land limits plant productivity and the deployment of biomass production systems (Yang *et al.*, 2011). Knowledge concerning the molecular mechanisms underlying drought tolerance is one of the critical factors needed for the development of drought tolerant bioenergy crops. Due to the large distribution of semi-arid agricultural lands, species with higher water-use efficiency (WUE) and drought tolerance are favored for biomass production (Somerville *et al.*, 2010). Genomics and functional genomics of plant responses to water deficit have been extensively studied in model plant species (Shinozaki, 1999; Shinozaki and Yamaguchi-Shinozaki, 2007). In general, plant response to drought stress tends to be dependent on species, genotypes and even specific tissues (Dinneny *et al.*, 2008; Iyer-Pascuzzi *et al.*, 2011; Munns and Tester, 2008; Shinozaki and Yamaguchi-Shinozaki, 2007). Some excellent reviews described the regulation of drought response in model plants like *Arabidopsis thaliana* and *Oryza sativa* (Hirayama and Shinozaki, 2010; Seki *et al.*, 2007; Shinozaki and Yamaguchi-Shinozaki, 2007; Yamaguchi-Shinozaki and Shinozaki, 2006). In this review, we summarize the recent progress in functional genomics of bioenergy crops such as *Populus* and *Panicum*, with a focus on the identification of commonality and specialty in drought responsive mechanisms among alternate bioenergy species (e.g., *Medicago, Jatropha*).First, genomic resources for bioenergy crops are described. Second, drought responsive pathways are discussed, along with genetic and epigenetic regulation of drought responses. Finally third, comparative and evolutionary genomics are examined to leverage the mounting genomic resources and to provide new insights into future routes of scientific investigation.

Prior to reviewing the genomics literature, an outline definition of drought tolerance is provided to create a common framework for the reader to place the functional genomics information. Drought tolerance, based on the terminology of Kramer (1980), consist of traits and mechanisms that postpone drought and function to maintain high plant water potential, or they allow the plant to tolerate dehydration with concomitant low water potential. Traits and processes, such as waxy leaf surfaces, leaf curling, leaf abscission, cessation of shoot growth, deep or extensive root development and effective stomatal control, all function to postpone drought. Water-use efficiency, given the associated improved stomatal regulation, falls under the classification of drought postponement. In contrast, dehydration tolerance mechanisms, in the terminology of Kramer (1980), allow plants to function under low water potential and include maintenance of low osmotic potential at full turgor and osmotic adjustment, the lowering of osmotic potential via the accumulation of compatible solutes, or both. In this review, therefore, drought tolerance refers to both drought postponement and dehydration tolerance mechanisms.

II. GENETICS AND GENOMICS RESOURCES

Genomic resources provide the foundation and tools for studying the molecular mechanisms underlying all plant phenotypes. One of the principal portals to genomic information relevant to bioenergy crops is the Phytozome (www.phytozome.net) portal. Other genomic resources publicly available for bioenergy crops are listed in Table 1. In this section, we describe the currently available genomics, transcriptomics and proteomics

TABLE 1
Summary of genomic resources available for drought research in bioenergy crops

Resources	Plant species	Description	References
MaizeGDB	*Zea mays*	QTL/SNP	(Lawrence *et al.*, 2004; Lawrence *et al.*, 2005)
MaizePLEXdb	*Zea mays*	Transcriptome/Drought	(Zheng *et al.*, 2010) http://www.plexdb.org/plex.php?database=maize
PoplarPLEXdb	*Populus balsamifera*	Drought Transcriptome	(Hamanishi *et al.*, 2010) http://www.plexdb.org/plex.php?database=Poplar
PopGenIE	*Populus*	Genome/Transcriptome	http://popgenie.org/(Sjodin *et al.*, 2009)
Switchgrass Functional Genomics Server	*Panicum virgatum*	EST/Expression Atlas/GBrowser	http://switchgrassgenomics.noble.org/
Jatropha Genome Database	*Jatropha curas*	Genome	http://www.kazusa.or.jp/jatropha/(Sato *et al.*, 2011)
SoyBase	*Glycine max*	Genome/Transcriptome	http://soybase.org/(Grant *et al.*, 2010)
CSGR	*Sorghum bicolor*	Genome/EST	http://csgr.pgml.uga.edu/Data/SorgSig.asp
MtGEA	*Medicago truncatula*	Transcriptome	http://mtgea.noble.org/v2/

resources. Bioenergy crops and related model species that exhibit variable drought tolerance and for which there is genomic information available are presented in Fig. 1.

A. QTL and Association Mapping

Quantitative trait loci (QTL) mapping approaches have been widely utilized for mapping drought tolerance related phenotypes in *Populus*. Among these, QTL for osmotic potential (Tschaplinski *et al.*, 2006) and WUE (Monclus *et al.*, 2012) have been successfully identified. In addition to loci for explicit drought response phenotypes, QTL were stably identified for *Populus* (P.)biomass productivity at sites contrasting in water availability (Slavov *et al.*, 2012). Genetic markers that are aligned to the *Populus* genome facilitate the potential identification of candidate genes (Monclus *et al.*, 2012; Slavov *et al.*, 2012). Despite the earlier successes, there has not been significant progress in utilization of such QTLs to identify specific genetic determinants of drought tolerance. Among the limitations of QTL mapping is the fact that such loci typically encompass tens to hundreds of genes due to limited recombination events among progeny and sparse marker coverage in the available genetic maps (Slavov *et al.*, 2012). This makes the molecular validation of candidate genes cumbersome and economically challenging.

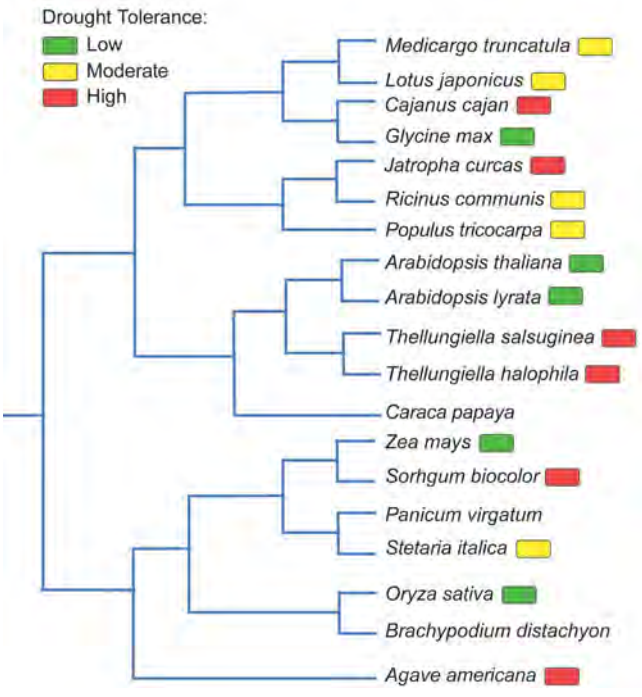

FIG. 1. Phylogenetic tree of bioenergy crops and related model species. The color bars indicate drought tolerance of corresponding species with information compiled from literature (Munns and Tester, 2008; Orsini *et al.*, 2010; Xoconostle-Cazares *et al.*, 2010; Yang *et al.*, 2011).

Conversely, recent successes in high-throughput single nucleotide polymorphism (SNP) genotyping and whole-genome resequencing to characterize polymorphisms in large assembled populations (Slavov *et al.*, 2012) and complementary statistical approaches, such as association mapping to identify marker-trait associations, offer opportunities for further characterization of valuable QTL intervals. In such studies, the non-random association between alleles and phenotypes (i.e., linkage disequilibrium) is evaluated and leads to identification of genetic associations that have been maintained through recombination events occurring over evolutionary time. Studies in several plant species have demonstrated the power of this method in identifying causal mutations down to the individual nucleotide (Buckler *et al.*, 2009). The possibility of applying this technique in *Populus* was recently supported by the findings of Slavov *et al*. (2012), who demonstrated that the extent of linkage disequilibrium in *P. trichocarpa* dissipated rapidly, suggesting that associations between markers and traits can be resolved down to the individual

gene level. Applications of association genetics have not been realized yet for the identification of drought tolerance genes.

B. Transcriptomics

Transcriptomic analysis has been extensively used to identify drought responsive genes in many plant species (Deyholos, 2010; Shinozaki *et al.*, 2003; Yamaguchi-Shinozaki and Shinozaki, 2006). Notably, transcriptome sequencing (RNA-Seq) has greatly improved the throughput of gene expression profiling in drought stressed individuals.

1. Transcriptome profiling

In *Populus*, microarrays have facilitated the identification of drought-responsive genes (Gailing *et al.*, 2009) and revealed that the time of day and genotype influenced the transcription level in response to drought (Raj *et al.*, 2011; Wilkins *et al.*, 2009). Whole-genome arrays have also been used to study intraspecific variation in drought tolerance in *P. balsamifera* (Hamanishi *et al.*, 2010). In *P. alba*, wood formation is related to water availability, but gene expression in multiple cellular functions, such as protein metabolism and cell wall formation, varies with drought (Berta *et al.*, 2010; Giovannelli *et al.*, 2007). Similarly, common drought-responsive genes in different tissues and genotypes appear to have specific functions in regulating stem development under drought (Berta *et al.*, 2010; Pallara *et al.*, 2012). Gender-specific analysis in *P. cathayana* and *P. yunnanensis* revealed that male and female individuals displayed differential physiological and biochemical responses to drought stress, with the female individuals being more sensitive to drought stress (Chen *et al.*, 2010; Xu *et al.*, 2008). Transcriptome sequencing, in response to osmotic perturbations, confirmed that several groups of genes displayed differential expression patterns between male and female clones in *P. yunnanensis* (Jiang *et al.*, 2012). Furthermore, transcriptome analysis of *P. euphratica* under various drought treatments (i.e., dehydration, salt accumulation and osmotic restoration) identified common and specific transcripts (Brinker *et al.*, 2010; Yan *et al.*, 2012). Using Affymetrix Gene Chip Poplar Genome Arrays, Willkins *et al.* (2009) identified divergent responses in gene expression profiles in response to drought stress between two *Populus* hybrids, suggesting that it may not be possible to describe a common genus-specific drought-driven transcriptome solely based on one or a few genotypes. Indeed, it has become increasingly more difficult to identify the *Populus*-specific drought transcriptome, because the whole-genome arrays have uncovered great variation in the transcriptomes even within a single species (Hamanishi *et al.*, 2010).

Genome-wide transcriptional changes during drought stress have been investigated in several other potential bioenergy crops, including *Sorghum bicolor*, *Panicum (Pa.) virgatum*, *Zea mays* and *Jatropha* (Buchanan *et al.*, 2005; Costa *et al.*, 2010; Dugas *et al.*, 2011; Jogaiah *et al.*, 2012; Kadam *et al.*, 2012). Kakumanu *et al.* (2012) compared drought-responsive gene expression in ovary and basal leaf meristem tissues in *Z. mays* using the RNA-Seq approach. Their results indicated that abscisic acid (ABA) and sugar signaling pathways were turned on during kernel development, despite the limitation of water in the short term. Using the *Zea mays* genome array, transcriptional analyses revealed that in drought-tolerant *Zea mays* varieties candidate genes in the ABA and carbohydrates pathways wereco-expressed under drought stress (Fuad-Hassan *et al.*, 2008; Setter *et al.*, 2011; Zheng *et al.*, 2010). Transcriptional profiling was also used to identify high-confidence drought-tolerance candidate genes in *Zea mays* (Lu *et al.*, 2010). A recent microarray gene expression analysis of drought responses induced by high salinity, PEG-induced osmotic stress and ABA treatments in roots and shoots of *Sorghum bicolor* revealed a complex gene regulatory network that was involved in drought signal transduction in a tissue-specific manner (Buchanan *et al.*, 2005). RNA-Seq analysis of multiple tissues in *Panicum hallii* was used to characterize the expression patterns of more than 14,000 annotated transcripts (Meyer *et al.*, 2012). A transcriptome database was recently created for *Panicum virgatum* (http://switchgrassgenomics.noble.org/). Sun *et al.* (2012) investigated gene expression in *Panicum virgatum* and identified two miRNAs that showed significant changes under high salinity stress. EST information was used to identify several drought-responsive genes in *Setaria italic* (Lata *et al.*, 2010; Puranik *et al.*, 2011; Sreenivasulu *et al.*, 2004). An EST library from salt-treated roots of *Jatropha curcas* was recently generated to identify drought responsive genes (Eswaran *et al.*, 2012).

2. Drought co-expression networks

Plant performance can be characterized using co-expression networks and the interaction of such genes can lead to the identification of the emergent properties of plant performance (Bennett and Monk, 2008). For a drought co-expression network, a model may be composed of subnetworks, termed modules, which contain many gene nodes that presumably function in the same biological process (e.g., osmotic adjustment). From a biological perspective, the level of biological organization is important in the emergent properties of a network (Lucas *et al.*, 2011). Although a number of drought-related transcriptional studies have been performed, relatively few have modeled the transcriptome using network approaches (Weston *et al.*, 2008) and fewer yet have modeled the drought-related transcriptome networks in bioenergy crops. The work by Zhang and colleagues (2012) provides an exception to this where the authors identified 15 gene modules from a subset of 2,607 *Oryza sativa* genes showing highly variable expression under drought stress.

C. Proteomics

The application of proteome-wide profiling approaches in characterizing plant phenotypes is occurring more often (Knight and Knight, 2001). However, drought-related proteomics resources for bioenergy crops are limited. This section summarizes recent progress in proteomic studies on drought tolerance in representative plant species (e.g., *Oryza sativa*, *Z. mays* and

Populus), including reviews of both whole-proteome studies and specialized investigations on specific proteins.

1. Proteomics research in monocots

Proteomic profiling, together with metabolic network analysis, in *O. sativa* seedlings revealed that the primary upregulated proteins belong to protein processing, protein chaperons, pathogen-related metabolism and enzymes for anabolic pathways, linking an elevated level of energy consumption during drought to conversion between storage substances (Mirzaei *et al.*, 2012; Shu *et al.*, 2011). Intriguingly, besides the usually upregulated components, such as the protective detoxification/oxidation-reduction reaction proteins (e.g., Cu-Zn superoxide dismutase) (Ke *et al.*, 2009; Mirzaei *et al.*, 2012), accumulation of several phosphoproteins was also evident (Ke *et al.*, 2009), agreeing with another report that the protein phosphorylation pattern in *O. sativa* leaf tissue was strongly influenced by the drought signaling hormone ABA (He and Li, 2008).

Proteomic evidence recently suggests that premature stomatal closure in drought-susceptible *Z. mays* inhibits photosynthesis, which is correlated with lower production of drought related proteins, whereas the drought-tolerant *Z. mays* maintains active photosynthesis through retaining stomatal opening and producing protective enzymes in response to desiccation stress (Benesova *et al.*, 2012). In wheat, though, drought-tolerant and -susceptible cultivars all seem to display decreased protein production related to photosynthesis and the Calvin cycle (Ford *et al.*, 2011). Alternatively, drought-tolerant wheat has higher capacity to maintain osmotic and ionic homeostasis and to achieve detoxification via accumulation of antioxidants, such as thioredoxin and glutathione S-transferase, thereby allowing a faster recovery from drought stress (Hajheidari *et al.*, 2007; Peng *et al.*, 2009).

Proteomic profiling in *Z. mays* revealed that the level of lignin content was lower in plants under water-deficit stress (Vincent *et al.*, 2005). Dehydration led to a reduction of lignin biosynthesis in the xylem of *Z mays*, due to the accumulation of cationic peroxidases and phenylpropanoids (Alvarez *et al.*, 2008). Consistent with those observations, recovery of phenylpropanoid biosynthesis enzymes, notably cinnamyl alcohol dehydrogenase and caffeate *O*-methyltransferase, occurs at a faster rate in drought-tolerant *Z. mays* (Hu *et al.*, 2009). In a drought-tolerant *O. sativa* cultivar, the damaged activities of Rubisco during drought appear to be compensated by an increased level of Rubisco activase and peptidyl-prolyl cis-trans isomerase (Ji *et al.*, 2012). Overall, the discussed proteomics studies from both *Zea mays* and *Oryza sativa* converge on one theme, in which numerous metabolic and physiological functions are compromised when the plants are subjected to drought stress, yet the rapidly upregulated activities of protective proteins provide the first line of defense to offset some of the adverse effects. Furthermore, once the drought condition is ameliorated upon re-watering, levels of heat shock proteins, molecular chaperones, aquaporins, G-proteins and stress-related proteins decrease sharply (Mirzaei *et al.*, 2012; Zang and Komatsu, 2007).

2. Proteomics research in dicots

Comprehensive proteomic analyses of multiple *Populus* tissues in response to drought-stress identified a broad spectrum of differentially expressed proteins, with up-regulated proteins in roots including 1) proteins responsible for breaking down and recycling of other proteins and 2) proteins related to secondary metabolite production and plant defense (e.g., flavonoid biosynthesis enzyme, leucoanthocyanidin reductase) (Plomion *et al.*, 2006). These drought-induced up-regulated proteins in *Populus* correspond well with those reported in *Arabidopsis* (Koussevitzky *et al.*, 2008). In *Arabidopsis* the MYB15 overexpression lines was demonstrated to achieve an improved drought tolerance as the result of a higher sensitivity to ABA-induced stomatal closure (Ding *et al.*, 2009), implying that tightly controlled stomatal closure has a positive downstream effect on the synthesis of stress-tolerant proteins. A recent proteomic study on nitrogen starvation during dehydration demonstrated that the decrease in certain amino acids (e.g., asparagine and glutamic acid) and Rubisco in *Medicago sativa* was linked to the inhibition of nitrogenase activity (Aranjuelo *et al.*, 2011). In *Brassica napus* a drought 22 kD (BnD22) protein was reported, via an enhancement in nitrogen recycling and utilization, to protect younger leaf tissue from nitrogen starvation caused by drought (Bazargani *et al.*, 2011).

In *Populus*, other factors are known to cause variation in the drought proteome, including tissue type (Durand *et al.*, 2011), genotype (Bonhomme *et al.*, 2009) and gender (Yang *et al.*, 2010). *Populus* species from higher altitude (e.g., *P. kangdingensis*), known to be adapted to drought, accumulate fewer oxidative molecules and have less of a decline in the level of proteins for photosynthesis, protein processing, redox homeostasis and carbohydrate metabolism (Yang *et al.*, 2010). Similar to *P. kangdingensis*, *P. euphratica*, known for its superior adaption to salt, drought and heat stress (Gu *et al.*, 1999; Gu *et al.*, 2004; Ma *et al.*, 1997), also maintains proteins related to photosynthesis, redox reaction, stress/defense, metabolic processing, protein refolding, amino acid synthesis, membrane transport and cytoskeleton structure under drought stress (Ferreira *et al.*, 2006). It is not surprising that diverse stresses often result in the accumulation of common stress proteins (described in section IIIC). A survey of over 300 proteins associated with the apoplast proteome of *P. deltoides* suggests that the multi-stress response in the apoplast constitutes an important adaptive trait in *Populus* (Pechanova *et al.*, 2010).

III. DROUGHT-RESPONSIVE SIGNALING PATHWAYS

Drought-responsive signaling pathways have been well-characterized in plants, including the ABA-dependent and the ABA-independent pathways (Fig. 2). Under drought stress, the accumulation of ABA activates the expression of

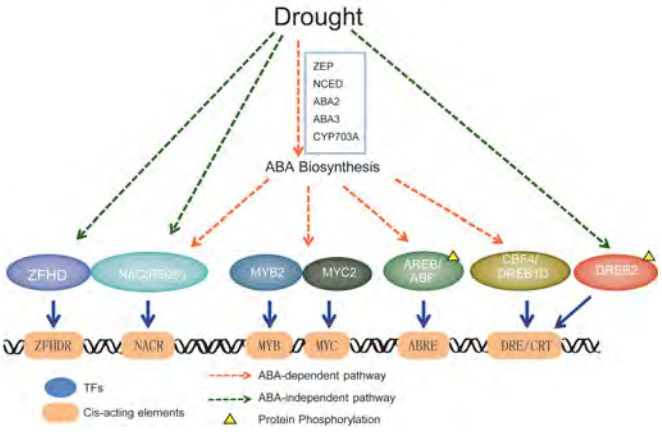

FIG. 2. Drought responsive pathways in plants. Drought commonly induces endogenous ABA production by modulating expression of ABA biosynthesis genes (Blue rectangle). The ABA-dependent pathway is indicated by red arrows and three ABA independent pathways are indicated by purple arrows. Transcription factors (TFs) including AREB/ABFs, MYB2, MYC2, RD26(NAC) and CBF4 are induced by ABA and bind to their corresponding cis-acting elements ABRE, MYB, MYC, NAC and DRE/CRT, respectively. TFs of ABA-independent pathway include ZFHD, DREB2 and NAC(RD26). RD26 is induced through both ABA-dependent and ABA-independent pathways. DREB2 and AREB/ABF are activated by protein phosphorylation. Adapted from (Hirayama and Shinozaki, 2010; Seki *et al.*, 2007; Tran *et al.*, 2007).

ABA-inducible transcriptional factors and consequently regulates the downstream genes involved in metabolism relevant to drought response (Shinozaki and Yamaguchi-Shinozaki, 2007; Tran *et al.*, 2007; Zhu, 2002). Still, many drought responses are mediated by transcriptional factors that are not regulated by ABA, but are induced under drought stress (Tran *et al.*, 2004).

A. ABA-Dependent Signal Transduction

The increase of endogenous ABA content under drought stress has been well-documented and the regulation of ABA biosynthesis pathway is associated with organ/tissue type and other environmental factors. In non-seed tissues, ABA biosynthesis occurs in plastids with the exception of the final two steps in which xanthoxin is converted to ABA in the cytosol (Seo and Koshiba, 2002). The initial step of ABA biosynthesis involves the zeaxanthin epoxidase (ZEP), which catalyzes two steps of epoxidation reactions converting zeaxanthin to all-trans-violaxanthin. The enzymes catalyzing all-trans-violaxanthin to 9-cis-neoxanthin have not been characterized yet. Another enzyme, 9-cis-epoxycarotenoid dioxygenase (NCED), considered rate limiting, utilizes oxidate 9-cis-violaxanthin or 9-cis-neoxanthin to produce xanthoxin in plastids. Xanthoxin is exported to the cytosol and catalyzed by a short-chain dehydrogenase/reductase (SDR/ABA2) into abscisic aldehyde (Seo and Koshiba, 2002). To produce ABA, aldehyde oxidase (AAO/AO), which is encoded by *ABA3* in *Arabidopsis*, is required to oxidize abscisic aldehyde. ABA can also be deactivated by the ABA hydroxylases (e.g., CYP707A3 in *Arabidopsis*), a key component in the ABA catabolic pathway, and dehydration can increase NCED expression levels, while decreasing CYP707A3 expression (Umezawa *et al.*, 2006).

Recently, the identification of ABA receptors has greatly improved our understanding of the ABA signaling pathway. Two types of ABA receptors in the Pyrabactin Resistance (PYR)/PYR-Like (PYL)/ Regulatory Components of ABA Receptor (RCAR) protein family have been identified (Park *et al.*, 2009; Shen *et al.*, 2006). In the absence of ABA, type 2C protein phosphatases (PP2Cs) inhibit the activity of sucrose non-fermenting-1 (SNF1)-related kinase 2 type of protein kinases (SnRK2s) that are positive regulators of ABA signaling. PP2Cs physically interact with SnRK2s and dephosphorylate Ser/Thr residues of SnRK2s (Raghavendra *et al.*, 2010; Weiner *et al.*, 2010). In the presence of ABA, binding of ABA to the PYR/PYL/RCAR receptors enables the interaction with PP2Cs and releases the PP2Cs inhibition of SnRK2 activity (Raghavendra *et al.*, 2010; Weiner *et al.*, 2010). The SnRK2 family proteins are plant-specific Ser/Thr kinases involved in abiotic stresses and members of subclass III, considered as major components in ABA-dependent signal transduction. SnRK2s can directly phosphorylate downstream targets including membrane proteins (e.g., SLAC1, KAT1 and AtRbohF) and transcription factors (e.g., ABF2 and ABF5) (Klingler *et al.*, 2010). ABA-inducible transcription factors (AREB/ABF) play a central role in drought-responsive gene expression, and the ABA responsive cis-elements (ABRE; T/CACGTGGC) have been widely found in the upstream regulatory regions of downstream genes (Hirayama and Shinozaki, 2010). MYB and MYC are induced by osmotic stress and can act cooperatively to regulate downstream genes, such as RD22 or AtADH1 (Abe *et al.*, 2003). CBF/DREB1 mediate gene expression in response to cold, but unlike other CBFs, CBF4 tends to uniquely mediate drought response (Haake *et al.*, 2002).

B. ABA-Independent Stress Signaling

Several drought-inducible genes do not respond to ABA treatment, indicating the existence of ABA-independent pathways (Shinozaki *et al.*, 2003; Yamaguchi-Shinozaki and Shinozaki, 2006). DRE/CRT is one of the major cis-elements present in the promoter region of various ABA-independent abiotic stress-responsive genes (Nakashima and Yamaguchi-Shinozaki, 2010). Osmotic stress activates other transcription factors including zinc finger homeodomain (ZFHD) and NAM/ATAF/CUC2 (NAC) proteins, which are independent of the ABA signaling pathway (Tran *et al.*, 2007; Vogel *et al.*, 2005). RAP2.1, an AP2/ERF transcription factor, was also reported as a negative transcriptional regulator in response to drought stresses in an ABA-independent manner (Dong and Liu, 2010).

Integration of the ABA-dependent and ABA-independent pathways was revealed by characterization of the *Arabidopsis* gene *RD29A*/*COR78*/*LT17*8 that was induced by drought, cold and ABA in the wild-type, as well as by drought in the ABA mutant *aba* or *abi* (Yamaguchi-Shinozaki and Shinozaki, 2006).

Recently, two protein kinases, *Arabidopsis* plasma membrane His kinase (ATHK1) and subclass III sucrose non-fermenting-1 related protein kinase 2 (SnRK2), were demonstrated to be involved in both ABA-dependent and -independent drought stress signaling pathways (Fujii *et al.*, 2011; Fujii and Zhu, 2009; Wohlbach *et al.*, 2008). The *Arabidopsis* trithorax-like factor ATX1, which trimethylates histone H3 at lysine 4 (H3K4me3), was also found to be involved in the dehydration stress signaling in both ABA-dependent and -independent manners (Ding *et al.*, 2011). More recently, a drought-induced ornithine δ-aminotransferase gene in *Oryza sativa*, *OsOAT*, was reported as a direct target of drought stress-responsive NAC transcription factor SNAC2 in both ABA-dependent and -independent pathways (You *et al.*, 2012).

C. Crosstalk between Drought and Other Abiotic Stress Pathways

As more transcriptome analyses have been attempted in diverse species, it is evident that the drought stress pathway is intertwined with other abiotic stresses (Yamaguchi-Shinozaki and Shinozaki, 2006), as illustrated in Fig. 3. Furthermore, an assortment of the drought- and salinity-induced genes were found to be stimulated by cold temperature (Rabbani *et al.*, 2003), implying a high degree of crosstalk initiated from a few master regulatory proteins. The Early Response to Dehydration (ERD1) protein in *Arabidopsis* is not only induced by drought, but is also induced during senescence, with two cis-acting elements responsible for dehydration and etiolation located separately in the promoter region (Simpson *et al.*, 2003). Upregulation of antioxidant enzymes, which produce reactive oxygen species (ROS), is thought to play a role in drought and related abiotic stresses; and hyperosmotic stress induced ROS production activates a cell wall diamine oxidase and a plasma membrane NADPH oxidase (Jiang and Zhang, 2002; Lin *et al.*, 2002), suggesting that ROS may mediate signal transduction under high osmotic stress condition. Calcium fluxes and phospholipids were shown to be second messengers of the drought signaling pathway (Boudsocq and Lauriere, 2005).

Other plant signaling molecules, such as jasmonic acid (JA) and salicylic acid (SA) also play important roles in abiotic stress signaling. SA has been proposed to act antagonistically with ABA under drought stress in several species (Yasuda *et al.*, 2008). The dosage-dependent manner of SA in drought tolerance suggests that SA and its downstream signals interact with ROS in the signaling cascade (Yuan and Lin, 2008). The participation of JA in response to drought and salinity has been reported in several species (Kramell *et al.*, 2000; Pedranzani *et al.*, 2003; Pedranzani *et al.*, 2007). The convergence of JA and ABA signaling occurs, in part, through a common set of transcription factors. For instance, AtMYC2 was first identified in the ABA-dependent drought pathway, whereas its mutation was characterized as jasmonate-insensitive 1 (jin1) (Abe *et al.*, 2003).

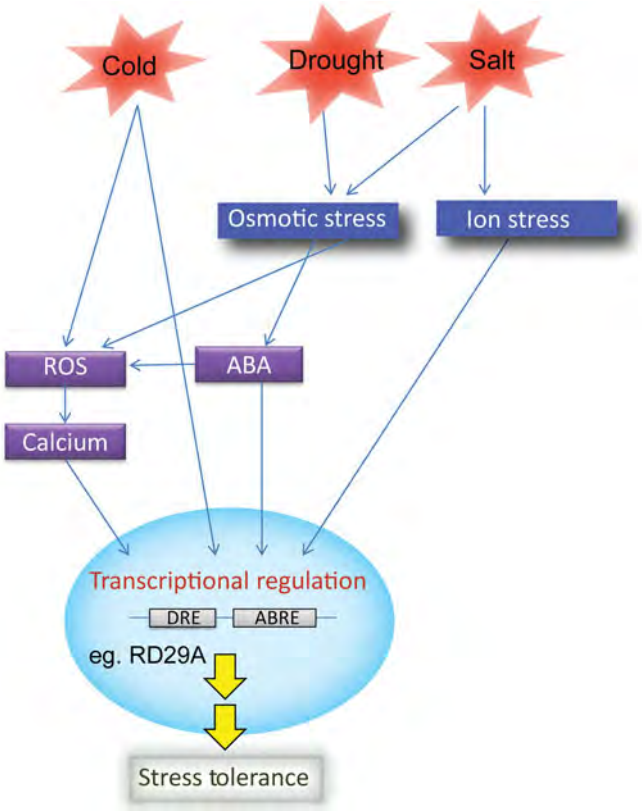

FIG. 3. Crosstalk between abiotic stress pathways. Blue boxes indicate three major abiotic stresses: cold, drought and salt. Drought and salt generate osmotic stress signal that is conveyed by ABA, ROS or calcium to regulate downstream gene expression. Salt also generates ion stress to regulate gene expression independently. Cold stress regulates gene expression by either ROS-dependent or ROS-independent pathways. Downstream gene like *RD29A* is regulated by both drought and cold signaling due to its dual cis-acting elements in the gene regulatory region. Integration of multiple signaling pathways results in plant stress tolerance.

IV. REGULATION OF DROUGHT RESPONSE

Unraveling the molecular regulatory mechanisms could further our understanding of drought adaption, ultimately facilitating genetic improvements in drought tolerance. Of course, plant drought response is controlled at genetic and/or epigenetic levels. This section summarizes the current knowledge about the genetic and epigenetic regulation of drought responses in plants, with a focus on bioenergy crops.

A. Genetic Regulation

Molecular, biochemical and genetic studies have established that drought stress signaling is regulated collectively by transcriptional activation of drought-induced genes, protein kinase activity, mitogen-activated protein kinase cascades, ubiquitin-dependent protein degradation, sumoylation and other protein post-translational processes. These genetic regulations can be divided into transcriptional, post- transcriptional and post-translational aspects.

1. Transcriptional regulation

Among the diverse molecular mechanisms, transcriptional reprogramming plays a central role in plant adaptation to drought (Shinozaki and Yamaguchi-Shinozaki, 2007; Tran *et al.*, 2007; Zhu, 2002). Some transcription factors serve as central hubs to modulate expression of multiple drought-regulated genes (Bartels and Sunkar, 2005; Fujii *et al.*, 2009; Shinozaki *et al.*, 2003; Thapa *et al.*, 2011; Yamaguchi-Shinozaki and Shinozaki, 2005; Yamaguchi-Shinozaki and Shinozaki, 2006; Zhu, 2002).

As noted above, transcription factors in the ABA-dependent pathways include 1) ABA-responsive element-binding protein/factor (AREB/ABF), 2) C-repeat-binding factor 4/dehydration-responsive element-binding protein 1D (CBF4/DREB1D), 3) myeloblastosis/myelocytomatosis (MYB/MYC), 4) Cys2His2 zinc-finger proteins (ZFP), and 5) WRKY domain binding transcription factors (WRKY) (Bartels and Sunkar, 2005; Fujii *et al.*, 2009; Shinozaki *et al.*, 2003; Thapa *et al.*, 2011; Yamaguchi-Shinozaki and Shinozaki, 2005; Yamaguchi-Shinozaki and Shinozaki, 2006; Zhu, 2002). ABA-independent pathways involve dehydration responsive element binding 2 (DREB2), NAM/ATAF/ CUC (NAC) and zinc-finger homeodomain (ZF-HD). Furthermore, some transcription factor families, such as APETALA 2/Ethylene Response Factor (AP2/ERF), include members involved in both ABA-dependent and ABA-independent pathways. Various drought responsive transcription factors have been identified in bioenergy crops (Table 2).

AREB/ABF, belonging to the basic region/leucine zipper motif (bZIP) class, binds to the G box-type ABA response element (ABRE) (i.e., PyACGTGGC) of many ABA-dependent genes (Kim, 2006). AP2/ERF includes CBF4/DREB1D (ABA-dependent) and DREB2 (ABA-independent) transcription factors, both of which regulate via the cis-acting dehydration-responsive /C-repeat (DRE/CRT) elements of three groups of drought/cold/salinity inducible genes (Abe *et al.*, 2003; Sakuma *et al.*, 2006). MYB/MYC family proteins, which are activated by drought and ABA treatment, bind to MYB and MYC elements within a 67-bp promoter region of the *RD22* gene in *Arabidopsis* (Abe *et al.*, 2003; Abe *et al.*, 1997; Zhou *et al.*, 2009). The NAC transcription factor family is unique to plants and consists of at least 100 members in both *Arabidopsis* and *Oryza sativa* (Fang *et al.*, 2008; Qu and Zhu, 2006; Tran *et al.*, 2007). The N-terminal DNA-binding domain of NAC transcription factors is highly conserved, whereas the C-terminal activation domain displays large variability (Hu *et al.*, 2008). The NAC domain interacts with ZFHD, which contains Zn-finger-like motifs upstream of a homeodomain (Tran *et al.*, 2007; Windhovel *et al.*, 2001; Yamaguchi-Shinozaki and Shinozaki, 2006). Transgenic plants with either overexpressed ZFHD or overexpressed NAC were shown to have a prominent improvement in drought tolerance (Tran *et al.*, 2007; Yamaguchi-Shinozaki and Shinozaki, 2006). ZFP, a large zinc-finger protein family, has also been implicated in salt, drought and cold response (Ciftci-Yilmaz and Mittler, 2008; Sakamoto *et al.*, 2004). Overexpression of GsZFP1, a newly isolated soybean ZFP that responded to ABA, resulted in decreased water loss rate and increased expression of other stress-inducible genes (Luo *et al.*, 2012). The WRKY transcription factor family has more than 70 members in both *A. thaliana* and *Oryza sativa* (Eulgem and Somssich, 2007). The WRKY domain typically interacts with W box (i.e., C/TTGACT/C) (Cai *et al.*, 2008; Ciolkowski *et al.*, 2008; Sun *et al.*, 2003). In addition to acting as a positive regulator of ABA-mediated signaling, many WRKY transcription factors have also been implicated in regulating other drought-responsive transcription factors, such as bZIP and MYB (Jiang and Yu, 2009; Rushton *et al.*, 2012; Shang *et al.*, 2010). Despite improved drought tolerance in *Arabidopsis* with ectopic expressed *OsWRKY45*, sensitivity toward ABA was found to be lowered in the transgenic plants (Qiu and Yu, 2009).

Multiple lines of evidence have demonstrated the possibility of manipulating transcription factors for enhanced drought tolerance, simply by overexpressing activators/down-regulating repressors to regulate stress tolerance genes or by introducing either a single or multiple site mutations to engineer alternative forms of transcription factors (Furihata *et al.*, 2006; Hossain *et al.*, 2010; Hu *et al.*, 2006; Kagaya *et al.*, 2002; Kim *et al.*, 2004; Maruyama *et al.*, 2004; Zhang *et al.*, 2005; Zhang, 2003; Zheng *et al.*, 2009). For instance, overexpression of AP2/ERF, NAC or MYB family members was reported to enhance levels of soluble carbohydrates and osmolytes in *Arabidopsis* and *Oryza sativa* under abiotic stress (Achard *et al.*, 2008; Mattana *et al.*, 2005; Song *et al.*, 2011; Takasaki *et al.*, 2010). Transgenic *Arabidopsis* with overexpressed soybean GmDREB2, as a means of activating other dehydration-inducible genes, was shown to have an improved tolerance to both drought and salt stresses, while still maintaining proper developmental and growth physiology (Chen *et al.*, 2007).

The promoter regions of many genes encoding dehydrins contain ABRE, DRE/CRT, MYB and MYC regulatory sequences (Jia *et al.*, 2006). Modulating the gene expression of transcription factors with modifiers and redesigning the promoter architecture have been instrumental in fine-tuning drought tolerance (Yamaguchi-Shinozaki and Shinozaki, 2005). For example, simply overexpressing native AREB1 does not confer drought tolerance; however, when the regulatory region between the activation and DNA-binding domain of AREB1 is deleted, a constitutively active AREB1 is expressed and the drought-tolerant phenotype is detected (Fujita *et al.*, 2005).

2. Post-transcriptional regulation

In plants, the accumulation of small RNAs under drought has attracted great attention to understand their role in stress-related responses (Covarrubias and Reyes, 2010; Khraiwesh *et al.*, 2012). In *Arabidopsis*, the levels of 117 miRNAs have been analyzed using miRNA chips and 17 stress-inducible miRNAs have been identified (Liu *et al.*, 2008). miR393, miR402, miR397b and miR319c were shown to be induced by drought stress whereas miR169 was down-regulated by drought in an

TABLE 2
Drought responsive transcription factors studied in bioenergy crops

Gene symbol	Plant species	Pathway	Description	References
ZmbZIP72	*Zea mays*	ABA-dependent	Positive	(Ying *et al.*, 2012)
ZmSNAC1	*Zea mays*	ABA, cold inducible	Positive	(Lu *et al.*, 2012)
ZmDBP4	*Zea mays*	ABA-independent	Positive	(Wang *et al.*, 2011)
ZmCBF3	*Zea mays*	ABA, Cold inducible	Positive	(Xu *et al.*, 2011)
ABP9	*Zea mays*	ABA, H_2O_2 inducible	Positive	(Zhang *et al.*, 2011)
ZmDBP3	*Zea mays*	Cold inducible	Positive	(Wang and Dong, 2009)
ZmDREB2A	*Zea mays*	Cold, drought inducible	Positive	(Qin *et al.*, 2007)
ZmDREB1A	*Zea mays*	Cold, drought	Positive	(Qin *et al.*, 2004)
DBF1,2	*Zea mays*	ABA-dependent	Positive	(Kizis and Pages, 2002)
PtaGTL1	*Populus tremula* × *P. alba (717-IB4)*	ABA-independent	Negative	(Weng *et al.*, 2012)
PeDREB2a	*Populus euphratica*	Cold, NaCl, GA_3 etc. inducible	Positive	(Zhou *et al.*, 2012)
PeSCL7	*Populus euphratica*	Drought inducible	Positive	(Ma *et al.*, 2010)
GmbZIP1	*Glycine max*	ABA inducible	Positive	(Gao *et al.*, 2011)
GmGT-2A/B	*Glycine max*	ABA-independent	Positive	(Xie *et al.*, 2009)
GmERF3	*Glycine max*	ABA, SA, JA, ethylene inducible	Positive	(Zhang *et al.*, 2009)
GmDREB3	*Glycine max*	ABA-independent	Positive	(Chen *et al.*, 2009)
GmDREB2	*Glycine max*	Drought, cold inducible	Positive	(Chen *et al.*, 2007)
GmMYB76, 177	*Glycine max*	ABA, cold inducible	Positive	(Liao *et al.*, 2008)
GmbZIP44, 62, 78	*Glycine max*	ABA, cold inducible	Negative	(Liao *et al.*, 2008)
GmWRKY54	*Glycine mac*	Cold, drought inducible	Positive	(Zhou *et al.*, 2008)
JcDREB	*Jatropha curas*	ABA-independent	Positive	(Tang *et al.*, 2011)
SbDREB2	*Sorghum bicolor*	Cold, drought inducible	Positive	(Bihani *et al.*, 2011)

ABA-dependent manner (Liu *et al.*, 2008). Similarly, it was reported that miR169g, which regulates expression of Nuclear Factor subunit A, was regulated by drought, possibly in an ABA-dependent pathway (Zhao *et al.*, 2009). Comparative profiling of miRNAs in root tissue between a salt-tolerant and a salt-sensitive *Zea mays* line revealed that members of the miR156, miR164, miR167 and miR396 families were down-regulated, while miR162, miR168, miR395 and miR474 families were up-regulated under salt treatments (Ding *et al.*, 2009). Recently, Zhou *et al*. (2010) identified 11 down-regulated miRNAs and eight up-regulated miRNAs in *Oryza sativa* under drought stress. More recently, it was reported that miR167, targeting IAA-Ala Resistant3, regulated root architecture under osmotic stress (Kinoshita *et al.*, 2012). Genome-wide identification of drought-responsive miRNAs were recently carried out in *Populus*, soybean, sugarcane, *Panicum virgatum* and *Medicago* with a number of conserved and non-conserved miRNAs related to drought response (Kulcheski *et al.*, 2011; Li *et al.*, 2011; Ren *et al.*, 2012; Sun *et al.*, 2012; Thiebaut *et al.*, 2012; Wang *et al.*, 2011). In *P. trichocarpa*, miR530a, miR1445, miR1446a-e, miR1447 and miR171l-n were found to be down-regulated, while miR482.2 and miR1450 were up-regulated under osmotic stress (Lu *et al.*, 2008). High-throughput sequencing in *P. euphratica* has identified 197 conserved miRNAs between *P. trichocarpa* and *P. euphratica* and 58 new miRNAs (Li *et al.*, 2011).

3. Post-translational regulation

In plants, protein post-translational modification plays pivotal roles in crosstalk between signaling cascades within highly interconnected networks in response to biotic and abiotic stimuli. Specific studies on protein post-translational modification in relation to drought-responsive pathways using woody bioenergy feedstock have not been reported, but efforts have been made in *Arabidopsis* and *Oryza sativa*. Our discussion will therefore focus on findings mainly from these two plants.

Phosphorylation by protein kinase, the most widely adopted post-translational regulation mechanism, regulates the expression of a number of dehydration-induced genes in plants. Under dehydration, because of osmolality imbalance, an influx of Ca^{2+} occurs and Ca^{2+}-dependent signaling responses have been reported, including post-translational modification of proteins (Tuteja and Mahajan, 2007). Altering the expression levels of Ca^{2+}-dependent protein kinases (CDPKs) has been suggested to influence the degree of drought tolerance in *Arabidopsis* (Harmon *et al.*, 2001; Hrabak *et al.*, 2003). CDPK activity has also been linked to the accumulation of Late Embryogenesis Abundant proteins (Serrano *et al.*, 2003; Xiong *et al.*, 2002), including many DREB2-induced genes that function in detoxification and cellular damage repair (Bartels and Sunkar, 2005; Umezawa *et al.*, 2006).

Mitogen-activated protein kinase (MAPK) represents a hierarchical protein kinase system, which responds to external stimuli in plants and other eukaryotes. The signaling pathway initiated from a stimulus at the cell surface is transduced by a sequential level of protein phosphorylation and activation in the order of MAPKK kinase, MAPK kinase and MAP kinase, leading eventually to translocation of phosphorylated transcription factors into the nucleus to activate other genes (Taj *et al.*, 2010; Treisman, 1996). It was reported that p44MMK4 kinase, transiently up-regulated by extreme drought in alfalfa, was involved in ABA-independent pathway (Jonak *et al.*, 1996). Recently, a nuclear protein kinase similar to Raf-like MAPKK kinase was found to confer drought tolerance by scavenging oxidative damage in *Oryza sativa* (Ning *et al.*, 2010). Another case implicating MAPK in drought response is a recent observation that *ZmMPK3* transcripts accumulated significantly in *Zea mays* seedlings upon exogenous treatments, including ABA and drought stress (Wang *et al.*, 2010). Furthermore, *Oryza sativa OsWRKY30*, a member of WRKY transcription factor family, has been shown to increase drought tolerance downstream of the MAPK cascade (Shen *et al.*, 2012). On the other hand, an *Oryza sativa* MAPK phosphatase, IBR5, induced by abiotic stress, negatively regulates drought tolerance in transgenic tobacco plants (Li *et al.*, 2012).

The ubiquitination/26S proteasome (UPS) system, based on poly-ubiquitination linked through Lysine-48, is a post-translational modification system that results in protein degradation and serves as an important regulator for many critical cellular processes in plants (Glickman and Adir, 2004; Kurepa *et al.*, 2003; Santner and Estelle, 2010; Smalle and Vierstra, 2004). In this system, a ubiquitin tag composed of 76 amino acids is ligated to the serine residue in the target protein through sequential actions of ubiquitin-activating enzyme (E1), ubiquitin-conjugating enzyme (E2) and ubiquitin ligase (E3) (Bachmair *et al.*, 2001; Dreher and Callis, 2007). Earlier observations revealed the diverse roles of different families of E3 ligases, such as RING-H2 zinc finger E3, Ring E3, C3H2C3-type RING E3, RING- E3 and U-box E3 proteins in the regulation of drought response in either a positive or negative fashion and in either ABA-dependent or ABA–independent pathways (Cho *et al.*, 2006; Cho *et al.*, 2008; Ko *et al.*, 2006; Lee *et al.*, 2009; Ryu *et al.*, 2010; Zhang *et al.*, 2007). Recently, OsDIS1, an *Oryza sativa* SINA type E3 ligase, was reported to mediate the degradation of a seine/threonine protein kinase, OsNek6, and overexpression of OsDIS1 resulted in a decline in drought tolerance (Ning *et al.*, 2011). Similarly, PUB19, an *Arabidopsis* U-box E3 ligase which is upregulated by drought, is a negative regulator of drought response; and downregulation of PUB19 increases the sensitivity of ABA-induced stomatal closing and consequently enhances drought tolerance (Liu *et al.*, 2011). In contrast, AtAIRP1, a RING E3 ligase, positively regulates the ABA-dependent drought response, and overexpression of AtAIRP1 imparts drought tolerance and rescues the loss-of-function ABA-insensitive phenotype (Ryu *et al.*, 2010). In *Oryza sativa*, U-box E3 ligase (PUB15), also a positive regulator, is upregulated by drought stress and possesses antioxidant activity that detoxifies reactive oxygen species (Park *et al.*, 2011). The expression of DREB2A is regulated by post-translational modification (Sakuma *et al.*, 2006). DRIP1 and DRIP2 are negative regulators that target DREB2A for 26S proteasome proteolysis, thus delaying the expression of DREB2A-driven drought-responsive genes (Qin *et al.*, 2008).

Another class of post-translational modification heavily involved in regulation of plant abiotic stress is sumoylation (small ubiquitin-related modifier [SUMO]), which also comprises steps of E1-activation, E2-conjugation and E3-ligation, with E3 ligase determining target specificity (Castro *et al.*, 2012; Colby *et al.*, 2006; Girdwood *et al.*, 2004; Johnson, 2004; Kerscher *et al.*, 2006; Kurepa *et al.*, 2003; Park *et al.*, 2011). In this system, SUMO protein is covalently attached to specific lysine residues of target proteins to antagonize protein degradation by ubiquitination (Johnson, 2004; Kerscher *et al.*, 2006). Sumoylation also mediates changes in protein-protein interactions, regulates protein sub-cellular localization, and exerts its effect at the transcriptional level (Colby *et al.*, 2006; Girdwood *et al.*, 2004; Johnson, 2004; Kurepa *et al.*, 2003). When subjected to dehydration, *Arabidopsis* SIZ1, a SUMO E3 ligase, controls the expression of about 300 ABA-independent drought-responsive genes, and regulates the accumulation of other SUMO-protein conjugates that induces cell expansion and proliferation (Catala *et al.*, 2007; Miura *et al.*, 2005). Consequently, a *siz1* mutant with a reduced level of SUMO-protein conjugates is defective in a number of physiological traits and more susceptible to abiotic stresses (Catala *et al.*, 2007; Lee *et al.*, 2007; Miura *et al.*, 2007; Miura *et al.*, 2005). ULP1c/d, a negative regulator of drought tolerance, and SUMO protease work in concert with SIZ1 to control the dynamics of SUMO conjugation/de-conjugation cycle of abiotic stress-related genes (Castro *et al.*, 2012; Conti *et al.*, 2008).

The sucrose non-fermenting-1-related protein kinase 2 (SnRK2) governs stomatal closure in response to reduced transpirational water loss imposed by drought (Mustilli *et al.*, 2002; Yoshida *et al.*, 2002). The SNF1-related protein kinase-1

(SnRK1) may also regulate drought response by altering the expression of genes involved in carbohydrate metabolism through the ratio of ATP/AMP as its signal (Celenza and Carlson, 1984; Hardie, 2007). In contrast, phosphatase antagonizes kinase activity by removing the phosphate tags. For example, the stress-activated MAPK pathway in plants and yeast is inactivated by MP2C phosphatase (Meskiene *et al.*, 1998). MP2C phosphatase has been proposed to be one component of an elaborate negative feedback regulatory network that requires a refractory period before MAPK signaling can be restarted again after inactivation (Meskiene *et al.*, 1998).

Poly ADP ribosylation is also thought to play a role in drought reponse as shown by the characterization of PARG1, a poly ADP ribose glycohydrolase 1 enzyme in *Arabdopsis* (Li *et al.*, 2011). The stomata of *parg1-3* mutant plants do not close under drought stress, with plants exhibiting an elevated level of cell damage in the presence of osmotic stress and an overall phenotype indicating reduced drought tolerance (Li *et al.*, 2011).

Protein farnesylation, characterized by the conjugation of C15-prenyl residues to the carboxyl termini of specific substrates, plays a role in the negative regulation of ABA signaling (Crowell, 2000; Galichet and Gruissem, 2003; Nambara and McCourt, 1999; Yalovsky *et al.*, 2000; Ziegelhoffer *et al.*, 2000). In plants, farnesyltransferase is heterodimer consisting of α- and β-subunits, each encoded by a specific gene family (Cutler *et al.*, 1996; Galichet and Gruissem, 2003; Nambara and McCourt, 1999). Down-regulation of *ERA1* gene (encoding a β-subunit of *Arabidopsis* farnesyltransferase) in *Brassica napus* was reported to improve drought tolerance via enhancing ABA sensitivity, which prompts stomatal closure under dehydration (Wang and Stormo, 2005).

Among the aforementioned post-transalatoinal modifications, SNF-related kinase, CDPK and MAPK-based signaling have all been observed to play a positive role in the increase of osmolytes, such as proline to stablize enzymes, cell structures and protein complexes under dessication (Fujii *et al.*, 2011). Increased levels of carbohydrates and proline can also be achieved by overexpreesoin of NAC and MYB family transciprtion factors, thus reinforceing the principle of heavy crosstalk between regulatory mechniams to defend against drought stress. Dormancy responses, described by reduced metabolism, inhibition of photosynthesis, and cessation of physiological activities until water becomes available, are prevalent in plant species found in arid and semi-arid environments (Hoekstra *et al.*, 2001; Koller, 1969; Mittler *et al.*, 2001). Pnueli *et al*. (2002) proposed that the dormancy state of a C3 drought-tolerant dessert legume was controlled by a specialized cell redox status that was dependent on post-translational modification.

B. Epigenetic Regulation

Besides genetic control, drought response can also be regulated through epigenetic mechanisms such as DNA methylation and histone modification.

1. DNA methylation

DNA methylation, defined as the addition of a methyl group at cytosine bases of DNA to form 5-methylcytosine, plays crucial roles in regulating genome-wide gene expression and maintaining genomic stability in response to drought stress (Boyko and Kovalchuk, 2008; Chinnusamy and Zhu, 2009; Hamanishi ET, 2011; Saze *et al.*, 2012; Wang *et al.*, 2011). DNA methylation provides a heritable stress-memory (Chinnusamy and Zhu, 2009). Genome-wide methylation in *Arabidopsis* was recently shown to increase in the progeny of plants exposed to extreme temperature, UV-B, flooding and salt stress, but decrease in the progeny of drought-stressed plants (Boyko *et al.*, 2010; Boyko and Kovalchuk, 2010; Lang-Mladek *et al.*, 2010). A genotype-dependent 5-methylcytosine pattern has been revealed in the shoot apices of drought-stressed hybrid poplars (*P. deltoides* × *P. nigra*) (Gourcilleau *et al.*, 2010). Using the clonally propagated *Populus* hybrid genotypes from DN34 (*P. deltoides* × *P. nigra*), Walker [*P. deltoides* × (*P. laurifolia* × *P. nigra*)] and Okanese [Walker × (*P. laurifolia* × P. *nigra*)], Raj *et al*. (2011) showed that ramets from clones of separate geographic origins developed different transcriptomes and DNA methylation levels in response to the same drought treatment. Their findings support the hypothesis that the transcriptome/DNA methylation-level response of a given genotype can be shaped by the history of the clones. They speculated that the older the clone, the more likely the ramets from different locations had a divergent history and, consequently, divergent drought transcriptome and DNA methylation.

Recently, Wang *et al*. (2011) compared the genome-wide DNA methylation status of two *Oryza sativa* cultivars with different tolerance to drought (i.e., the drought-tolerant line DK151 and its drought-sensitive parent IR64) through the methylation-sensitive amplified polymorphism analysis (MSAP), and found significant differences in the methylation patterns between the two genomes. In *Arabidopsis* two novel *Microrchidia* (*MORC*) adenosine triphosphatase (ATPase) family genes (i.e., *AtMORC1* and *AtMORC6*), which cause derepression of DNA-methylated genes, play conserved roles in regulating gene silencing in eukaryotes through higher-order compaction of methylated and chromatin silencing (Moissiard *et al.*, 2012). A mutation in a plant-specific *MOM1* gene was also shown to affect gene silencing without affecting DNA methylation in *Arabidopsis*; however, *mom1* mutants did not show chromocenter decondensation and, therefore, were likely to act via an alternate mechanism (Amedeo *et al.*, 2000; Probst *et al.*, 2003). Fan *et al*. (2012) showed that exogenous nitric oxide treatment decreased the global DNA methylation levels of *Dendrobium huoshanense* in response to drought stress.

2. Histone modification

Post-translational modification of specific residues on the four core histones (H2A, H2B, H3 and H4) play major roles in regulating genome function, presumably by recruiting of transcription factors or other protein complexes that affect chromatin

structure and state (Hake *et al.*, 2007; Ruthenburg *et al.*, 2007). Tri-methylation of H3 at lysine 4 (H3K4me3), which is catalyzed by a specific histone methyltransferase of the Trithorax (TrxG) group, leads to gene transcription, whereas trimethylation of H3 at lysine 27 (H3K27me3) by a specific methyltransferase of the Polycomb group leads to the repression of gene expression (Alexandre *et al.*, 2009; Alvarez-Venegas, 2010; Liu *et al.*, 2010). Upon water deficiency, nucleosome pattern and histone modification, specifically on the H3 N-tail of four *Arabidopsis* drought-reponsive genes, are altered to activate their coding region (Kim *et al.*, 2008). Papaefthimiou and Tsaftaris (2012) also identified another putative plant-specific PKDM7 subfamily histone demethylase gene, *HvPKDM7-1*, that was significantly induced by drought stress. Qian *et al*. (2012) identified a novel gene, *increased DNA methylation 1* (*IDM1*), required for preventing DNA hypermethylation of highly homologous multicopy genes and other repetitive sequences.

Histone modifications have been detected on the N-terminal tails of H3 in association with four drought-stress responsive genes (i.e., *RD29A, RD29B, RD20* and *Atg20880*) in *Arabidopsis* under drought stress (Kim *et al.*, 2008). van Dijk *et al*. (2010) compared the genome-wide epigenomic modification of H3K4me1, H3K4me2 and H3K4me3 patterns in chromatin isolated from *Arabidopsis* rosette leaves before and after dehydration stress through genome-wide analysis, and found a substantial change in H3K4me3 abundance occurred upon dehydration stress, whereas there were only moderate changes in H3K4me1 and H3K4me2 levels. A recent study on the expression of three major drought stress-responsive genes (*RD20*, *RD29A* and *AtGOLS2*) revealed that the transcriptional activity and chromatin status were rapidly changed from an active to inactive mode during the process of recovery from drought stress, indicating that histone modifications are correlated with the inactivation of drought-inducible genes during the recovery process by rehydration (Kim *et al.*, 2012). It was also shown that most drought-induced DNA methylation/demethylation loci could be reversed to their original status after recovery (Wang *et al.*, 2011).

Histone modifications are often found to be induced by ABA in response to the drought stress (Chinnusamy *et al.*, 2008). ABA treatment causes severe reduction in the expression of *AtHD2C*, a plant-specific histone deacetylase gene, whereas overexpression of *AtHD2C* results in insensitivity to ABA and enhanced drought tolerance (Sridha and Wu, 2006). The transgenic *Arabidopsis* co-suppression lines (*msi1-cs*) of *MSI1* gene, encoding a subunit of Polycomb group protein complexes and chromatin assembly factor 1, have an increased drought stress tolerance phenotype (Alexandre *et al.*, 2009).

V. COMPARATIVE AND EVOLUTIONARY GENOMICS

Comparative analyses of sequenced genomes or transcriptomes across phyla could provide new insights into drought tolerance beyond the knowledge obtained from genomics studies on individual species. By comparing the drought-induced transcriptome of *Sorghum bicolor* with other transcriptomes in *Oryza sativa*, *Zea mays* and *Arabidopsis*, Dugas *et al.* (2011) identified more than 50 drought-responsive genes of unknown function. Six drought-associated gene clusters have been identified by comparing large-scale protein sequences that occur in drought tolerant species (foxtail millet and *Sorghum bicolor*) and drought susceptible species (*Zea mays* and *Oryza sativa*) (Bennetzen *et al.*, 2012). Recently, a homolog of an *Arabidopsis* drought tolerance DNA-binding transcription factor was identified in the *Sorghum bicolor* genome by *in silico* targeted genome mining and comparative analysis of structural and functional properties (Shanker *et al.*, 2012). Comparative evolutionary analyses of multiple sequenced plant genomes have discovered more than 100 non-family genes (i.e., 1–2 copies per genome) that were associated with response to water deficiency (Ye *et al.*, 2013). Comparative genomics analysis has also been performed to examine drought tolerance at the genotype level. For instance, comparative transcriptome profiling of two contrasting *Populus* genotypes differing in drought tolerance has identified several candidate genes preferentially involved in early and long-term responses to drought (Cohen *et al.*, 2010).

VI. FUTURE PERSPECTIVES

Drought response involves multiple signaling pathways that are subject to both genetic and epigenetic regulation. Genetic improvement in drought tolerance is a viable solution to overcome the bottleneck of sustainable production of bioenergy crops in arid and semi-arid regions. Successful genetic modifications benefit from a deep understanding of drought responsive pathways in the target crops. Unraveling the complexity of drought response pathways will require a systems biology approach, including genomics, transcriptomics, proteomics, metabolomics and phenomics. It is apparent that our current understanding of the molecular mechanisms underlying drought tolerance in bioenergy crops is very limited, relative to model plants like *Arabidopsis*. Although the knowledge gained from model plants can be transferred to non-model crops using translational genomics approaches, future genome-scale studies on drought signaling pathways in non-model bioenergy crops are necessary, given that drought response is dependent on species and genotype. The current second generation and emerging third generation DNA sequencing technology, high-throughput phenotyping platforms, and improved informatics resources will greatly expedite gene discovery in bioenergy crops.

One trend in drought genomics research is to understand the molecular and biochemical basis of Crassulacean Acid Metabolism (CAM), which enables a significant increase in WUE relative to C3 and C4 plants (Borland *et al.*, 2009). CAM plants, such as Agave and *Opuntia*, are emerging biofuel crops with great potential for sustainable biomass production in semi-arid areas (Borland *et al.*, 2009; Yang *et al.*, 2011). Future exploration of genomics and functional genomics in this understudied domain may open a new door to genetic improvement

in WUE in bioenergy crops, as shown in genetic engineering for other traits (Ye *et al*., 2011).

ACKNOWLEDGMENTS

This material is based in part upon work supported by the Department of Energy, Office of Science, Genomic Science Program under Award Number DE-SC0008834, the U.S. DOE BioEnergy Science Center and the Laboratory Directed Research and Development Program of Oak Ridge National Laboratory. The BioEnergy Science Center is a U.S. Department of Energy Bioenergy Research Center supported by the Office of Biological and Environmental Research in the DOE Office of Science. The Oak Ridge National Laboratory is managed by UT-Battelle, LLC for the U.S. Department of Energy under Contract Number DE-AC05-00OR22725.

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