

# Examining the drought stress transcriptome in cotton leaf and root tissue

Paxton Payton · Kameswara Rao Kottapalli ·  
Hirut Kebede · James R. Mahan ·  
Robert J. Wright · Randy D. Allen

Received: 1 October 2010 / Accepted: 8 December 2010 / Published online: 28 December 2010  
© Springer Science+Business Media B.V. (outside the USA) 2010

**Abstract** Growth, yield, and yield quality of cotton are greatly affected by water-deficit stress. We have identified the genes and associated metabolic pathways involved in the water-deficit stress response in leaf and root. Gene expression profiles were developed for leaf and root tissues subjected to slow-onset water deficit under controlled, glasshouse conditions. The water-deficit stress was characterized by leaf water potential of  $-23.1$  bars for stressed tissue compared to  $-8.7$  bars for fully-irrigated control plants and a corresponding decrease in net carbon assimilation to approximately 60% of the rates seen in the irrigated controls

( $30.3 \pm 4.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  compared to  $17.8 \pm 5.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Profiling experiments revealed 2,106 stress-responsive transcripts, 879 classified as stress-induced, 1,163 stress-repressed, and 64 showed reciprocal expression patterns in root and leaf. The majority of stress-responsive transcripts had tissue-specific expression patterns and only 173 genes showed similar patterns of stress responsive expression in both tissues. A variety of putative metabolic and regulatory pathways were identified using MapMan software and the potential targets for candidate gene selection and ectopic expression to alter these pathways and responses are discussed.

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10529-010-0499-y](https://doi.org/10.1007/s10529-010-0499-y)) contains supplementary material, which is available to authorized users.

P. Payton (✉) · K. R. Kottapalli · J. R. Mahan  
USDA-ARS Cropping Systems Research Laboratory,  
Lubbock, TX 79415, USA  
e-mail: [paxton.payton@ars.usda.gov](mailto:paxton.payton@ars.usda.gov)

K. R. Kottapalli · H. Kebede · R. J. Wright  
Department of Plant and Soil Science,  
Texas Tech University, Lubbock, TX 79409, USA

H. Kebede  
USDA-ARS Crop Genetics Research Unit, Stoneville,  
MI 38776, USA

R. D. Allen  
Department of Biochemistry and Molecular Biology,  
Oklahoma State University, Stillwater, OK 73401, USA

**Keywords** Cotton · Drought stress · Leaf · Root · Transcript profile

## Introduction

Although cotton exhibits moderately high tolerance during vegetative development, water-deficit stress is one of the major limiting factors in its production. Recent advances in DNA sequencing and functional genomics technologies provide powerful tools for the genetic dissection of abiotic stress tolerance in crop plants (Valliyodan and Nguyen 2006). Large-scale genome projects have generated a mass of knowledge regarding the structural organization and function of stress-responsive genes in plants (Hamel et al. 2006). Searchable databases and analytic tools available to

the research community offer the capacity to query these data. These comparative tools from related fields enable the identification of genes and gene products, and may reveal functional relationships between a genotype and observed phenotype (Edwards and Batley 2004; Mayes et al. 2005). There is an opportunity to make direct and meaningful comparisons from data generated by both structural and functional approaches to provide solutions for crop improvement, especially when combined with physiological data. In accordance with those goals, an established set of data related to tissue-specific responses, developmental stages, abiotic stress, and biotic factors is required to enhance our ability to integrate structural, physiological, and functional genomics with phenotypes of interest.

The development of drought-tolerant crops has been hindered by our limited knowledge of more precise physiological parameters that reflect genetic potential for improved productivity or genetic limitations under water-limited and thermally stressful environments. The potential to identify key traits that limit yield under abiotic stress conditions hinges upon our understanding of the responses at both the physiological and molecular levels and integrating these responses with whole-plant phenotypes. This indirect approach, combined with traditional empirical breeding strategies, will hasten yield improvement (Araus et al. 2002). Our present ability to study plant responses at the transcriptome level has provided insight into the complex nature of multi-genic responses (Bray 2002, 2004; Rizhsky et al. 2004; Mantri et al. 2007; Shinozaki and Yamaguchi-Shinozaki 2007; Taliercio et al. 2009; Urano et al. 2010). More recently, positional cloning and candidate gene approaches have begun to identify a limited number of structural genes or transcription factors controlling the larger response to abiotic and biotic stimuli (Urano et al. 2010).

For cotton, an initial community-wide effort produced 185,198 Expressed Sequence Tags (ESTs) from 30 cDNA libraries, sampling a variety of tissues, primarily fiber, as well as tissues subjected to abiotic stresses such as chilling temperatures and water-deficit (Udall et al. 2006). Subsequently, a subset of these sequences was used to generate a publicly available oligonucleotide microarray for gene expression studies. Even though this array did not provide complete transcriptome coverage, particularly for stress-related

genes, together with the assembled EST database, described by Udall et al. (2006), it has provided a foundation for more robust functional analysis of a multitude of developmental responses in cotton.

Our long-term goal is to explore the regulatory networks that control the expression of stress-responsive genes. The principal aim of this study was to identify cotton genes implicated in water-deficit stress in leaf and root material exposed to slow-onset water deficit, similar to that which occurs under field conditions during irrigation intervals or between rainfall events. The results of this study provide insight into the distinct differences in the mechanisms involved in these tissues under soil water deficits and establishes a collection of potential candidate genes for functional gene expression studies related to improving stress tolerance in cotton.

## Materials and methods

### Water-deficit stress treatment

Cotton plants (FiberMax 989, Bayer CropScience, Inc.) were grown under glasshouse conditions (approx. 28/20°C, day/night) in 25 l pots containing a 2:1:1 mix of potting soil (Sunshine Mix #1; SunGro Horticultural, Canada):field soil (Amarillo sandy loam):sand. Plants were grown 12 weeks and irrigated to field capacity as needed, generally every 4–6 days, and fertilized weekly with 50% Hoagland's solution. Water-deficit stress was imposed by withholding irrigation and monitored based on leaf water potential measured with a pressure bomb. Additionally, leaf-level net carbon assimilation was measured on the 4th apical leaf using a portable infrared gas analyzer (Li-COR, Model LI-6400, Lincoln, NE, USA). Leaf-to-air vapor pressure deficit (VPD), air temperature, and CO<sub>2</sub> concentration (400 μmol mol<sup>-1</sup>) of the cuvette were set to ambient environmental values for each measurement period and maintained constant for all measurements across pots. Irradiance was set to saturating conditions (2000 μmol m<sup>-2</sup> s<sup>-1</sup>) using a light-emitting diode (Licor LI-6400-002). Data were logged three times for each leaf and then averaged for each plant to be used as a statistical unit. At the time of leaf and root tissue harvest, leaf water potentials averaged -8.7 bars (±0.37 SE) for fully-irrigated control plants and -23.1 bars (±2.28 SE) for stressed

plants. Leaf photosynthetic rates had decreased to approximately 60% of the rates seen in the irrigated controls ( $30.3 \pm 4.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  compared to  $17.8 \pm 5.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). The youngest, nearly fully-expanded leaf (4th leaf from the apical meristem) was sampled from each plant and immediately frozen in liquid nitrogen. Root tissue, both tap and lateral root, was harvested by sampling lateral roots in two sequential steps of flash freezing in liquid nitrogen. For the first step, pots were cut away from the plant, as much soil as possible was removed by gentle shaking, and roots were placed in liquid N<sub>2</sub>. This step was achieved in approximately 60 s. The second step involved isolating as much root tissue from the remaining soil with forceps and a small screen in liquid N<sub>2</sub>. Frozen tissue samples were transferred to a 50 ml conical vial in liquid N<sub>2</sub> and subsequently moved to a freezer for storage at  $-80^\circ\text{C}$ .

#### Gene expression analysis

Gene expression profiling experiments were carried out using the cotton oligonucleotide microarray described by Gene Expression Omnibus Platform GPL4305 and series GSE8719 (<http://www.ncbi.nlm.nih.gov/geo>). The array is composed of 12,006 oligonucleotides derived from an assembly of more than 180,000 *Gossypium* ESTs sequenced from 30 cDNA libraries ([www.cottonevolution.info/microarray](http://www.cottonevolution.info/microarray)). Expression data were subjected to LOWESS normalization and a Benjamini and Hochberg multiple testing correction. Differential expression was defined as  $\geq 2$  fold change in expression level at  $P \leq 0.05$  in at least 4 of 6 replicate hybridizations of 3 biological replicates in dye-swap comparisons.

Total RNA was isolated using the modified hot-borate method of Wilkins and Smart (1996). Target RNA (25  $\mu\text{g}$ ), quantified spectrophotometrically (Nanodrop Technologies, Inc., Wilmington, DE), was labeled using the amino-allyl MessageAmp labeling kit (Ambion, Austin, TX). Hybridizations were carried out at  $55^\circ\text{C}$  for 18 h. The hybridized chips were scanned using an Axon 4000B laser scanner. Data were analyzed using GeneSpring 7.0 software (Agilent Technologies, Santa Clara, CA).

Reverse transcription (RT)-PCR analysis was conducted on selected differentially expressed genes to validate the microarray result. cDNA was synthesized

from 4  $\mu\text{g}$  total RNA from leaves and roots of water-deficit stressed and control plants using MMLV reverse transcriptase and oligo-dT (20 mer) in a 50  $\mu\text{l}$  reaction volume. The cDNA was amplified using specific primers designed for the selected genes. The PCR contained 100  $\mu\text{M}$  dNTPs, 25 mM MgCl<sub>2</sub>, 1X Taq polymerase, PCR buffer, 100  $\mu\text{M}$  primers and 2  $\mu\text{l}$  cDNA reaction mixture. The PCR was carried out as follows, 5 min at  $94^\circ\text{C}$ , followed by 30 cycles of 40 s of denaturation at  $94^\circ\text{C}$ , 40 s of annealing at  $58^\circ\text{C}$  and extension for 1 min at  $72^\circ\text{C}$ , and a single extension cycle of 7 min at  $72^\circ\text{C}$ . PCR products were resolved in 1% agarose gel by electrophoresis and stained with ethidium bromide.

#### MapMan analysis

MapMan software version 2.20 was used to display expression profiles at the pathway level (Thimm et al. 2004; <http://gabi.rzpd.de/projects/MapMan/>). The assembled EST sequences used to generate a mapping file using Mercator tools and log ratio expression values from stressed versus well-watered controls were used to visualize the cotton transcript expression data. The set of cotton genes represented in the mapping file, MapMan bin identifiers, and array identifiers are listed in Supplementary Table 1 and can be downloaded at [www.csrl.ars.usda.gov/psgd/droughtstresspublication.aspx](http://www.csrl.ars.usda.gov/psgd/droughtstresspublication.aspx). The graphical representations generated from the stressed to control expression ratios of the differentially expressed genes are presented as metabolism overview, regulation overview, and transcription overview.

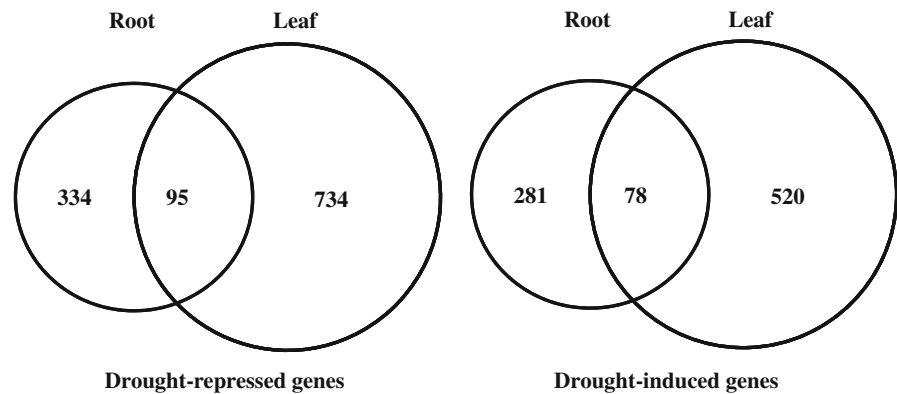
## Results and discussion

#### Gene expression

Transcriptional responses to imposed water-deficit stress in leaf and root tissue of 12-week old cotton plants revealed 2,106 stress-responsive transcripts (Fig. 1). The entire set of differentially expressed genes can be viewed in Supplementary Table 1 and downloaded at [www.csrl.ars.usda.gov/psgd/droughtstresspublication.aspx](http://www.csrl.ars.usda.gov/psgd/droughtstresspublication.aspx).

A subset of transcripts was selected for RT-PCR to validate the microarray experiments (Table 1). A total of 879 transcripts were classified as stress-induced

**Fig. 1** Venn-diagram of transcripts showing differential expression in cotton leaf and root tissue exposed to slow-onset water deficit stress. Differential expression was defined as  $\geq 2$  fold change in expression at  $P \leq 0.05$



and 1,163 stress-repressed transcripts in root and/or leaf (Fig. 1). Almost twice as many stress-responsive genes were identified in leaf compared to root, 1,491 and 852, respectively, and only 173 genes showed similar patterns of stress responsive expression in both tissues. The significant difference in expression profiles between these two tissues is likely due to both the diverse functions of these tissues and the lack of root-specific ESTs on the array. Additionally, 64 transcripts showed reciprocal expression patterns in root and leaf (15 induced in root, but repressed in leaf; 49 induced in leaf but repressed in root).

The functional groups identified as stress-responsive in leaf and root were in many cases similar, however, gene expression patterns within those groups were distinctly different. Figures 2 and 3 show the MapMan overview of water-deficit stress responsive transcripts in leaf and root, respectively. Cell signaling, cell wall metabolism, membrane and lipid metabolism, secondary metabolism, particularly terpene and flavanoid biosynthesis, and carbon metabolism showed distinctly different responses in leaf and root.

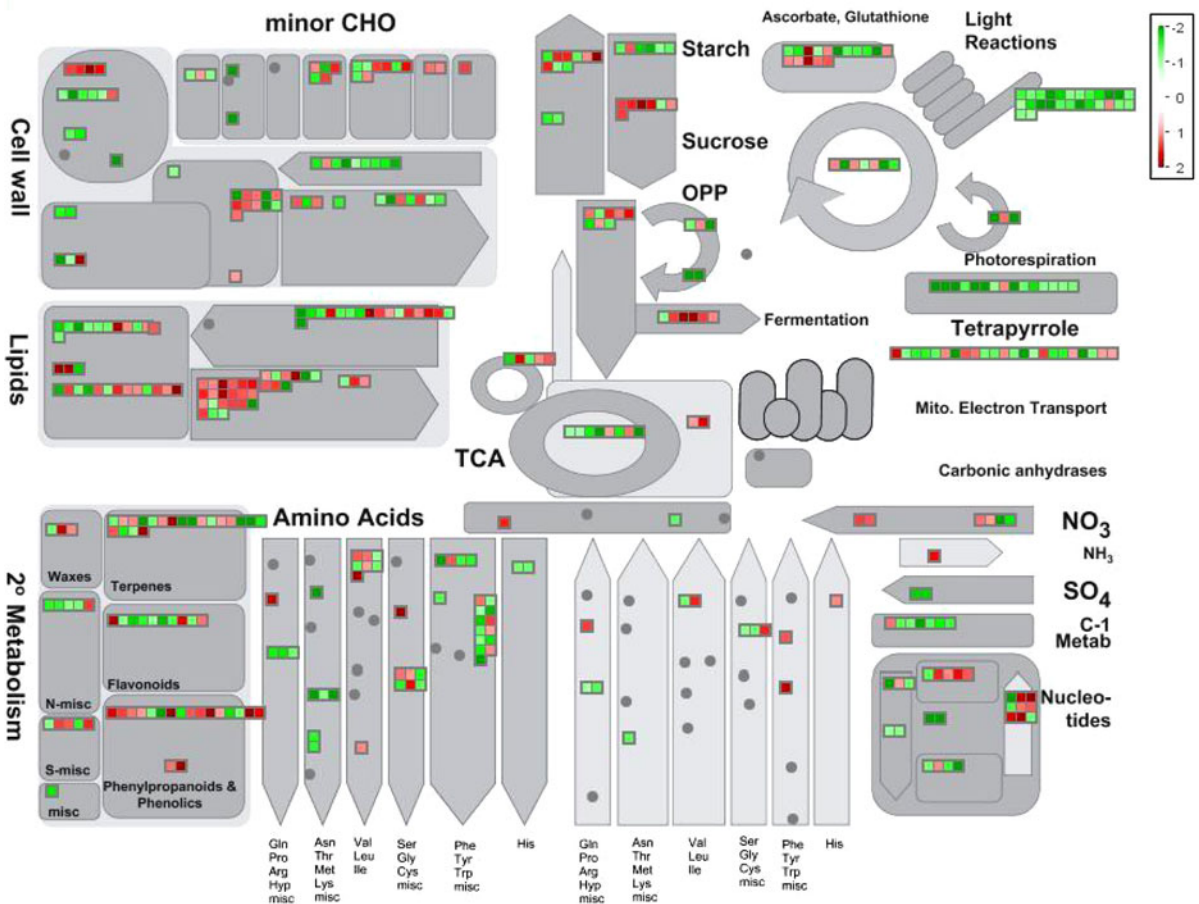
Table 1 shows a subset of transcripts which showed tissue-specific induction in response to water-deficit stress. The four major functional groups showing stress induction in leaf were cell signaling, stress response, regulation of transcription, and hormone biosynthesis or signaling. For root, the major responsive categories were stress response, carbon metabolism, regulation of transcription, and cell signaling (Supplementary Table 1). Comparisons of similar functional groups showing stress induction in leaf and root revealed the distinct differences in potential mechanisms affected by water-deficit. In

leaves, the majority of induced transcripts in the Stress Response functional group were heat shock factors and pathogenesis-related response proteins. This observation, along with the fact that numerous cell wall-related enzymes and lipid biosynthesis proteins were also shown to be stress-responsive (Supplementary Table 1) indicates that the primary defense response in leaf tissue is related to maintaining membrane and cell wall integrity.

For roots, there did not appear to be an abundance of a single class of genes induced by drought stress in the Stress Response functional group, which included well-characterized stress-responsive genes like heat shock factors, early light-inducible proteins, DREB transcription factors, and BURP domain proteins (Zhu 2002; Seki et al. 2003; Jia et al. 2006; Cramer et al. 2007; Shinozaki and Yamaguchi-Shinozaki 2007; Catterou et al. 2001). Root tissue also showed a significant induction of transcripts related to carbon/sugar metabolism suggesting the importance of the synthesis of sugars as osmoregulators, another commonly observed response to water deficit stress and a response that has been shown to correlate with increased yield and dry matter production (Subbarao et al. 2000; Niknam et al. 2003; Moinuddin and Renu 2004; Moinuddin et al. 2005; Cramer et al. 2007; Charlton et al. 2008; Kottapalli et al. 2009). This group of candidate genes may be involved in osmotic adjustment by osmotic-stress signaling leading to the expression of early response transcriptional activators, which then activate downstream stress tolerance effector genes (Shinozaki and Yamaguchi-Shinozaki 1999). Similarly, transcripts showing decreased expression/repression under water-deficit stress in root tissue represented the majority of functional

**Table 1** RT-PCR expression analysis of selected differentially expressed transcripts in cotton leaf and root subjected to water-deficit stress

Gene ID	Microarray		RT-PCR				Putative homology
	Root <sub>st/c</sub>	Leaf <sub>st/c</sub>	Root <sub>st</sub>	Root <sub>c</sub>	Leaf <sub>st</sub>	Leaf <sub>c</sub>	
Cotton12_04395_01	4.18	1.73					Ethylene response factor ERF3a
Cotton12_07910_01	0.67	0.09					Ethylene repressed major latex protein (MLP)
Cotton12_19658_01	4.18	1.28					Hypothetical protein At1g09310
Cotton12_02930_01	1.07	2.40					4-Coumarate:CoA ligase
Cotton12_04760_01	5.44	3.75					Isoprenylated protein
Cotton12_13170_01	0.21	0.70					BZIP transcription factor BZI-2
Cotton12_09309_01	2.17	1.56					DNA-binding protein

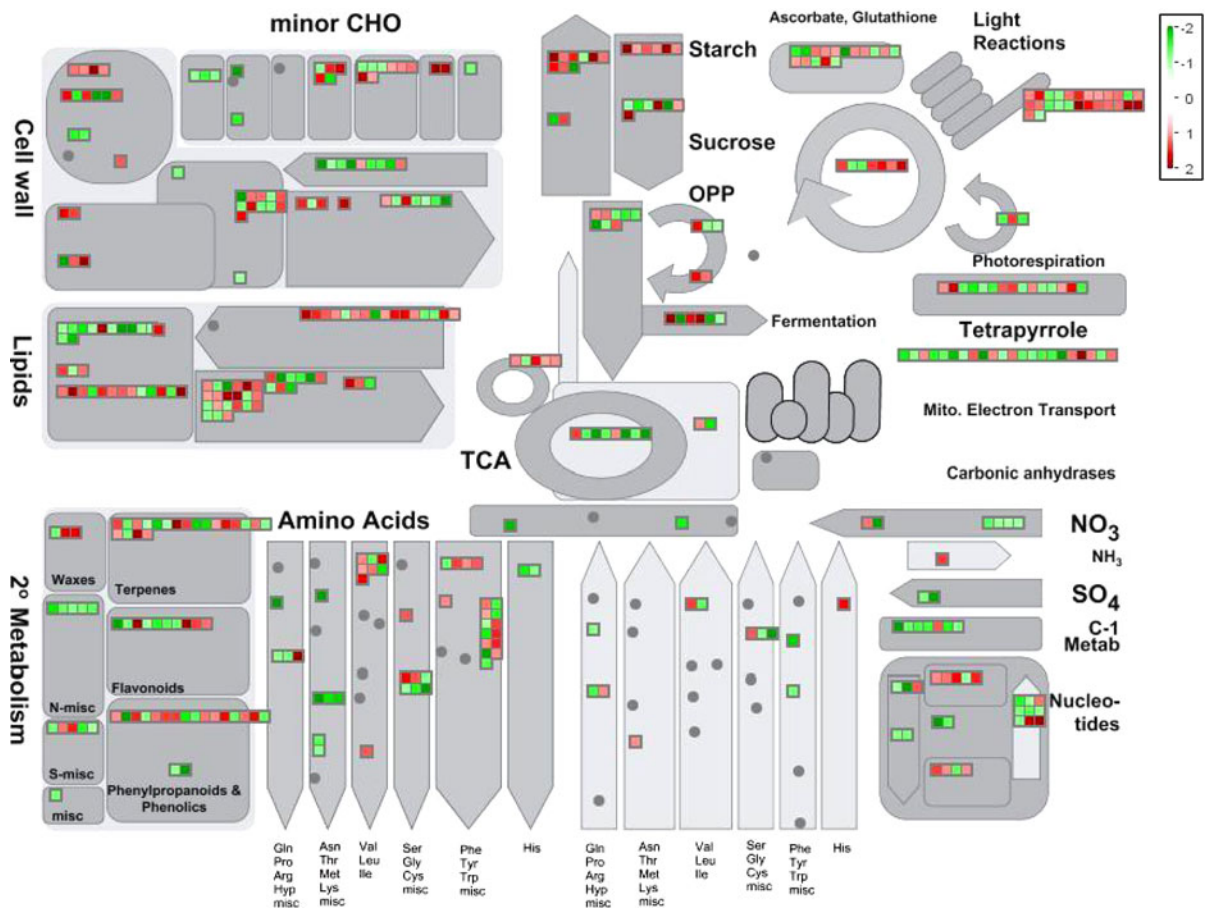


**Fig. 2** MapMan metabolic overview of water-deficit stress responsive genes in cotton leaf. *Boxes* represent log<sub>2</sub> expression values of stress-responsive genes. Genes in *red* are up-regulated in response to stress and those in *green* are repressed

groups assigned by MapMan software. Paradoxically, many of the same gene families, albeit different putative genes, identified as up-regulated by stress, were also part of the repressed transcripts. In

particular, many of the Stress Response functional group transcripts were related to pathogen responsive proteins. Additionally, there were several transcripts with homology to metal toxicity (e.g., aluminum-





**Fig. 3** MapMan metabolic overview of water-deficit stress responsive genes in cotton root. Boxes represent log<sub>2</sub> expression values of stress-responsive genes. Genes in red are up-regulated in response to stress and those in green are repressed

induced protein) which suggests that down-regulation of genes that inhibit root growth are possible initial steps in stimulation of root growth under deficit conditions (Pan et al. 2004). For leaf tissue, the Protein Synthesis and Protein Degradation functional groups represented the largest fraction of repressed genes.

Gene expression analysis revealed a large number candidate transcription factors differentially expressed under water-deficit condition, in leaf and/or root, are involved in a network that coordinates the response to adverse environmental conditions. For leaf, this functional group had an abundance of WRKY transcription factors and ethylene and auxin-responsive factors, as well as transcription factors associated with ABA-mediated stomatal movement and plant water balance (*AtGPA1*), heat shock (*Hsp20.1*), and transcriptional activation (zinc finger-like protein) (Wang et al. 2001; Abe et al. 2002; Pendley and Assmann 2004; Rizhsky

et al. 2004; Davletov et al. 2005). Again, for root tissues, there were no over-represented gene families in this functional group.

In addition to known stress-responsive genes, we have identified a number of novel, uncharacterized transcripts that show tissue-specific expression patterns. The fact that a significant number of stress responsive gene families show tissue specific expression, but also reciprocal responses to water-deficit stress, the implied cross-talk between several pathways and mechanisms and the fact that the largest number of stress-responsive transcripts (1,131) in both leaf and root have unknown functions highlights the complexity of abiotic stress responses in plants and the need for functional analysis to determine the underlying regulatory mechanisms involved in this response. The identification of viable candidate genes and pathways is the primary challenge for enhancing

abiotic stress tolerance in crop plants and will continue to be so for the near future (Yang et al. 2010). In this study, candidate genes that may influence water deficit stress response in cotton have been identified. While these results are primarily archival, they provide additional information regarding the water-deficit stress response in an economically important crop plant and insight into the tissue-specific nature of this response.

**Acknowledgments** This work was supported by USDA/Southwest Consortium on Plant Genetics and Water Conservation Award No. SWC-03N02, USDA-ARS CRIS 6208-21000-013-00D, and the USDA-ARS Ogallala Aquifer Initiative. We would like to thank Scot Dowd for his assistance in the assembly of the ESTs, Marc Lohse and the MapMan team for their support in generating the cotton mapping file.

## References

- Abe H, Urao T, Ito T, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2002) *Arabidopsis* AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. *Plant Cell* 15:1–16
- Araus JL, Slafer GA, Reynolds MP, Royo C (2002) Plant breeding and drought in C3 cereals: what should we breed for? *Ann Bot-Lond* 89:925–940
- Bray EA (2002) Classification of genes differentially expressed during water-deficit stress in *Arabidopsis thaliana*: an analysis using microarray and differential expression data. *Ann Bot-Lond* 89:803–811
- Bray EA (2004) Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. *J Exp Bot* 55:2331–2341
- Catterou M, Dubois F, Schaller H, Aubanelle L, Vilcot B, Sangwan-Norreel BS, Sangwan RS (2001) Brassinosteroids, microtubules and cell elongation in *Arabidopsis thaliana*. I. Molecular, cellular and physiological characterization of the *Arabidopsis* bull mutant, defective in the delta 7-sterol-C5-desaturation step leading to brassinosteroid biosynthesis. *Planta* 212:659–672
- Charlton AJ, Donarski JA, Harrison M, Jones SA, Godward J, Oehlschlager S, Arques JL, Ambrose M, Chinoy C, Mullineaux PM et al (2008) Responses of the pea (*Pisum sativum* L.) leaf metabolome to drought stress assessed by nuclear magnetic resonance spectroscopy. *Metabolomics* 4:312–327
- Cramer GR, Ergül A, Grimplet J, Tillett RL, Tattersall EA, Bohlman MC, Vincent D, Sonderegger J, Evans J, Osborne C, Quilici D, Schlauch KA, Schooley DA, Cushman JC (2007) Water and salinity stress in grapevines: early and late changes in transcript and metabolite profiles. *Funct Integr Genomics* 7:111–134
- Davletov S, Schlauch K, Couto J, Mittler R (2005) The zinc-finger protein Zat12 plays a central role in reactive oxygen and abiotic stress signaling in *Arabidopsis*. *Plant Physiol* 139:847–856
- Edwards D, Batley J (2004) Plant bioinformatics: from genome to phenome. *Trends Biotech* 22:232–237
- Hamel LP, Nicole M, Sritubtim S, Morency M-J, Ellis M, Ehling J, Beaudoin N, Barbazuk B, Klessig D, Lee J, Martin G, Mundy J, Ohashi Y, Scheel D, Sheen J, Xing T, Zhang S, Seguin S, Ellis B (2006) Ancient signals: comparative genomics of plant MAPK and MAPKK gene families. *Trends Plant Sci* 11:192–198
- Jia J, Junjie F, Jun Z, Xin Z, Junling H, Jianhua W, Meng W, Ying Z, Xiaoping C, Jinpeng Z, Jinfeng Z, Zhen S, Yuping L, Guoying W (2006) Annotation and expression profile analysis of 2073 full-length cDNAs from stress-induced maize (*Zea mays* L.) seedlings. *Plant J* 48:710–727
- Kottapalli KR, Rakwal R, Shibato J, Burow G, Burke J, Puppala N, Burow M, Payton P (2009) Proteomics of water-deficit stress in U.S. peanut mini-core accessions. *Plant Cell Environ* 32:380–407
- Mantri NL, Ford R, Coram TE, Pang EC (2007) Transcriptional profiling of chickpea genes differentially regulated in response to high-salinity, cold and drought. *BMC Genomics* 8:303
- Mayes S, Parsley K, Sylvester-Bradley R, May S, Foulkes J (2005) Integrating genetic information into plant breeding programmes: how will we produce varieties from molecular variation, using bioinformatics? *Ann Appl Biol* 146: 223–237
- Moinuddin RA, Renu K-C (2004) Osmotic adjustment in chickpea in relation to seed yield and yield parameters. *Crop Sci* 44:449–455
- Moinuddin RA, Fisher A, Sayre KD, Reynolds MP (2005) Osmotic adjustment in wheat in relation to grain yield under water deficit environments. *Agron J* 97:1062–1071
- Niknam SR, Ma Q, Turner DW (2003) Osmotic adjustment and seed yield of *Brassica napus* and *B. juncea* genotypes in a water-limited environment in south-western Australia. *Aust J Exp Agr* 43:1127–1135
- Pan JW, Ye D, Wang LL, Hua J, Zhao GF, Pan WH, Han N, Zhu MY (2004) Root border cell development is a temperature-insensitive and Al-sensitive process in barley. *Plant Cell Physiol* 45:751–760
- Pendley S, Assmann SM (2004) The *Arabidopsis* putative G protein-coupled receptor GCR1 interacts with the G protein  $\alpha$  subunit GPA1 and regulates abscisic acid signaling. *Plant Cell* 16:1616–1632
- Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, Mittler R (2004) When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiol* 134:1683–1696
- Seki M, Kamei A, Yamaguchi-Shinozaki K, Shinozaki K (2003) Molecular responses to drought, salinity and frost: common and different paths for plant protection. *Curr Opin Biotech* 14:194–199
- Shinozaki K, Yamaguchi-Shinozaki K (1999) Molecular response to drought stress. In: Shinozaki K, Yamaguchi-Shinozaki K (eds) *Molecular responses to cold, drought, heat and salt stress in higher plants*. Landes Company, Texas, pp 11–25
- Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. *J Exp Bot* 58:221–227

- Subbarao GV, Chauhan YS, Johnson C (2000) Patterns of osmotic adjustment in pigeonpea—its importance as a mechanism of drought resistance. *Eur J Agron* 12:239–249
- Taliercio EW, Romano G, Scheffler J, Ayre BG (2009) Expression of genes associated with carbohydrate metabolism in cotton stems and roots. *BMC Plant Biol* 9:11
- Thimm O, Bläsing O, Gibon Y, Nagel A, Meyer S, Krüger P, Selbig J, Müller LA, Rhee SY, Stitt M (2004) MAPMAN: a user-driven tool to display genomics data sets onto diagrams of metabolic pathways and other biological processes. *Plant J* 37:914–939
- Udall JA, Swanson JM, Haller K, Rapp RA (2006) A global assembly of cotton ESTs. *Genome Res* 16:441–450
- Urano K, Kurihara Y, Seki M, Shinozaki K (2010) ‘Omics’ analyses of regulatory networks in plant abiotic stress responses. *Curr Opin Plant Biol* 13:132–138
- Valliyodan B, Nguyen HT (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Curr Opin Plant Biol* 9:189–195
- Wang X-Q, Ullah H, Jones AM, Assmann S (2001) G protein regulation of ion channels and abscisic acid signaling in *Arabidopsis* guard cells. *Science* 292:2070–2072
- Xu H, Li Y, Yan Y, Wang K, Gao Y, Hu Y (2010) Genome-scale identification of soybean BURP domain-containing genes and their expression under stress treatments. *BMC Plant Biol* 10:197
- Zhu JK (2002) Salt and drought stress signal transduction in plants. *Ann Rev Plant Biol* 53:247–273