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Revealing Response of Plants to Biotic and Abiotic Stresses with Microarray Technology

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ABSTRACT

DNA microarrays became a widely employed tool in functional genomics and global gene expression analysis. They have been intensely used to investigate plant transcriptomes to answer various biological questions involving stress response and tolerance. Identification of stress-related genes via microarrays provides valuable information to improve biotic and abiotic stress tolerance in plants. Since these stresses are the major factors that limit plant growth and production worldwide, in this review recent progresses resulting from gene expression analysis using microarrays under biotic and abiotic stresses are summarized. Moreover microarray technology, manufacturing of arrays, experimental approaches in cDNA and oligonucleotide microarray platforms and data analysis, which are followed by microarray expression profiling studies in plant sciences, are briefly explained.

Keywords: cold, crosstalk, pathogen response, salinity, signaling, tolerance
Abbreviations: **ABA**, abscisic acid; **ABRE**, ABA-responsive element; **ABREB**, ABRE-binding protein; **ACC**, aminocyclopropane carboxylic acid; **AM**, arbuscular mycorrhizal; **Apx**, ascorbate peroxidase; **Cat**, catalase; **CBF**, CRT-binding factor; **cGMP**, 3',5'-cyclic guanyl monophosphate; **CRT**, C-repeat; **DRE**, dehydration-responsive element; **DREB**, DRE-binding protein, **ET**, ethylene; **ERE**, ET-responsive element; **EREBP**, ERE-binding protein; **EST**, expressed sequence tag; **Fov**, *Fusarium oxysporum* f. sp. *vasinfectum*; **GST**, glutathione-*S*-transferase; **H_2O_2**, hydrogen peroxide; **HSF**, heat shock TF; **HSP**, heat shock protein; **HR**, hypersensitive response; **JA**, jasmonic acid; **LEA**, late embryogenesis abundant; **LOX**, lipoxygenase; **MAPK**, mitogen activated protein kinase; **MeJA**, methyl jasmonate; **MKP**, MAPK phosphatase; **NO**, nitric oxide; **PCD**, programmed cell death; **PCR**, polymerase chain reaction; **PI**, protease inhibitor; **PP**, protein phosphatase, **PR**, pathogenesis-related; **qRT-PCR**, quantitative real time PCR; **QTL**, quantitative trait loci; **ROS**, reactive oxygen species; **RT-PCR**, reverse transcription PCR; **SA**, salicylic acid; **SAGE**, serial analysis of gene expression; **SAR**, systemic acquired resistance; **SCN**, soybean cyst nematode; **SOD**, superoxide dismutase; **TF**, transcription factor

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INTRODUCTION

Complete genome sequence information from model organisms and key plant species including *Arabidopsis thaliana*, *Oryza sativa* and *Populus trichocarpa* have been available for a while. This genomic information has yielded the ability to perform high-throughput, genome-wide screens of gene function and has boosted application of a range of new technologies to functional plant gene analysis (Holtorf *et al.* 2002). Such technologies allow analysis of different constituents namely the transcripts, proteins and metabolites of a cell that help to deduce gene function. This is where genomics turns out to be functional genomics. Functional genomics, which includes transcriptomics, proteomics and metabolomics, aims to determine the biological functions of genes and their products. The goal is not simply to provide a catalogue of all the genes, gene products and information about their functions, but to understand how the components work together to comprise functioning cells and organisms.

Different screening approaches and methodologies have been developed forming separate fields within functional genomics. Such screening approaches are transcriptomics, proteomics and metabolomics. Other methodologies of functional plant genomics like forward and reverse genetic approaches, RNA interference and transgenics are inefficient when it comes to performing high-throughput functional genomic analyses, despite the existence of dense genetic and physical maps in model organisms (Camilleri *et al.* 1998; Holtorf *et al.* 2002). Gene function, however, can not solely be inferred by using only one approach. Gathering all the information collected by different functional genomics tools is the only way for assigning functions to unknown plant genes.

Gene expression analysis

Transcriptomics, defining gene expression analysis by mRNA profiling, is considered to be the most prominent and powerful tool for functional genomics. Gene expression analysis might be divided into two main categories according to the number of genes investigated in a single experiment. First one of these categories is directed to the analysis of a single gene at a time, whereas the second one provides a global view of genome and its transcript profile. Whole genome transcript profiling, having advanced from one-gene-at-a-time methods, supplies information on both physical and functional annotation of genome and its components like regulatory regions (Donson *et al.* 2002).

Until the development of high-throughput technologies, molecular analysis and functional annotation of genes generally focused on a single gene level. Measurement of mRNA abundance and changes in gene expression at the level of single mRNA are performed by various techniques (Lockhart and Winzeler 2000). These techniques are time-consuming, labor-intensive and less informative compared to high-throughput screening methods. Moreover interactions between different genes and regulatory sequences or relations of pathways working together or in an opposite manner can not be resolved by analyses at single gene level. Most widely employed expression analyses at single gene level include northern blotting and quantitative real time PCR (qRT-PCR). Besides being the choice of methodology of single-gene-at-a-time, two are frequently utilized as confirmation methods for high-throughput analysis techniques such as microarrays.

Global gene expression analysis

Qualitative and quantitative determination of transcript profiles of a genome and identification of differentially regulated genes are of great importance. Specific metabolic or morphogenetic functions of genes might be assigned by comparing the concentration of individual mRNAs present in samples originating from different genotypes, tissues, developmental stages, growth or environmental conditions. Analyses of transcript patterns are valuable in assessing roles of novel sequences in an organism, since similarity of expression patterns of sequences of unknown function with those of known genes might indicate functional homology (Kuhn 2001). For instance, similarly regulated genes might be involved in same or similar pathways or responses providing information on how cells function and components of cell work together. Moreover, expression under specific conditions allows the comparison of the promoter or regulatory sequences of genes. Common *cis*-elements might be localized within a genome and their presence or activity might be correlated with specific features of the expression profile of corresponding gene, gene groups or genomes.

Determination of transcript profiles and patterns or identification of differentially regulated genes in plants can be performed by various techniques such as DNA microarrays, serial analysis of gene expression (SAGE), cDNA fragment sizing combined with amplified fragment length polymorphism, differential display, differential screening of cDNA libraries, expressed sequence tag (EST) sequencing and massively parallel signature sequencing. These methods can be divided into two classes; direct or indirect analysis. Direct analysis includes procedures involving nucleotide sequencing and fragment sizing whereas indirect analysis employs nucleic acid hybridization of mRNA or cDNA fragments (Donson *et al.* 2002). All global methods of gene expression analyses demand powerful information and data management systems, automation, data analysis and data mining systems.

Array-based gene expression monitoring

Hybridization has generally been preferred in quantification of RNA levels. With the availability of nucleotide sequences and EST clones as physical reagents, hybridization-based gene expression analyses now allow for simultaneous

analysis of tens of thousands of genes in a genome. The interest in this form of transcript profiling has been spurred by the development of two parallel microarray-based technologies; cDNA microarrays (Schena *et al.* 1995) and oligonucleotide microarrays (Lockhart *et al.* 1996).

Hybridization partners in microarrays are referred as probe and target. Probe is the stretch of gene-specific DNA attached to a solid surface, making up the array itself, and target is the labeled RNA or DNA strand in solution. Microarray technologies have been extensively developed by increasing the number of probes on an array and by decreasing the area of array surface. Therefore, microarrays have become a standard tool and method-of-choice in functional genomics and global gene expression analysis.

DNA microarrays, being high-density and high-throughput, allow quantitative analysis of thousands of genes, expression patterns, and gene networks in parallel. Microarrays nowadays provide information on primary DNA sequence in coding and regulatory regions, polymorphic variation within a species or subgroup, interaction between genes and regulatory sequences, time and place of expression of RNAs during development, physiological response, environmental stress and disease, subcellular localization and intermolecular interactions of RNA molecules.

However focus of current array-based plant genomics studies is the monitoring of RNA expression levels. There are several different approaches that can be employed to determine gene function using expression data. The primary method depends on correlation of temporal and spatial expression patterns related with a specific phenotype or response. A second method involves the association of unknown genes with known genes based on co-expression and co-regulation (Rensink and Buell 2005).

The enormously growing interest in array technologies has been sparked by two key innovations. The first was the use of non-porous solid supports like glass, which has facilitated the miniaturization and fluorescence-based detection. Second was the development of methods for high-density spatial synthesis of oligonucleotides and spotting of *in situ* synthesized probes onto solid surfaces.

On a whole genome level, microarrays provide a high-throughput platform to measure gene expression and thereby generate functional data for many genes simultaneously. However, microarrays only measure expression levels for those genes for which a probe, either a clone or sequence, is available.

Probe design and array manufacturing

Two major types of microarrays include oligonucleotide and cDNA based chips (**Fig. 1**). One of the former, named GeneChip, is commercially manufactured by Affymetrix and contains 25 bp long oligonucleotide probes, which are complementary to the 3′ end of expressed sequences in a genome (Lipshutz *et al.* 1999; Aharoni and Vorst 2001). Oligonucleotides are directly synthesized on a solid matrix using photolithographic masks to determine the correct sequence (Lockhart *et al.* 1996). Other approaches of *in situ* synthesis of oligonucleotides include ink-jet technology used by Agilent and electrochemical synthesis used by CombiMatrix.

On the other hand, cDNA microarrays contain PCR amplified cDNA fragments, which are spotted onto glass surfaces by printers or arrayers, as probes. A particularly attractive aspect of the cDNA microarrays is that it is ratio-based, with two cDNA samples under analysis being hybridized in parallel to probes on a single array (**Fig. 1**). This removes the variability of fabrication and individual hybridizations from the equation. Therefore, result is the relative increase of an mRNA between different treatments or tissues that is of interest. For copy-number calculations, however, highly optimized kinetics of oligonucleotide arrays offers better solutions (Donson *et al.* 2002).

Probe design is an important issue for oligonucleotide microarrays. The sequence information is gathered from genomic or EST sequence databases and handled *in silico* for determination of probe-complementary regions. The probes are designed to complement to the 3′ end of expressed sequences. GeneChips involve probe pairs that each consist of 25 bp oligonucleotides. Each probe pair has a perfect-match (PM) and a mismatch (MM) probe. The MM probe has identical sequence to the PM probe, except at the central base and functions as an internal control. On the other hand, computer-based sequence design is not employed for cDNA microarrays; rather the probes are PCR-amplified from an already available cDNA library. Therefore the sequences of the probes are not known exactly.

Construction of arrays and placement of probes onto specific locations on solid surface are done via separate techniques for oligonucleotide and cDNA arrays (**Fig. 1**). GeneChips use light-directed synthesis for the construction of high-density DNA probe arrays using two techniques: photolithography and solid-phase DNA synthesis. Synthetic linkers, modified with photochemically removable protecting groups, are attached to a glass substrate and light through a photolithographic mask is directed to specific areas on the surface to produce localized photodeprotection. The first of a series of chemical building blocks, hydroxyl-protected deoxynucleosides, is incubated with the surface, and chemical coupling occurs at those sites that have been illuminated in the preceding step. Next, light is directed to different regions of the substrate by a new mask, and the chemical cycle is repeated (Lockhart *et al.* 1996). The dimensions of a square spot, referred as feature, might be as small as 5 × 5 μm. The amount of nucleic acid information encoded on the array in the form of different probes is limited only by the physical size of the array and the achievable lithographic resolution.

Oligonucleotide synthesis performed by Agilent employs the ink jet technology in which four cartridges are loaded with different nucleotides (A, C, G and T). Moving printer head deposits specific nucleotides to the locations on substrate where they are needed, to establish a specific sequence base by base. Electrochemical synthesis of oligonucleotides uses small electrodes embedded into substrate to manage individual reaction sites. Solutions containing specific bases are washed over the substrate and the electrodes are activated in necessary positions in a predetermined sequence that allows oligonucleotides to be constructed base by base.

cDNA microarrays use spotters or arrayers to transfer and place probe solution onto specific regions of substrate. Principal components of an arrayer are a computer-controlled three-axis robot and a unique pen tip assembly. The robot is designed to automatically collect samples from either 96- or 384-well microtitre plates, with up to 12 pens simultaneously. Each pen collects from between 250 to 500 nL of solution per pen and deposits 0.25–1 nL on each slide, creating spots that range from 100–150 μm in diameter (Cheung *et al.* 1999).

Target preparation, hybridization and scanning

Two types of microarrays also differ with respect to sample preparation and labeling (**Fig. 1**). GeneChip microarrays require isolation of RNA, double-stranded cDNA synthesis, *in vitro* transcription of cRNA and labeling of cRNA with biotin during transcription. Similarly, cDNA microarray sample preparation starts with isolation of RNA and conversion to single-stranded cDNA, however during cDNA synthesis, the target is labeled with fluorescent dyes, Cy3 or Cy5. Labeled cDNA targets are mixed and directly hybridized to arrays (Schulze and Downward 2001).

Hybridization and washing stages of microarrays also differ significantly in oligonucleotide or cDNA arrays. The conditions of hybridization and stringency of wash buffers are highly optimized in both systems. In cDNA microarray analyses, during hybridization, two targets to be compared and labeled with separate dyes are hybridized to a single array. On the other hand, a single sample is hybridized to a

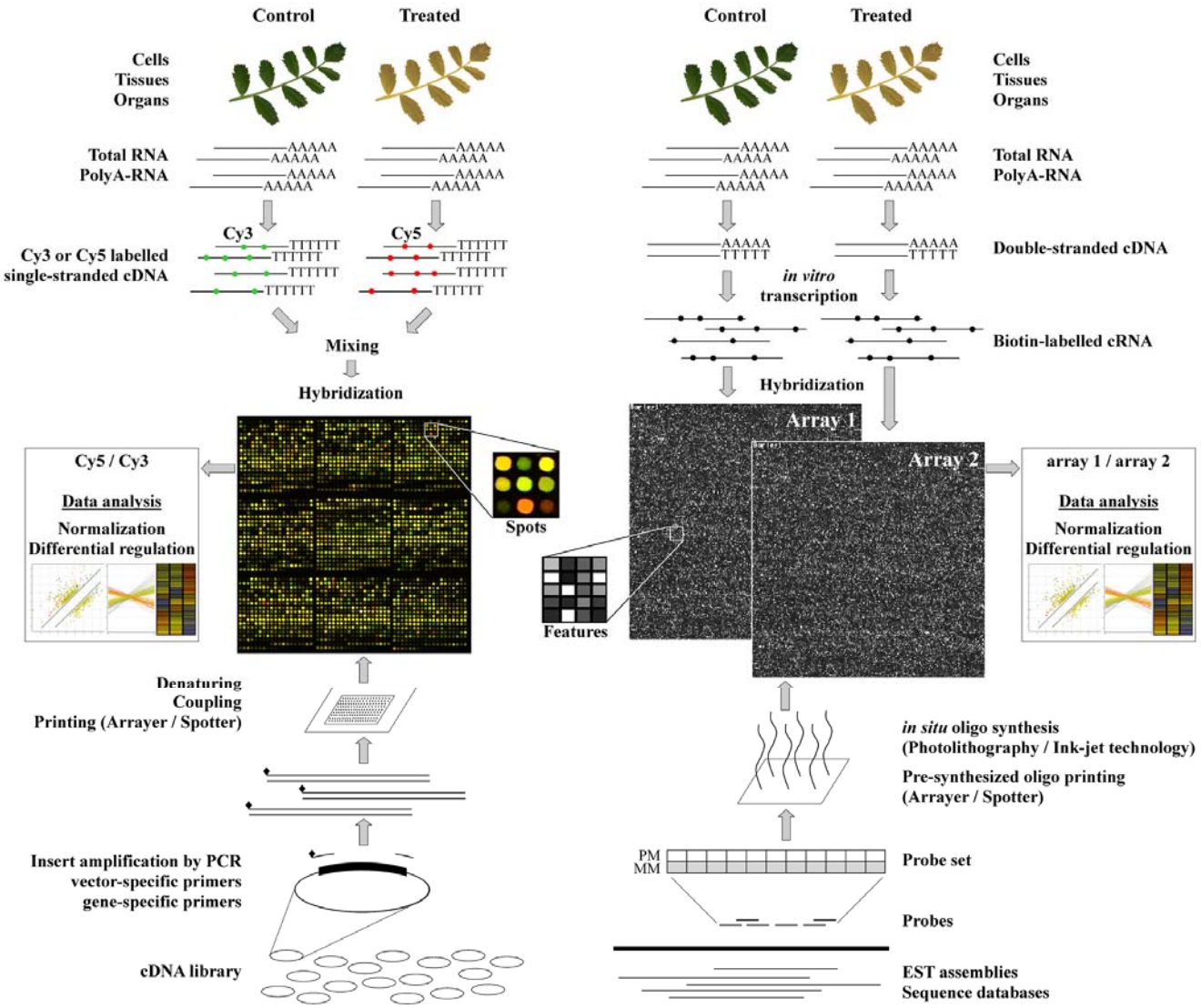

Fig. 1 Schematic overview of array and target preparation for cDNA and oligonucleotide microarrays. Left and right panes represent cDNA and oligonucleotide arrays, respectively. Top and bottom panes represent target and array preparation, respectively. Middle pane displays array images and data analyses. Inlets show spots and features in cDNA and oligonucleotide arrays, respectively. Top left pane: Total RNA or polyA-RNA is isolated from cells, tissues or organs of two different samples (Control and Treated) and is used to synthesize single-stranded cDNA in the presence of nucleotides labeled with two different fluorescent dyes (Cy3 and Cy5). Both target samples are mixed and hybridized to a single array surface resulting in competitive binding of differentially labeled targets to the corresponding array elements, probes. Scanning of the array with two different wavelengths corresponding to the dyes used provides ratios of signal intensities (Cy5 / Cy3) and ratios of mRNA abundance for the genes represented on the array. Bottom left pane: Inserts from cDNA libraries are amplified using PCR with either vector- or gene-specific primers. PCR amplicons are printed at specific sites on glass slides using arrayers or spotters. Through the use of chemical linkers, coupling and denaturing, selective covalent attachment of the coding strand to the surface is achieved. Top right pane: Total RNA or polyA-RNA is isolated from cells, tissues or organs of two different samples (Control and Treated) and is first reverse transcribed using T7 promoter:oligo(dT) primer fusion in the first strand cDNA synthesis. Second strand cDNA synthesis generates double-stranded cDNA carrying a transcriptional start site for T7 RNA polymerase. During *in vitro* transcription double-stranded cDNA is used as a template and biotin-labeled nucleotides are incorporated into the newly synthesized cRNA molecules. Resulting biotin-labeled cRNA from each target sample is hybridized to a separate array. Target binding to probes on the array is detected by staining with a fluorescent dye coupled to streptavidin. Scanning of the array with a single wavelength provides signal intensities of probe sets. Ratios of signal intensities for a single probe set from two different arrays (array 1 / array 2), calculated *in silico*, provides relative mRNA abundance for the genes represented on the array. Bottom right pane: Sequences of short oligonucleotides (probes) (25- or 60-mers) often complementary to the most unique part of the transcript in the 3′ end of the mRNA reference sequence, generated from EST assemblies or sequence databases, for each gene are selected *in silico*. Probe sets of a number of perfect-mach (PM) and mismatch (MM) pairs for each transcript are generated. MM probe has identical sequence to the PM probe, except at the central base. Elements on the array are generated either by *in situ* oligo synthesis using photolithography or ink-jet technology or by printing pre-synthesized oligos using arrayers or spotters. Middle pane: Data analyses are performed after preprocessing and normalization of the expression values represented as mRNA abundance. Various algorithms and software programs are employed for the determination and clustering of differentially regulated genes.

single array in GeneChip microarray analyses, since labeling is done with biotin only. Staining is done with streptavidin-phycoerythrin and biotinylated anti-streptavidin antibody during washing of arrays.

Array scanning in both types of microarrays is performed with fluorescence detecting scanners. The intensity of fluorescence signal that is produced as a result of hybridization between probes and labeled targets provides quantitative values for gene expression. Since separate dyes are employed for labeling samples in cDNA microarrays, two-color scanning is performed. However one-color scanning is done for GeneChip arrays. Two images of cDNA arrays are then merged and manipulated *in silico* to produce a composite image, which goes through preprocessing before expression values are analyzed. In oligonucleotide arrays quantitative expression values are assigned to each

feature on an array and these values are preprocessed using algorithms specifically designed for these arrays. Comparison of expression values from different conditions or samples is done *in silico*.

Data analysis for microarrays

Microarray data analysis has five key components; experimental design, preprocessing, inference, classification and validation (Allison *et al.* 2006). First of all development of an experimental plan or design is extremely important to maximize the quality and quantity of information obtained as a result of a microarray experiment. Second, preprocessing includes processing of the microarray image and normalization of the data to remove systemic variations. Other potential preprocessing steps include transformation of data, data filtering and background subtraction. Third component of microarray data analysis is inference, which entails testing statistical hypotheses. Another component is classification of data, which refers to analytical approaches that attempt to divide data into classes with no prior information or into predefined classes. Last component is validation of the findings which defines process of confirming the reliability of the inferences and conclusions drawn in the study.

Data analysis of microarrays employs various algorithms like Micro Array Suite 5 (MAS5) or Robust Multi-Array Average (RMA) for most of the key components of analysis. Decision for the algorithm to be used for preprocessing and normalization should be done according to experimental question in the study. Other components like experimental design should intensely be studied with respect to replicate number, sample size, pooling of samples, quality of samples and steps of procedures (Irizarry *et al.* 2003; Allison *et al.* 2006).

Applications of microarray technology

Microarray studies find multiple uses and applications in various aspects of basic and applied sciences. Microarray technology might be employed in agricultural biotechnology for developing perfect, improved strains of plants; in environmental sciences for testing causes for environmental degradation or outbreaks; in food industry for testing contaminants; or for designing the best livestock and grading their quality and safety. Moreover it might be used for identity testing like paternal testing, for prescribing the best combination of medicines for an individual or for diagnosis of human diseases like leukemia. Besides these applications, microarrays might be used in basic research for identification of key genes and regulatory sequences in a genome of an organism especially through expression analyses.

Nowadays microarrays are designed for various DNA-analysis purposes including; detection of polymorphisms, analysis of single nucleotide polymorphisms (SNP), resequencing and genotyping (Hacia 1999; Hoheisel 2006). There are also arrays designed for analysis of gene regulation or alternative splicing.

Microarray studies in plant sciences

DNA microarrays have been intensely used to investigate plant transcriptomes to answer various biological questions involving tolerance to biotic diseases or abiotic stresses, germination, growth and development, fertilization, flowering and nutritional requirements, toxicity or deficiency. Moreover, detection of polymorphic variations, mutational analyses, transcriptional regulation and alternative splicing might be investigated in detail. Intensive microarray studies have been carried out using model plants like *Arabidopsis*. Additionally, expression analyses with crop plants such as maize, rice, wheat, barley, soybean, potato, and tomato have been reported.

GLOBAL PROFILING UNDER BIOTIC INTERACTIONS

Genomic technologies provide the research of entire developmental or biochemical pathways, gene networks, chromosomal location of relevant genes and their evolutionary history. In the area of plant-pathogen interactions, transcript profiling has provided insight to the mechanisms underlying specific gene resistance and basal defense, host/non-host resistance, biotrophy/necrotrophy, and pathogenicity of vascular/nonvascular pathogens, among many others. In this way, genomic technologies have facilitated a system-wide approach to unifying themes and unique features in the interactions of hosts and pathogens (Wise *et al.* 2007).

Signaling pathways, molecules and hormones involved in biotic stresses

Herbivore and pathogen resistances are known to be mediated by jasmonic acid (JA), salicylic acid (SA), ethylene (ET) along with glucosinolates and their hydrolysis products. The implications of JA, ET, SA, and other signals in responses to biotic stress are less understood. The use of microarray analysis containing insect- and defense-regulated genes provides ways to understand their effects.

cDNA analysis of *Arabidopsis* was carried out after inoculation with an incompatible fungal pathogen *Alternaria brassicicola* or treatment with the defense-related signaling molecules SA, methyl jasmonate (MeJA), or ET. The results showed that under one or more treatments the steady-state abundance of 705 mRNAs were observed to be changing including known and putative defense-related genes and 106 genes with no previously described function or homology. Coordinated defense responses including 169 mRNAs were found to be regulated by multiple treatments/-defense pathways. Since co-induction and co-repression was observed after SA and MeJA treatments, existence of a substantial network of regulatory interactions and coordination during plant defense among the different defense signaling pathways was proposed between the salicylate and jasmonate pathways (Schenk *et al.* 2000).

When the mRNA levels of 402 distinct transcription factor (TF) genes of *Arabidopsis* were examined at different developmental stages and under various stress conditions some were reported to be up-regulated together with other regulatory pathways, suggesting their multifunctional nature. In certain mutant lines that are defective in SA, JA, or ET signaling the expression of 74 TF genes responsive to bacterial pathogen infection was reduced or abolished showing the control of these genes by these plant hormones. It was also suggested that these TF genes were also involved in the regulation of additional downstream responses mediated by these hormones. The differential expression of certain genes was found to be common at various stress treatments, suggesting extensive overlapping responses to these stresses (Chen *et al.* 2002).

A large-scale gene expression study was conducted in the C4 monocot sorghum (*Sorghum bicolor*) roots and shoots in response to the signaling compounds SA, MeJA, and the ET precursor aminocyclopropane carboxylic acid (ACC). Numerous gene clusters were identified in which expression was correlated with particular signaling compound and tissue combinations. It was observed that many genes previously implicated in defense responded to the treatments. It was concluded that responses to SA, MeJA, and combined SA-MeJA revealed patterns of both antagonisms and synergistic effects on regulation of some genes. This leads to a crosstalk that effects transcriptional co-regulation by SA and JA (Salzman *et al.* 2005).

The effect of MeJA treatment on gene expression in sugarcane root signaling between roots and shoots was studied with 829 ESTs obtained from sugarcane roots treated with the defense-regulator MeJA. 21 ESTs were observed to be induced and 23 to be reduced by MeJA in roots. Repeated foliar application of MeJA had no apparent effects

on plant growth and was demonstrated to increase lipoxygenase (*LOX*) transcripts in roots, but did not increase transcript levels of other genes tested (Bower *et al.* 2005). *A. thaliana* responses to MeJA were investigated by 2,467 selected genes of primary and secondary metabolism (Jost *et al.* 2005). 97 and 64 genes were identified that were up- or down-regulated respectively. Among the genes that were affected the most were sulfur-related genes. In addition, increased expression of genes of sulfur-rich defense proteins and of enzymes involved in glucosinolate metabolism was observed. According to the results, it was suggested that the regulation of sulfur-related genes and plant defenses are connected.

MeJA is known to have highly specific and persistent effects in regulating the expression of genes associated with plant defense. The effects of MeJA were more intensely studied compared to other signaling molecules. The molecular genetic mechanisms that MeJA is involved in have been investigated by microarray analyses, the use of knockout lines and by functional gene expression studies in *A. thaliana* and other systems (Pickett *et al.* 2007).

Transgenic *Arabidopsis* plants overexpressing jasmonate carboxyl methyltransferase gene (*AtJMT*) were analyzed by GeneChip arrays and the expression of 168 genes were shown to be altered. Among them, 80 were up-regulated, including those involved in defense, oxidative stress tolerance and senescence whereas 88 genes were down-regulated that function in photosynthesis and cold/drought stress responses. The results of the study confirmed that MeJA is a key control point for jasmonate-responsive gene expression in plants (Jung *et al.* 2007a).

The microarray analysis to investigate the regulatory network of MeJA-induced genes in adventitious root cultures of the medicinal herb *Bupleurum kaoi* showed that the genes up-regulated by MeJA included those involved in saikosaponin, amino acid, phenylpropanoid and jasmonate biosynthesis, defense signaling, plant hormone regulation and stress protection. The results of the study indicated interactions between signaling pathways leading to transcriptional regulation in *B. kaoi* adventitious roots (Chen *et al.* 2007). *A. thaliana* jasmonate responsive genes were screened and the data showed that the external application of 100 mM MeJA resulted in significant changes in the expression levels of 137 genes in the rosette leaves of 5-week-old *Arabidopsis* plants (Jung *et al.* 2007b). Among the up-regulated genes were jasmonate biosynthesis, defense, oxidative stress responses, senescence, and cell wall modification. In contrast, the expression of genes involved in chlorophyll constitution and photosynthesis were shown to be down-regulated. The most important finding of the study was the observation of antagonistic relation of jasmonate and abscisic acid (ABA) signaling pathways in abiotic stress responses.

Transcriptome analyses of sugarcane in response to environmental changes were performed by cDNA microarrays representing 1,545 genes. Also the responses to ABA and MeJA were assayed. The arrayed elements corresponded mostly to genes involved in signal transduction, hormone biosynthesis, TFs, novel genes and genes corresponding to unknown proteins. Among the analyzed genes 179 of them were shown to be differentially expressed in at least one of the treatments (Rocha *et al.* 2007).

ET-regulated gene expression in leaves of *A. thaliana* was investigated with a microarray containing about 6,000 unique genes. For the analysis ET-insensitive mutant *etr1-1*, the ET-constitutive mutant *ctr1-1*, ET-treated wild-type and untreated wild-type plants were used. The study led to the identification of ET-regulated genes involved in its own biosynthesis and signal transduction pathway. A large number of TFs, some putative signaling components, and primary metabolic genes were shown to be highly regulated by ET. Genes of chloroplast structural proteins and photosynthetic genes were generally down-regulated. Plant defense genes were differentially regulated, with some genes within this class highly up-regulated. Other ET-regulated genes identified were known sugar-, auxin-, wounding- and JA-related genes, suggesting the existence of coordinated interactions between ET and other hormonal and defense signaling path-ways (van Zhong and Burns 2003).

Defense systems against biotic stresses were shown by analysis of both JA and SA levels during herbivore attack on *Nicotiana attenuata*. The transcript level of *NaNPR1* was observed to be increasing with SA treatment and silencing of this gene made plants susceptible to herbivore and pathogen attack. Microarray analysis revealed that there was down-regulation of many JA-elicited genes and up-regulation of SA biosynthetic genes at *NPR-1* silenced plants. It was concluded that during herbivore attack, *NPR1* negatively regulated SA production triggering JA-mediated defenses; while in *NPR1* silenced plants SA production was increased and JA related defense diminished making the plants susceptible to herbivores (Rayapuram and Baldwin 2007).

Emerging evidence indicated that auxin, an essential plant hormone in regulating plant growth and development, is also involved in plant disease susceptibility. *GH3.5*, a member of the GH3 family of early auxin-responsive genes in *Arabidopsis*, encodes a protein possessing *in vitro* adenylation activity on both indole-3-acetic acid (IAA) and SA. Zhang *et al.* (2007a) showed that during pathogen infection *GH3.5* acts as a bifunctional modulator in both SA and auxin signaling, inducing the former and repressing the latter by up-regulating SA-responsive genes and basal defense components, and down-regulating auxin repressor genes (Zhang *et al.* 2007a).

Fungal infections and symbiotic interactions with fungi

Pathogen attack initiates a cascade of signal transduction pathways so that a systemic or induced resistance begins in tissue remote to the initial infection. The analysis of transcriptional changes that occur during systemic defense responses in *Arabidopsis* plants caused by fungal pathogen *A. brassicicola* revealed the presence of 25 up-regulated and 10 down-regulated genes in distal tissue of inoculated plants (Schenk *et al.* 2003). Genes with altered expression in distal tissue included those with putative functions in cellular housekeeping, indicating that plants modify these vital processes to facilitate a coordinated response to pathogen attack. Transcriptional up-regulation of genes encoding enzymes functioning in the β-oxidation pathway of fatty acids, genes involved in cell wall synthesis and modification and genes putatively involved in signal transduction were observed. The results of the study confirmed the notion that the distal tissues of pathogen-challenged plants prepared themselves for subsequent pathogen attacks.

The attack of *A. brassicicola* induces hypersensitive response (HR) in wild-type *A. thaliana* plant. This response requires the presence of *PAD3*. In order to determine the effect, cDNA microarray analysis of *Arabidopsis* was carried out after inoculation with *A. brassicicola*. The cDNA microarrays were also done to analyze *Arabidopsis* responses after treatment with signal molecules, reactive oxygen species (ROS)-inducing compounds and UV-C. It was reported that the mutation of *pad3-1* changed both accumulation of camalexin and timing of expression of many defense-related genes in response to *A. brassicicola* (Narusaka *et al.* 2003).

After the infection of fungal pathogen *A. alternate*, none of the ecotypes of *Arabidopsis* plants showed hypersensitive cell death. On the contrary, accumulations of detectable levels of ROS or phytoalexin took place in those ecotypes. The non-host penetration resistance to *A. alternata* was examined by expression patterns of 7,000 genes by cDNA microarray analysis in *Arabidopsis* plants after inoculation with *A. alternata*. The results revealed that the expressions of 48 genes were induced among which there were genes associated with hypersensitive reaction. It was concluded that even though *A. alternata* had no visible ef-

fect on the plants, there exists a non-host penetration resistance to *A. alternata* that was associated with activation of the jasmonate- and ET-signaling pathways (Narusaka *et al.* 2005).

cDNA microarray analysis was used to monitor global changes in gene expression in tobacco cells treated with an oligoglucan from the fungus *A. alterna* or with laminarin (Shinya *et al.* 2007). Among the 265 genes identified after the treatment, a novel tobacco R2R3 MYB-type TF homolog (*NtMYBGR1*) and two DC1 domain-containing genes (*NtDC1A* and *NtDC1B*) were identified. It was reported that *NtMYBGR1* specifically regulated defense responses in BY-2 tobacco cells by enhancing phenylpropanoid metabolism in response to glucan and laminarin elicitors.

According to microarray gene expression changes, in hypocotyl tissues of cotton infected with *Fusarium oxysporum* f. sp. *vasinfectum* (Fov) but not in infected root tissues, increased expressions of defense-related genes were observed. In infected roots, especially at the early stages of infection more genes were repressed than were induced. It was the first research showing the repression of drought-responsive proteins such as aquaporins in both roots and hypocotyls as a response to pathogen attack. This response was proposed to be specific to vascular wilt diseases. Gene expression results implicated the roles of phytohormones ET and auxin in the disease process (Dowd *et al.* 2004).

In another study microarray and qRT-PCR technology were used to identify genes expressed in root and hypocotyl tissues of cotton after Fov infection. Fov genes are believed to be associated with pathogenicity. 218 fungal clones representing 174 Fov non-redundant genes that were expressed *in planta* were identified. The Fov genes identified were predominately of unknown function or associated with fungal growth and energy production. 11 of the identified fungal genes were shown to be preferentially expressed in plant tissue among which a putative oxidoreductase gene (with homology to *AtsC* which is related to virulence in *Agrobacterium tumefaciens*) was found (McFadden *et al.* 2006).

The necrosis- and ET-inducing peptide (Nep1) from *F. oxysporum* f. sp. *erythroxyli* treated *A. thaliana* showed retarded root and cotyledon growth. Nep1 was observed to be triggering cell death and generating necrotic spots. Microarray analysis after Nep1 treatment showed altered expression of genes encoding especially chloroplast and mitochondria localized proteins. Other genes involved in response to short-term Nep1 treatment were involved in ROS production, signal transduction, ET biosynthesis, membrane modification, apoptosis, and stress. The results of the study were consistent with Nep1 facilitating cell death as a component of diseases caused by necrotrophic plant pathogens (Bae *et al.* 2006).

The significance analysis of microarrays was used to identify transcripts that showed a differential response between *F. graminearum* challenged wheat versus control plants. 185 and 16 ESTs were found to be up- and down-regulated in the six organs constituting the wheat spike. Many up-regulated ESTs showed no homology, whereas others showed homology with genes involved in defense and stress responses, the oxidative burst of hydrogen peroxide (H_2O_2) and the phenylpropanoid pathway. The study allowed identification of the differential expression of genes in an organ specific manner in response to *F. graminearum* infection (Golkari *et al.* 2007).

When expression patterns of 20 defense-related ESTs were studied in chickpea (*Cicer arietinum*) after inoculation with ascochyta blight (*Ascochyta rabiei*), 10 of the defense-related ESTs displayed up- or down-regulation in resistant accession ICC3996 and/or susceptible cultivar Lasseter compared to uninoculated control samples. The microarray expression analysis of defense-related ESTs in chickpea represented the first study of this type (Coram and Pang 2005). In another study the ascochyta blight resistance of *C. arietinum* genotypes including resistant, moderately resistant, susceptible and wild relative was studied by microarray technology (Coram and Pang 2006). Out of 756 genes, 97 resulted in the differential expression in at least one genotype at one time point. The genes that act as signature for *A. rabiei* resistance were coding for several pathogenesis-related (PR) proteins, SNAKIN2 antimicrobial peptide, proline-rich protein, disease resistance response protein DRRG49-C, environmental stress-inducible protein, leucine-zipper protein, polymorphic antigen membrane protein, Ca^{2+}-binding protein and several unknown proteins.

The responses to defense signaling compounds SA, MeJA and ACC were studied in three *C. arietinum* genotypes with ranging levels of resistance to ascochyta blight (Coram and Pang 2007). The results of the study showed differential expression of 425 transcripts with the genotype that is resistant to *A. rabiei* showing a more substantial range of defense-related gene induction by all treatments. The involvement of SA, MeJA and ACC signaling together with *A. rabiei*-specific signaling mechanisms for resistance was studied. The results provided novel insights to the molecular control of chickpea cellular processes, which might assist the understanding of chickpea defense mechanisms and allow development of disease resistant cultivars.

Arabidopsis cDNA arrays were used to screen the local-defense-associated genes in canola (*Brassica napus*) when challenged with *Sclerotinia sclerotiorum*. 36 unique genes that were up-regulated and 25 unique genes that were down-regulated were screened out from the local tissue around the necrosis (Liu *et al.* 2005). The pathogen-induced gene expression changes in *B. napus* due to the fungal pathogen *S. sclerotiorum* were analyzed using microarrays. Inoculation with pathogen led to increased or decreased expressions of more than 300 transcripts when compared to uninoculated controls. Among the induced genes were JA biosynthesis and signaling, ROS metabolism, and cell wall structure and function. These genes might be playing important roles in mediating plant responses to the pathogen (Yang *et al.* 2007).

Many plants in natural ecosystems have a symbiotic relation with arbuscular mycorrhizal (AM) fungi. This relation increases the resistance to abiotic and biotic stresses. Specific plant genes exhibiting common responses to different AM fungi were identified in *Medicago truncatula* (Massoumou *et al.* 2007). Transcriptional activities of the selected plant genes were compared during root interactions with 7 AM fungi belonging to different species and under widely different biological conditions. It was observed that among the tested genes 10 of them were commonly induced by all the tested AM fungal species. Unique transcription of plant genes were observed at mycorrhizal roots and several were already active at the appressorium stage of fungal development. The study concluded that plants should possess a mycorrhiza-specific genetic program which is co-modulated by a broad spectrum of AM fungi (Massoumou *et al.* 2007). In a study, a 16,000-feature oligonucleotide array and qRT-PCR were used to explore transcriptional changes triggered in *M. truncatula* roots and shoots as a result of AM symbiosis (Liu *et al.* 2007). Experimental evidence supported the local and systemic changes in gene expression, including the induction of a functional defense response.

The genes providing partial resistance of sunflower (*Helianthus annuus*) to the necrotrophic fungus *Phoma macdonaldii* were analyzed by a cDNA microarray containing genes putatively involved in primary metabolic pathways, signal transduction and biotic stress responses. 38 genes were identified to be differentially expressed among genotypes, treatments and times that were mostly related to plant defense, signaling pathways and amino acid metabolism. At the end of the study a model that points the negative regulation of a dual-specificity mitogen activated protein kinase (MAPK) phosphatase (MKP) due to the significant increase in expression of certain genes in sunflower defense mechanisms was proposed. It was also noted that the activation of protein phosphatase 2A (PP2A) causing cell death inhibition, could limit pathogen development (Alignan *et al.* 2006).

Chitin which is a major constituent of fungi, insects and nematodes act as an elicitor of plant defense responses. After the attack of fungal species chitin oligomers are released from fungal cell walls by endochitinase. These oligomers trigger defense and related cellular responses in many plants. The gene expression profile of *Arabidopsis* in response to chitin treatment was analyzed by an *Arabidopsis* microarray consisting of 2,375 EST clones (Ramonell *et al.* 2002). Transcript levels for 71 ESTs, representing 61 genes were altered. Among these transcripts were genes that were enriched with both the W-box promoter element and a novel regulatory element. Some genes coding for several proteins involved in cell wall strengthening and wall deposition were found to be down-regulated.

The microarray analysis of *Arabidopsis* for the expression patterns of TF and ubiquitin-ligase genes were analyzed under chitooctaose treatment at different exposure times using GeneChip *Arabidopsis* whole-genome array. Among the 118 TF genes and 30 ubiquitin-ligase genes that were responsive to the chitin treatment were 27 APETALA2/ET-responsive element binding proteins, 14 C2H2 zinc finger proteins, 11 MYB domain-containing proteins, and 14 WRKY domain TFs. The researchers proposed transcript-specific regulation of these TF genes since transcript variants from a few of these genes were found to respond differentially to chitin (Libault *et al.* 2007).

The responses of wheat leaves infected with *Meloidogyne graminicola* were determined; and microarray transcript profiling of *M. graminicola* was analyzed to identify adaptive responses of the fungus to its changing environment (Keon *et al.* 2007). The results of the study figured out that in susceptible hosts the symptoms were similar to HR whereas a rapid and localized form of host programmed cell death (PCD) is more commonly associated with disease-resistance mechanisms. Microarray analysis of the fungal genes supported the hypothesis that host plant PCD plays an important role in susceptibility towards fungal pathogens with necrotrophic lifestyles.

Spring dead spot is a serious root-rot fungal disease of turf-type bermudagrass (*Cynodon dactylcui*), caused by *Ophiosphaerella herpotricha*. In order to identify the genes associated with the plant and fungal interaction, microarray technology was used. A total of 323 genes were identified with the analysis between fungal infected tolerant cultivar (Yukon) and susceptible cultivar (Jackpot) and between fungal infected and non-infected Jackpot. The results of the study proposed that the higher expression of genes involved in defense response and signal transduction might associate with improved tolerance to fungal infection (Zhang *et al.* 2006).

CON7 gene of *Magnaporthe grisea* is predicted to encode a TF and was previously shown to be essential for appressorium formation and growth *in planta*. Microarray-based gene expression analysis identified several genes whose transcription during germination depends on promoter of *CON7* (Con7p). These proteins mainly included several genes that encode G protein-coupled receptors and factors determining cell wall structure or function. The results of the study suggested that *CON7* encodes a TF required for the transcription of several genes which participate in disease-related morphogenesis in *M. grisea* (Odenbach *et al.* 2007).

Plant cells release oligogalacturonides (OGs) due to pathogen attack. It was shown that OGs increase resistance in *Arabidopsis* to fungal pathogen *Botrytis cinerea* independently of JA-, SA-, and ET-mediated signaling. Microarray analysis showed that about 50% of the genes regulated by OGs changed upon infection by *B. cinerea.* Elicitors released from the cell wall during pathogen infection contributed to basal resistance against fungal pathogens through a signaling pathway also activated by pathogen-associated molecular pattern molecules (Ferrari *et al.* 2007).

The tolerance mechanism of tomato (*Lycopersicon esculentum*) to fungal wilt pathogen, *Verticillium dahliae*, was examined and compared to a susceptible infection. It was observed that some genes like foliar necrosis and cell death were down-regulated in tolerant ones. The researchers suggested reprogramming of chlorosis, necrosis and wilt symptoms which were observed in the susceptible interaction to limit the growth of the fungal pathogen, and protect the general tomato population (Robb *et al.* 2007).

The changes in gene transcript abundance in conifer *Pinus sylvestris* root tissues infected by *Heterobasidion annosum* were analyzed by a cDNA microarray containing 2,109 ESTs from *P. taeda* (Adomas *et al.* 2007). A total of 179 ESTs differentially expressed at 1, 5 or 15 days post inoculations were identified. It was also observed that the total number of genes differentially expressed during the infection increased over time; and the most abundant group of genes up-regulated upon infection coded for enzymes involved in metabolism (phenylpropanoid pathway) and defense-related proteins with antimicrobial properties. The report of Adomas *et al.* (2007) together with the previous studies documented in crop pathology suggested that angiosperms and gymnosperms use similar genetic programs in responding to invasive growth by microbial pathogens.

Powdery mildew disease

The effects of basal responses on the onset of Mla- (mildew resistance locus a) specified resistance were investigated by meta-analysis of GeneChip mRNA expression for 155 basal defense-related genes. The gene expression of barley (*Hordeum vulgare*) was assayed after different h of inoculation with *Blumeria graminis* f. sp. *hordei*; the causal agent of powdery mildew disease. It was reported that transcripts hyperaccumulated from 0 to 16 h after inoculation in both compatible and incompatible interactions in plants having the fast-acting Mla1, Mla6, or Mla13 alleles. However 16 h after inoculation, suppression of basal defense-related transcripts was observed only in compatible interactions, whereas these transcripts were sustained or increased in incompatible interactions. The report hypothesizes that the regulation of basal defense influences host-cell accessibility to the fungal pathogen and drives allelic diversification of gene-specific resistance phenotypes (Caldo *et al.* 2006).

The effect of silicon (Si) on plants was investigated by performing microarray analysis of both control and powdery mildew-stressed *Arabidopsis*, with or without Si application (Fauteux *et al.* 2006). According to results the expression of all genes except two was unaffected in control plants, a result contradicting reports of a possible direct effect of Si as a fertilizer. On the other hand inoculation of plants treated with Si or not, altered the expression of a set of nearly 4,000 genes. Among the up-regulated ones were defense-related genes and down-regulated ones were genes belonging to primary metabolism. Other genes that were altered were resistance (R) genes, stress-related TFs, genes involved in signal transduction, the biosynthesis of stress hormones (SA, JA, ET), and the metabolism of ROS. The results of the study showed that Si is not an essential element for the metabolism of unstressed plants, but it has a role for modulation of a more efficient response to pathogen stress.

Microarray analysis of *M. truncatula* after the attack by *Erysiphe pisi* revealed induction of 55 genes that were associated with the basal defense response. These included PR genes and other genes involved in defense, signal transduction, senescence, cell wall metabolism and abiotic stress (Foster-Hartnett *et al.* 2007).

In order to elucidate the molecular basis of rice defense to fungal pathogen *Rhizoctonia solani*, RNA isolated from *R. solani*-infected leaves of Jasmine 85 was used for SAGE library construction and microarray hybridization. It was reported that about 70% of the genes identified in the SAGE libraries had similar expression patterns (up- or down-regulated) in the microarray data. Some candidate SAGE tags and microarray genes were found to be located in known sheath blight quantitative trait loci (QTL) regions (Venu *et al.* 2007).

Viral infections

Plant viruses do not contain common nucleotide sequences and form a diverse group among plant pathogens. Microarray technology provides the basis of specific testing for individual and even combination of viruses (Boonham *et al.* 2007). Various signaling pathways induce different responses in host cells upon viral infection. Moreover, resistant and susceptible cells respond differently to virus infection. These effects range from non-specific changes in gene expression due to the general accumulation of viral proteins to those responses that are initiated by the specific interactions between virus and host proteins. The studies have identified distinct sets of genes that have altered expression profiles in response to viruses, including stress- and defense-related genes. Together with interference of hormone signaling, the activities of viral RNA silencing suppressors influence plant gene expression and lead to developmental abnormalities (Whitham *et al.* 2006).

The unique gene expression changes of *N. benthamiana* upon infection by distinct enveloped viruses were assayed by microarray technology. Infection by *Impatiens necrotic spot virus* (INSV) resulted in differential expression of 275, 2,646 and 4,165 genes after 2, 4 and 5 days, respectively. In contrast, 35, 665 and 1,458 genes were expressed differentially in response to *Sonchus yellow net virus* (SYNV) after 5, 11 and 14 days, respectively. Interestingly heat shock protein (HSP) induction was observed with infection by INSV but not SYNV. On the contrary, when infected with INSV all histone genes were down-regulated. It was concluded that the infection by INSV resulted in larger fold changes in host gene expression relative to infection by SYNV (Senthil *et al.* 2005).

The responses elicited by viruses in susceptible hosts were analyzed by the use of model plant *Arabidopsis* that were either mock inoculated or inoculated with *Cucumber mosaic cucumovirus*, *Oil seed rape tobamovirus*, *Turnip vein clearing tobamovirus*, *Potato virus X potexvirus*, or *Turnip mosaic potyvirus*. Microarray analysis revealed coordinated changes in gene expression in response to infection by different viruses that can be virus-general and virus-specific. Analyses of the promoters of these genes further suggested that diverse RNA viruses elicit common responses in susceptible plant hosts through signaling pathways that have not been previously characterized (Whitham *et al.* 2003).

The plant immune system constitutes resistance genes and involves HR leading to cell death. *Arabidopsis* microarray analysis was used to monitor the changes for *RCY1*-mediated resistance to *Cucumber mosaic virus* strain Y (CMV-Y). The results pointed the presence of 444 putative factors belonging to nine different functional classes that showed significant transcript regulation during *Arabidopsis*-CMV-Y interaction. Most of the genes were with unknown functions others were genes of kinases and phosphatases, protein degradation machinery/proteases, transcriptional regulators, and others. About 80 defense-responsive genes that might participate in resistance gene-mediated defense against both viral and bacterial pathogens were identified (Marathe *et al.* 2004).

cDNA microarrays were used to analyze gene expression changes in susceptible potato (*Solanum tuberosum*) cv. 'Igor' after infection with *Potato virus Y* causing potato tuber necrotic ringspot disease. After 14 days of inoculation, gene expression changes were more pronounced and observed mostly on leaves of plants grown from infected tubers. The up-regulated genes included genes for HSPs, catalase (Cat) 1, β-1,3-glucanase, wound inducing gene, and genes involved in photosynthesis (Pompe-Novak *et al.* 2005).

Plants respond to viruses with both specific and general changes. In order to identify gene expression changes that are concomitant with virus symptoms, comparative expression profiling experiments on *N. benthamiana* leaves infected with one of three different fruit tree viruses with distinct symptoms were performed. Viral infections were induced by *Plum pox potyvirus* (PPV; leaf distortion and mosaic), *Tomato ringspot nepovirus* (ToRSV; tissue necrosis and general chlorosis), and *Prunus necrotic ringspot ilarvirus* (PNRSV; subtle chlorotic mottling). Severities of the symptoms were in correlation with the number of genes being expressed: 1,082 (ToRSV), 744 (PPV), and 89 (PNRSV). Genes associated with plastid function were repressed both in PPV- and ToRSV-infected leaves. PPV uniquely induced the expression of large numbers of cytosolic ribosomal genes whereas ToRSV repressed the expression of plastidic ribosomal genes (Dardick 2007).

Several reports on senescence-associated genes (SAGs) have pointed out that some of the genes induced during senescence take role in HR at pathogen infections and lead to necrotic symptoms. Espinoza *et al.* (2007a) analyzed the transcript profiles of *Arabidopsis* ecotype Uk-4 infected with *Tobacco mosaic virus* strain Cg (TMV-Cg) and *Vitis vinifera* cv. 'Carmenere' infected with *Grapevine leaf roll-associated virus* strain 3 (GLRaV-3) by using microarray slides of *Arabidopsis*. A large number of SAGs encoding proteases, lipases, proteins involved in the mobilization of nutrients and minerals, transporters, TFs, proteins related to translation and antioxidant enzymes exhibited altered expression. Some virus-induced genes were also expressed at elevated levels during natural senescence in healthy plants. The results of the study revealed that a part of the response of plant to virus infection appeared to be the activation of the senescence program (Espinoza *et al.* 2007a).

Gene expression in the *V. vinifera* red wine cultivars Carmenere and Cabernet-Sauvignon naturally infected with GLRaV-3 were evaluated by microarray technology with the *V. vinifera* GeneChip. Differential expressions of genes related to a wide spectrum of biological functions, including processes of translation and protein targeting, metabolism, transport, and cell defense were observed. Highest number of genes that were induced was associated with membrane and endomembrane systems whereas chloroplastic genes were mostly repressed (Espinoza *et al.* 2007b).

Bacterial invasions and diseases

One of the early studies showing gene expression changes by bacterial interaction was done on model plant *Arabidopsis*. An increase of defense-related transcripts in the shoots of *Arabidopsis* plants infected with the rhizobacterium *Pseudomonas thivervalensis* was determined with cDNA microarray analyses (Cartieaux *et al.* 2003).

The transcript modifications taking place during the interaction between *Arabidopsis* and growth-promoting rhizobacterium *P. fluorescens* FPT9601-T5 were investigated with microarray analysis of approximately 22,800 genes (Wang *et al.* 2005). The study revealed 95 up-regulated and 105 down-regulated genes. Up-regulated genes included the ones related to metabolism, signal transduction, and stress response. Interestingly it was noted that upon FPT9601-T5 colonization, putative auxin-regulated genes and nodulin-like genes were up-regulated, and some ET-responsive genes were down-regulated. In a recent study, microarray analysis revealed that the R2R3-MYB-like TF gene *MYB72* was specifically induced in the roots of *Arabidopsis* upon colonization by non-pathogenic *P. fluorescens* WCS417r (van der Ent *et al.* 2008).

T-DNA insertion lines and microarray analysis enabled identification of a gene involved in the establishment of SAR at *Arabidopsis* leaves inoculated with avirulent or virulent strains of the bacterial pathogen *P. syringae*. Due to its homology to flavin-dependent monooxygenases (FMO) the gene was designated as *FMO1*. The results of the study suggested that the gene product of *FMO1* is present in systemic tissue and that it is critical for the development of SAR. The possible role of *FMO1* was hypothesized to be the synthesis of a metabolite required for the transduction or amplification of a signal during the early phases of SAR establishment in systemic leaves (Mishina and Zeier 2006).

P. syringae pv. tomato DC3000 is a pathogen infecting tomato and *Arabidopsis* plants. The bacterium induces genes encoding the type III secretion system and substrate proteins (collectively called TTSS genes) in minimal medium. The microarray analysis pointed out that the induction of TTSS genes was associated with down-regulation of the housekeeping genes slowing the basic cellular activities (Lan *et al.* 2006). Moreover, the disease resistance gene *MbR7* of wild apple species *Malus baccata* was expressed in *Arabidopsis* (Lee *et al.* 2007a). It was shown that the expression enhanced the resistance against a virulent pathogen, *P. syringae* pv. tomato DC3000. The microarray analysis of *Arabidopsis* plants carrying *MbR7* revealed that the *MbR7* gene likely activates a downstream resistance pathway without interaction with pathogens.

P. syringae effectors were reported to be acting on the ABA signaling pathway using microarray analysis. According to the analysis there was a 42% overlap between the genes up-regulated by effector delivery and ABA-responsive genes and components of networks induced by osmotic stress and drought. It was suggested that a major virulence strategy was effector-mediated manipulation of plant hormone homeostasis, which might lead to the suppression of defense responses (de Torres-Zabala *et al.* 2007).

The *AtPTR3* of *Arabidopsis* is a wound-induced peptide transporter gene and it is regulated by several signaling compounds, most clearly by SA, but also by MeJA and ABA. Microarray data showed that the *AtPTR3* expression was also induced by *Pseudomonas* elicitors and by avirulent *P. syringae* pathovars and type III secretion mutants. The results suggested that *AtPTR3* protects the plant against biotic and abiotic stresses (Karim *et al.* 2007).

Microarray expression profiling of an *Arabidopsis* mutant, *cir1* (constitutively induced resistance 1) which was shown to be resistant to *P. syringae* pv. tomato DC3000 was reported. The mutant was assayed with microarray expression profiling for the genes taking role in the defense system. The induction of the genes encoding Na^+-inducible Ca^{2+}-binding protein, *AtP2C-HA* (PP2C), *AtGSTF7* (glutathione-*S*-transferase; GST), tryptophan synthase β-like and *AtPAL1* (phenylalanine ammonia lyase 1), and the repression of *AtEREBP-4* (ET-responsive element binding protein 4) and *HFR1* (long hypocotyl in far-red 1) in *cir1* were found to be common for *Arabidopsis* plants infected with *P. syringae* (Naidoo *et al.* 2007).

Microarray expression profiling was used to identify novel components of *Arabidopsis* basal resistance against the bacterial pathogen *P. syringae* pv. tomato. With the use of *cir1* mutant, two genes, *At4g23810* and *At2g40000*, encoding the TF WRKY53 and the nematode resistance protein-like HSPRO2, were identified. Compared to complemented lines, knockout mutants of both genes were more susceptible to *P. syringae* infection with increased growth of the pathogen *in planta*. In response to pathogen attack, WRKY53 and HSPRO2 appeared to be functioning in downstream of SA signaling and negatively regulated by signaling through JA and ET (Murray *et al.* 2007).

Xanthomonas campestris pv. vesicatoria (Xcv) is the causal agent of spot disease in tomato and pepper. A large set of cDNAs were identified to be induced or repressed during the resistance response of Hawaii 7981 plants to Xcv T3 bacteria. 426 non-redundant genes that were differentially expressed after infection were designated as XRE (*Xanthomonas*-regulated) genes. These genes were further classified into more than 20 functional classes, largely involving genes taking role in defense, stress responses, protein synthesis, signaling, and photosynthesis. Detailed analysis of these genes showed that 77% of the identified XRE genes were directly modulated by expression of the AvrXv3 effector protein. Interestingly, 64% of the XRE genes were also shown to be induced in tomato during an incompatible interaction with an avirulent strain of *P.* syringae pv. tomato (Gibly *et al.* 2004).

cDNA from *X. campestris* pv. malvacearum inoculated and non-inoculated leaves of cotton line Im216 resistant to bacterial blight was used to determine HR. The analysis yielded 121 unique non-redundant sequences, consisting of 97 with similarity to sequences submitted to GenBank and 24 without good matches. The unique sequences and some identified genes were amplified by PCR and were arrayed onto glass slides. These microarrays were used to analyze transcripts in Im216 leaves over the extended period of 8-60 h after inoculation. The results showed that 98% of the genes were significantly up-regulated at one or more of the sampling times. Among these up-regulated genes 63% had sequence similarity to genes that function in disease/defense, protein synthesis/turnover, secondary metabolism, signaling, stress/PCD, or code for PR proteins or retrotransposon-like proteins that take role in defense responses (Patil *et al.* 2005).

The type III effector AvrXv3 from Xcv was known to elicit a resistance response in the tomato line Hawaii 7981. Tomato plants tested after inoculation with isogenic Xcv strains differing only by the *avrXv3* gene revealed that transcript levels of 139 genes were observed to be increasing within 8 h, and a massive shift in expression of 1,294 genes was detected at 12 h. AvrXv3 up-regulated a large number of genes encoding TFs and signaling components, genes involved in defense and stress responses, lipid metabolism, protein degradation, and secondary metabolism whereas genes related to photosynthesis and protein synthesis were generally down-regulated. Many novel genes encoding proteins of unknown function were also identified. A partial overlap and a similar distribution in functional classes were determined between AvrXv3-modulated genes and those differentially expressed in tomato plants recognizing other bacterial effectors (Balaji *et al.* 2007). Global expression analysis of tomato during disease development caused by *Clavibacter michiganensis* subsp. *michiganensis* (Cmm) at 4 and 8 days after inoculation was performed (Balaji *et al.* 2008). Among 9,254 tomato genes represented on the array, 122 were reported to be differentially expressed in Cmm-infected plants, compared to mock-inoculated ones. It was also found that Cmm infection induced genes involved in ET biosynthesis and activated basal defense responses, including induction of defense-related genes, production of free oxygen radicals, enhanced protein turnover, and hormone synthesis.

cDNA microarrays proved the presence of a putative cytochrome P450 gene in chili pepper (*Capsicum annuum* L.) (*CaCYP1*) following induction of the leaf HR by inoculation of pepper plants with the non-host pathogen *X. axonopodis*. *CaCYP1* expression was observed to be increasing also after SA and ABA treatments. The results indicated that *CaCYP1* might play a role in plant defense response pathways that involve SA and ABA signaling pathways (Kim *et al.* 2006).

It was previously observed that *Trichoderma hamatum* 382 is able to protect tomato against bacterial spot and its pathogen *X. euvesicatoria* 110c. In order to determine the mechanism by which *T. hamatum* 382 induced resistance in tomato, oligonucleotide microarrays were used; and the results revealed that *T. hamatum* 382 consistently modulated the expression of genes in tomato leaves. Among them were the genes having functions associated with biotic or abiotic stress, as well as RNA, DNA, and protein metabolism. The results of the study showed that *T. hamatum* 382 actively induces systemic changes through modulation of the expression of stress and metabolism genes (Alfano *et al.* 2007).

An *indica* rice cultivar IET8585 (Ajaya) withstands diverse races of the *X. oryzae* pathogen attack, and bacterial leaf blight (blb). The microarray analysis revealed differential expression of numerous genes in blb-infected resistant IET8585 cultivar over the susceptible IR24. Hypersensitive cell death in the resistant cultivar upon bacterial infection might be due to the higher expression of *EREBP* TF along with lower expression of alcohol dehydrogenase gene and ROS scavenging system. It was also suggested that induction of glutathione-mediated detoxification and flavonoid biosynthetic pathways along with up-regulation of defense

genes during infection might inhibit pathogen spread in the host tissues (Kottapalli *et al.* 2007).

The acyl-coA elongase complex synthesizes very-long-chain fatty acids. In a recent report, microarray analyses of *Arabidopsis* plants upon infiltration with avirulent strain 147 of *X. campestris* pv *campestris* were conducted. The genes encoding the four enzymes forming the acyl-coA elongase complex were proposed to be the putative targets of *MYB30*, which might be regulating the HR via synthesis of very-long-chain fatty acids (Raffaele *et al.* 2008).

Gene expression differences of ginseng hairy roots after infection by *A. rhizogenes* were investigated by using a cDNA microarray approach and 250 genes were analyzed (Chung *et al.* 2003). Among them, 63 were differentially expressed in a hairy root line containing a high level of ginsenosides. 29% of the genes that were differentially expressed were genes related to metabolism and 17% were related to stress responses. Most of them were primarily associated with ribosomal proteins, thereby functioning in protein synthesis and their expression was down-regulated in hairy roots having less lateral branching which might be a phenotype resulting from manipulation of metabolic activities by the translational machinery.

A. tumefaciens lacks the HR-inducing *hrp* genes. An *Arabidopsis* 26,000-gene oligonucleotide microarray was used to understand the timing and extent of the plant transcriptional response to this pathogen. The response was found to be different at 48 h after infection but not earlier. The induced genes included genes encoding known defense proteins, and the repressed ones were enriched with genes characteristic of cell proliferation (Ditt *et al.* 2006).

Agrobacterium effect on gene expression was determined by a functional genomics approach in *A. thaliana*. The increase in the levels of anions, sugars, and amino acids were correlated with changes in the gene expression of specific enzymes and solute transporters. The expression profiles of the genes taking role in the energy metabolism, such as those involved in photosynthesis, mitochondrial electron transport, and fermentation, suggested that tumors produce carbon (C) and nitrogen (N) compounds heterotrophically and gain energy mainly anaerobically (Deeken *et al.* 2006).

The *Rhizobium*-legume symbiosis provides the exchange of nutrients in the root nodule. Bacteria within the nodule reduce molecular N for plant use and plants provide bacteria with C-containing compounds (Starker *et al.* 2006). In order to predict regulation of plant genes for nodule initiation, the gene expression profiling was carried out in early stages of the symbiosis between *M. truncatula* roots and *Sinorhizobium meliloti* (Lohar *et al.* 2006). The plants at defined stages of inoculation (1-72 h post inoculation) were analyzed by using a microarray with about 6,000 cDNAs. Hundreds of genes of both known and unknown function were significantly regulated; and according to expression profiles four stages of the interaction were recognized.

Microarray analysis was carried out in order to see the effect of *S. meliloti* lipopolysaccharide (LPS) and an elicitor invertase on defense-associated gene expression (Tellstrom *et al.* 2007). The results showed that there exists a gene expression pattern characteristic for a defense response. Concurrent treatment of *M. truncatula* suspension-cultured cells with invertase and *S. meliloti* LPS led to a lower level of induction of defense-associated genes compared to induction rates in cells treated with invertase alone. The report concluded that LPS of the symbiont both suppresses fast defense responses (i.e. oxidative burst) and exerts long-term influences (i.e. transcriptional adjustment to pathogen attack).

Using cDNA microarray analysis, a cDNA clone, *CaATL1* (*C. annuum* L. AT-hook-like gene 1), from a chili pepper plant was isolated and shown to be incompatibly interacting with bacterial pathogens. In pepper plants expression of *CaATL1* was specifically induced in host- and non-host-resistant responses against bacterial and viral pathogens. In addition, SA and ethephone treatments induced expression of *CaATL1* where MeJA treatment resulted in mild induction. This was the first study showing the evidence of a role for a plant AT-hook motif-containing TF in pathogen defense response (Kim *et al.* 2007a).

During pathogen attack microbial surfaces are recognized by plant cells with a system called pathogen-associated molecular pattern (PAMP)-triggered immunity. *Arabidopsis* plants treated with a bacterial peptidoglycan from *Staphylococcus aureus* resulted in the activation of plant responses. Peptidoglycan-treated *Arabidopsis* leaves tested by microarray analysis revealed enhanced transcript levels for 236 genes (Gust *et al.* 2007).

Oomycete pathogenesis

Together with the induction of systemic acquired resistance (SAR), developmental processes of host plants might take role in the resistance response to pathogens. In *N. tabacum*, the vegetative-to-flowering transition came along with a susceptibility-to-resistance transition to the oomycete *Phytophthora parasitica*, the causal agent of black shank disease (Hugot *et al.* 2004). The study showed up-regulation of genes involved in SAR and peroxidase cross-linking of structural proteins to cell wall at late developmental stages of leaves. These genes were hypothesized to govern extracellular events that lead to expression of developmental resistance.

The characterization of a non-host pathosystem between the model plant *A. thaliana* and oomycete pathogen *P. infestans* was done by a microarray analysis of 11,000 *Arabidopsis* cDNAs 16 h after infection. A significant overlap between *Arabidopsis* non-host response and other defense-related treatments described in the literature was observed. The results of the study also confirmed a clear association of activation of JA pathway with the non-host response to *P. infestans* (Huitema *et al.* 2003).

The microarray analysis of a moderately resistant potato leaves that were inoculated with *P. infestans* for 2 to 72 h revealed the presence of 348 *P. infestans*-responsive genes (Wang *et al.* 2005). These functional genes were found to be mostly related to metabolism, plant defense, signaling, and transcription regulation. Based on the results, potato defense against *P. infestans* was discriminated into distinct stages. Furthermore, 114 novel genes with unknown functions were also isolated.

The molecular aspects of resistance mechanisms of potato to *P. infestans* were analyzed by using cDNA microarrays of 100 ESTs selected from a subtractive cDNA library (Tian *et al.* 2006). Among these clones 76 were differentially expressed in infected plants compared with mock-inoculated control plants. The expression of genes were post-inoculation time dependent some being induced later than others and some being up-regulated at all times. The largest set of up-regulated genes (35%) was found to be related to the primary/secondary metabolism according to BLAST algorithm searches. Furthermore, certain genes with known or putative functions including disease defense or cell rescue (18%), transcription, signal transduction, cellular transporter/transport facilitation, development, protein synthesis/destination, as well as those playing roles in cellular organization were differentially regulated. Besides, 15 genes encoding proteins of unknown function were also revealed.

RPP7 was found to be a specific disease resistance gene of *A. thaliana* against *Hyaloperonospora parasitica*. The function of it is independent of the defense hormone SA and most known genes required for plant immune responses. Another gene associated with *RPP7* suppression was found to be *EDM2* (enhanced downy mildew 2). Microarray analysis of the mutants of these genes, *rpp7* or *edm2* plants, defined a set of defense-associated genes, the expression of which were suppressed during successful parasite colonization of either (Eulgem *et al.* 2007).

Parasitic interaction of *M. truncatula* and the oomycete

Aphanomyces euteiches triggers the expression of a plant protease inhibitor (PI) encoding gene, *MtTi2*. Global expression profiles of RNA silenced *Medicago*, *MtTi2i* roots, was investigated using an 8,000 gene containing *M. truncula* microarray to reveal the effects of suppression of *MtTi2*. The analysis showed differential regulation of genes in *MtTi2i*- and wild type roots. The results suggested endogenous functions of *MtTi2* other than direct suppression of the pathogen (Nyamsuren *et al.* 2007).

Aphid infestation and wounding

Localized changes in transcript levels of certain genes upon compatible aphid feeding on leaves of *A. thaliana* have been described previously. These genes were also associated with infection, mechanical damage, chewing herbivory, or resource allocation shifts. The results of a gene expression analysis carried out after 72 or 96 h of *Myzus persicae* feeding on *A. thaliana* leaves revealed that genes involved in oxidative stress, Ca^{2+}-dependent signaling, PR responses, and signaling were key components of response (Moran *et al.* 2002).

It was known that *S. bicolor* activates JA- and SA-regulated genes and genes that take part in wounding and SA signaling pathways when attacked by a phloem-feeding greenbug aphid (*Schizaphis graminum*). A microarray consisting of 672 cDNAs was used for expression profiling and 82 transcripts were found to be responsive to greenbug feeding, MeJA, or SA application (Zhu-Salzman *et al.* 2004). DNA sequencing analyses indicated that these transcripts encoded proteins functioning in direct defense, defense signaling, oxidative burst, secondary metabolism, abiotic stress, cell maintenance, and photosynthesis, as well as proteins of unknown function. The activation of certain genes by greenbug infestation indicated that there might be unique signal transduction events independent of JA- and SA-regulated pathways. According to the results of the study it was concluded that even though plants regulate defense gene expression when attacked by phloem-feeding aphids, aphids are able to avoid triggering activation of some effective plant defensive machinery, possibly through their particular mode of feeding.

The effects of phloem-feeding by greenbug and sorghum genes responsive to greenbugs were investigated with cDNA microarray and northern blot analyses (Park *et al.* 2006). The results showed that 157 differentially expressed genes of sorghum had functional roles in metabolic pathways, such as defense, signal transduction, cell wall fortification, oxidative burst/stress, photosynthesis, development, cell maintenance and abiotic stress. As well as the well-known defense related regulators like SA, JA, and ABA, mediation of the defense responses against greenbug phloem-feeding in sorghum involved auxin and gibberellic acid.

A cDNA microarray of 240 defense-related *N. attenuata* genes was used in the analysis of gene expression in native tobacco plants infested with the aphid *M. nicotianae* (Voelckel *et al.* 2004). Contrary to the strong responses to tissue-feeding lepidopteran larvae and mesophyll-sucking insect attacks, the responses to phloem-feeding aphids were observed to be weaker. Expression of trypsin protease inhibitors (*TPI*), *LOX*, and xyloglucan-endotransglycosylase genes were increased and that of small RUBISCO subunit and ubiquitin carrier protein genes were decreased upon feeding by *M. nicotianae*. Aphid-specific changes included the up-regulation of glutamate synthase and the down-regulation of a germin-like protein. The results of the study showed that the genes for hydroperoxide lyase and *TPI* which mediate the synthesis of compounds reported to be toxic for aphids were either not under transcriptional control or not important in *N. attenuata*.

The wheat expression profiles for the genes associated with plant defense against *Diuraphis noxia* (Russian wheat aphid, RWA) reported 29 transcripts associated with the feeding response. These transcripts encoded proteins functioning in direct defense and signaling, oxidative burst, cell wall degradation, cell maintenance, photosynthesis, and energy production. It was concluded that the ability to maintain photosynthetic function may be the key factor determining the survival of the resistant plants in response to RWA feeding (Botha *et al.* 2006).

Oligonucleotide microarrays and qRT-PCR analysis were used to characterize transcriptional profiles of different *A. thaliana* ecotypes (Wassilewskija; Ws, Cape Verde Islands; Cvi, and Landsberg erecta; Ler), with different predominant glucosinolate hydrolysis products, in response to infestation with *M. persicae* or *Brevicoryne brassicae* (Kusnierczyk *et al.* 2007). The results showed common induction of general stress-responsive genes and suppression of myrosinases, enzymes hydrolyzing glucosinolates, in all ecotypes. Different gene inductions at specific defense systems were observed in different ecotypes suggesting slightly different defense strategies. In Cvi, highest up-regulations were reported to be that of genes belonging to JA synthesis pathway while in Ler that of genes belonging to indole glucosinolate synthesis pathway. It was suggested that the defense system was both herbivore and ecotype specific.

Insect and worm attack

When plants are attacked by herbivores they release leaf volatiles that could result in the induction of defense responses against aggressive biotic agents. In order to analyze the gene expressions in lima bean leaves that were exposed to volatiles released from the neighboring leaves infested with spider mites cDNA microarray analysis was carried out. The infestation with spider mites and the herbivory-induced volatiles enhanced the expression of 97 and 227 genes, respectively. These genes were categorized as being related to response to pathogenesis, wounding, hormones, ET biosynthesis, flavonoid biosynthesis, transcriptional modifications, chaperones, secondary signaling messengers, membrane transports, protein degradations, and photosynthesis. It was concluded that herbivorous damage and herbivory-induced volatiles resulted in drastic changes of metabolism in leaves (Arimura *et al.* 2000).

The events taking place in intact tomato (*L. esculentum*) plants at the first 5 days of attack by spider mites (*Tetranychus urticae*) were analyzed by combined metabolomics and transcriptomics approach. Time dependent changes were reported on expression levels of genes. PI activity was observed to be doubled and the transcription of genes involved in JA-, SA-, and ET-regulated defenses and phospholipid metabolism had been activated on day one and those involved in the secondary metabolism on day four. It was concluded that complementation of direct defense response against spider mites in tomato was done by activation of indirect defenses (Kant *et al.* 2004).

In plants SA, JA, and ET signaling pathways interact upon pathogen and insect attack. *Arabidopsis* plants exposed to different pathogens and insects were investigated for the analysis of integrated mechanisms of these signaling pathways. It was observed that the timing and quantity of SA, JA, and ET production varied with pathogen type; however overexpression of stress-related genes was the common point. It was concluded that the complex attacker specific defense was due to the attacker induced signals and crosstalk between SA, JA, and ET signaling pathways (de Vos *et al.* 2005).

Microarray analysis of 115 transcripts of *N. attenuata* after attack by *Manduca sexta* larvae revealed 73 differentially expressed genes. The analysis revealed understanding of the signaling and transcriptional basis of direct and indirect defenses used against herbivores. Simultaneous activation of SA-, ET-, cytokinin-, WRKY-, MYB-, and oxylipin-signaling pathways were observed leading to regulation of terpenoid-, pathogen-, and cell wall-related transcripts in defense responses. The defense responses showed down-regulation of photosynthesis-related transcripts and up-regulation of transcripts associated with protein and nuc-

leotide turnover, and carbohydrate metabolism. The complexity of the defense system against herbivore attack was mainly due to the up-regulation of defense-associated and down-regulation of growth-associated transcripts together with alteration of transcripts for a variety of genes (Hui *et al.* 2003).

The differences at the transcriptional responses due to attack by a specialist *M. sexta* or two generalist species *Heliothis virescens* and *Spodoptera exigua* were determined by cDNA microarray analysis of *N. attenuata*. The differences in plant responses were found to be correlated with the profile of larval elicitors like fatty acid-amino acid conjugates (FAC) and it was concluded that variation in FAC composition might shape the interaction between generalist or specialist lepidopteran larvae and plants (Voelckel and Baldwin 2004).

Using DNA microarrays, gene expressions in damaged and in distal *A. thaliana* leaves in response to the specialist insect, *Pieris rapae* were analyzed. More than 100 insect-responsive genes having role in pathogenesis, indole glucosinolate metabolism, detoxification and cell survival, and signal transduction were observed to be differentially expressed. When wild-type and jasmonate mutant plants were compared, approximately 75% of *Pieris*-regulated genes were observed to be controlled totally or in part by JA. The comparison of response to larvae of the specialist *P. rapae* and to a generalist insect, *Spodoptera littoralis* revealed almost identical transcript profiles (Reymond *et al.* 2004).

Insect eggs represent a threat for plants as hatching larvae rapidly start feeding. The whole-genome microarray was used to analyze the expression profile of *Arabidopsis* leaves after oviposition by two pierid butterflies. It was shown that the expression of hundreds of genes changed with deposition of eggs and response was similar to that observed during HR with up-regulation of defense and stress related genes and down-regulation of ones taking role in growth and photosynthesis (Little *et al.* 2007).

A. thaliana mutants impaired in JA, ET, and SA signaling pathways were challenged with the specialist small cabbage white (*P. rapae*) and the generalist Egyptian cotton worm (*S. littoralis*), and transcriptional profiles of plants were monitored with microarrays. JA was shown to act as a major signal controlling the up-regulation of defense genes in response to either insect. Altered transcript profiles were observed in ET and SA mutants after *S. littoralis* herbivory but not after *P. rapae* herbivory. On the contrary, both insects yielded similar transcriptome changes in the ABA-biosynthetic mutants and ABA controlled transcript levels in insect-attacked plants. The study proposed a new role for ABA in defense against insects in *Arabidopsis* and identified some components important for plant resistance to herbivory (Bodenhausen and Reymond 2007).

A cDNA microarray containing 960 random clones represented with cDNA probes prepared from mRNAs of control and planthopper-infested wild rice (*O. minuta*) revealed differential expression of 383 clones upon infestation. These transcripts were categorized into 3 main groups; subcellular localization, metabolism, and protein fate. The study showed that resistance of *O. minuta* to insect infestation might be maintained by an elevated expression of defense-related genes together with enhanced metabolic activities (Cho *et al.* 2005).

cDNA microarray containing 15,496 unique genes was utilized to monitor gene expression in poplar leaves in response to herbivory by forest tent caterpillars (*Malacosoma disstria*). The analysis showed 1,191 genes to be up-regulated, compared to only 537 down-regulated ones after 24 h of feeding. Functional classification of this induced gene set revealed genes with roles in plant defense, octadecanoid and ET signaling, transport, secondary metabolism and transcriptional regulation (Ralph *et al.* 2006a).

Conifers have higher resistance to a large number of potential insect herbivores or pathogens but the genomic basis of defense and resistance mechanisms is largely unknown. cDNA microarrays representing approximately 5,500 unique genes were used to monitor gene expression in Sitka spruce (*Picea sitchensis*) bark in response to herbivory by white pine weevils (*Pissodes strobi*) or wounding, and in young shoot tips in response to western spruce budworm (*Choristoneura occidentalis*) feeding. All treatments caused substantial changes of the host transcriptome after 1 or 2 days of treatment. Differentially expressed gene sets were similar for each treatment. The up-regulated genes were determined to be involved in plant defense, octadecanoid and ET signaling, transport, secondary metabolism, and transcriptional regulation and down-regulated ones were genes involved in primary metabolic processes such as photosynthesis (Ralph *et al.* 2006b).

The phloem-feeding insect-plant interactions were studied using silverleaf whitefly (SLWF; *Bemisia tabaci* type B) and *Arabidopsis*. Microarray studies with ATH1 Gene Chip brought out 700 transcripts to be up-regulated and 556 down-regulated by SLWF nymphs. The results also showed the response to SLWF-instar feeding to be qualitatively and quantitatively different from that to chewing insects and aphids (Kempema *et al.* 2007).

Nematode infections

Compatible interaction of soybean cyst nematode (SCN), *Heterodera glycines*, with soybean (*Glycine max*) roots 2 days after infection was analyzed by a cDNA microarray. The results indicated induction of 8% of the genes monitored and more than 50% of these were with unknown functions. Certain genes like repetitive proline-rich glycoprotein, stress-induced gene *SAM22*, β-1,3-endoglucanase, peroxidase, and those involved in carbohydrate metabolism, plant defense, and signaling were among the highly expressed genes after 2 days of inoculation with SCN (Khan *et al.* 2004).

Changes in gene expression within roots of *G. max* cv. Kent, susceptible to infection by SCN, at different time points were monitored using microarrays containing more than 6,000 cDNA inserts. Some genes like *WRKY6* TF, trehalose phosphate synthase, *EIF4a*, *Skp1*, *CLB1*, *LOX*, calmodulin, phospholipase C, metallothionein-like protein, and chalcone reductase were observed to be differentially induced at most of the time points. The stress-related gene, *SAM-22*, phospholipase D and 12-oxophytodienoate reductase were induced at the early time-points. On the other hand, the ribosomal protein, initiation and elongation factor genes and the transcripts of proteins involved in C metabolism and transport were more abundant at later stages (Alkharouf *et al.* 2006).

Parallel genome-wide analysis of gene expression changes in the host soybean and the pathogen SCN was performed during infection. Among 35,611 soybean transcripts represented on GeneChip arrays, 429 were observed to be differentially expressed in infected root tissues. These included genes which were encoding enzymes involved in primary metabolism, biosynthesis of phenolic compounds, lignin, and flavonoids, and genes related to stress and defense responses, cell wall modification, cellular signaling, and transcriptional regulation. Among 7,431 SCN transcripts analyzed, 1,850 genes showed differential expression across different stages of nematode parasitism and development (Ithal *et al.* 2007).

In a time-course microarray analysis of soybean roots during an infection by incompatible and compatible populations of SCN (*H. glycines*), it was revealed that infection by individual incompatible and compatible populations influenced the transcription of soybean genes differently, a substantial difference being early at 12 h post infection. Amplitude differences in transcript abundances were also observed. It was concluded that host roots responded differentially to different pathogen races even before feeding site selection (Klink *et al.* 2007a). Syncytial cells in soybean roots infected by incompatible and compatible populations of SCN were collected using laser capture microdissection and assayed by microarray analysis. Differentially ex-

pressed genes in syncytial cells that were determined as not differentially expressed in the whole root analyses were identified (Klink *et al.* 2007b). Genes encoding *LOX*, *HSP 70*, and superoxide dismutase (*SOD*) were shown to be elevated almost 10-fold or more, while genes encoding several TFs and DNA binding proteins were elevated at lower levels in syncytial cells from incompatible roots. The research showed that gene expression differed in syncytial cells compared to whole roots infected with nematodes and the expression depends on the developmental stage of the syncytial cells.

The root knot nematode *Meloidogyne javanicaa* is a plant parasite that establishes and maintains a permanent feeding site within plant roots. Compatible interaction of *Meloidogyne* spp. cause re-differentiation of root cells into multinucleate nematode feeding cells (giant cells) which provide nutrition for nematodes. A tomato spotted microarray chip was used to analyze the gene expression in compatible response of tomato to root knot nematodes (Bar-Or *et al.* 2005). According to the results of the study significant changes were reported in the steady-state levels of transcripts of several functional categories, including PR genes, hormone-associated genes and development-associated TFs. Giant cell-enriched root tissues of *Arabidopsis* were used to investigate the plant response to root-knot nematodes (Jammes *et al.* 2005). Out of 22,089 genes monitored 3,373 genes were shown to display significant differential expression. It was also shown that the down regulation of certain genes might be essential for proper gall formation. Jammes *et al.* (2005) provided new insights into nematode feeding-cell formation, and role of suppression of plant defense in development of nematode feeding-site.

The giant cells show increased transport activity across the plasma membrane. The *Arabidopsis* ATH1 GeneChip was used to identify transporter genes that were regulated by nematode infestation over a 4-week period. Expression of 50 transporter genes from 18 different gene families was shown to be significantly altered. The results of the study showed regulation of multiple transport processes that might play important roles in establishment and maintenance of nematode feeding-site (Hammes *et al.* 2005).

Whole genome microarrays for plant gene expression in mature *M. incognita*-induced galls in *Arabidopsis* revealed differential expression of 959 genes among which two-thirds of them were down-regulated (Fuller *et al.* 2007).

Rust diseases

Plant pathogen interaction between three-week-old soybean plants and Asian soybean rust (ASR) was analyzed by transcriptome profiling using soybean microarrays. A total of 112 genes were found to be differentially expressed; 46 being up-regulated and 66 down-regulated. General defense and stress-related genes constituted the largest subset of differentially expressed genes. It was concluded that the failure to develop rust resistance in the soybean might be due to low and non-specific innate response to the pathogen (Panthee *et al.* 2007).

In another study on ASR, soybean mRNAs were profiled in mock-inoculated and infected leaves of a soybean accession (PI230970) carrying the *Rpp2* resistance gene and a susceptible genotype (Embrapa-48). The profiles of differentially expressed genes revealed a biphasic response which was dependent on genotype of soybean and stage of fungal growth. The obtained data suggested that ASR initially induced a non-specific response in both genotypes. This transient response was suppressed when early steps in colonization were completed. Extensive expression changes in soybean containing *Rpp2* resistance gene started prior to onset of rapid fungal growth which was observed in susceptible genotype (van de Mortel *et al.* 2007).

Populus 15.5K cDNA microarray was used to study the transcriptional response of hybrid poplar (*P. tyichocarpa* × *P. deltoides*) to poplar leaf rust (*Melampsora medusae*) infection (Miranda *et al.* 2007). 20% of genes were shown to be differentially regulated where a number of pathogen-defense genes encoding *PR-1*, chitinases, and other PR proteins were consistently up-regulated. The expression changes were time dependent and the largest number of changes in gene expression was observed late during the infection. Interestingly, inoculation repressed genes that were previously characterized to be wound- and herbivore-induced defense genes suggesting suppression of early host responses.

The *Lr34/Yr18* gene of wheat takes role in resistance to leaf rust, yellow rust, and several other diseases of wheat. The lack of knowledge motivated scientists for microarray analysis of rust- and mock-inoculated flag leaves of two pairs of wheat near isogenic lines for *Lr34/Yr18* (Hulbert *et al.* 2007). ABA inducible, osmotic stress, cold stress, and/or seed maturation related 57 genes were observed to be up-regulated in mock-inoculated leaf tips of resistant plants. PR proteins were not up-regulated in resistant flag leaves of mock-inoculated plants. However, they were up-regulated in both resistant and susceptible flag leaves of rust-inoculated plants. On the other hand higher expression levels of PR genes in resistant plants suggested a possible role for *Lr34/Yr18* in defense responses.

Response to wounding

Local responses due to wounding in *A. thaliana* leaves were observed by microarray analysis (Delessert *et al.* 2004). The analyzed parameters were spatial expression (local, adjacent and systemic), timing of expression (0.5, 4, 8, 17 h), and effect of hormone treatments (MeJA, ET and ABA). It was observed that the genes which responded systemically at early stages encoded predominantly signal transduction and regulatory factors and many of these genes were controlled by MeJA. The genes that were specifically expressed at wounding site responded slowly and they were mainly related to metabolism and lignin biosynthesis. It was proposed that ET and ABA took role in local response and they regulated photosynthetic and drought responsive genes, respectively. These results showed that raising a systemic response to wounding has priority in defense, and the local response at the wound site is established later.

12-Oxophytodienoate reductases (OPRs) belong to a family of flavin-dependent oxidoreductases. Three isoforms of OPRs were characterized and only one of them, OPR3 was found to be participating in the octadecanoid pathway for JA biosynthesis. The expression of *L. esculentum OPR3* was analyzed using a microarray (Strassner *et al.* 2002). *LeOPR3* was found to be up-regulated after wounding and the accumulation of octadecanoid pathway transcripts was found to be more rapid and transient in wounded leaves compared to unwounded leaves. It was concluded that transcriptional activation of the octadecanoid pathway and accumulation of JA were not required for activation of defense gene expression in systematic tissues.

A study showing the effects of bestatin, a potent inhibitor of some aminopeptidases which acts as an inducer of wound-response genes in tomato (*L. esculentum*) revealed that bestatin exerts its effect by activating JA signaling in plants. *Arabidopsis* whole-genome chip was used to confirm that the gene expression profile of bestatin-treated plants was similar to that of JA-treated plants (Zheng *et al.* 2006). The evidences led researchers to hypothesize that bestatin exerts its effects through the modulation of some key regulators in JA signaling.

It is known that MKPs which are negative regulators of MAPKs take role in abiotic stress responses in dicotyledons. In order to determine their roles in monocotyledons, rice microarray analysis was carried out (Katou *et al.* 2007). Five putative MKPs in rice were identified among which *OsMKP1* expression is rapidly induced by wounding. The loss of function mutant *osmkp1* was analyzed by microarray and the results showed that 13 and 8 genes were up- and down-regulated in *osmkp1*, respectively. Among the up-regulated genes, expressions of 5 genes were shown to be res-

ponding to wounding, indicating constitutive activation of wound responses in *osmkp1*. The researchers suggested involvement of *OsMKP1* in the negative regulation of rice wound responses.

Systemic acquired resistance

Together with basal response, plants also have SAR that might be induced in tissues remote from pathogen infection sites. The initiation of local defense and SAR requires transcriptional reprogramming at infected plants. A cDNA microarray consisting of 23-30% of *Arabidopsis* genes was used to monitor gene-expression changes under 14 different SAR-inducing or SAR-repressing conditions (Maleck *et al.* 2000). The results of the study revealed the presence of regulons, genes with common regulation patterns. Among these, the regulon containing *PR-1*, a reliable marker gene for SAR in *A. thaliana*, was observed to be containing known PR genes and novel genes likely to function during SAR and disease resistance. The study also reported identification of a common promoter element in genes of this regulon that binds members of a plant-specific TF family.

SAR is an inducible plant defense response involving a series of transcriptional events induced by SA through the transcription cofactor NPR1. A microarray analysis on *Arabidopsis* plants expressing the NPR1:GR (glucocorticoid receptor) fusion protein was used to determine regulatory nodes of SAR (Wang *et al.* 2006a). NPR1 was found to be regulating a NPR1-dependent transcription via up-regulation of 8 WRKY TF genes. Previously this large family of 74 TFs has been shown to take role in various defense responses, but Wang *et al.* (2006a) provided the understanding of both positive and negative regulation of WRKY factors on SAR.

Upon pathogen attack *Coffea arabica* activates SAR as the main defense mechanism. The report of de Nardi *et al.* (2006) focuses on the effect of a SAR chemical inducer, benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH) on the expression profile of *C. arabica*. 1,587 non-redundant ESTs were created by the use of mRNA isolated from leaves and embryonic roots. Microarray analysis revealed the presence of 55 induced and 16 repressed genes via competitive hybridization between untreated and BTH-treated leaves. These numbers in roots were 37 and 42 for induced and repressed genes, respectively. Overall a systemic increase in PR protein synthesis, in the oxidative burst, and in the cell wall strengthening processes was observed with a site specific manner.

The activation path for establishing SAR remains unclear. In a study it was shown that even though there was no pathogen-associated molecular pattern contact, systemically responding leaves rapidly activated a SAR transcriptional response that had strong similarity to local basal defense (Truman *et al.* 2007). The study revealed that JA might be central to systemic defense, initiating the signaling cascade for SAR. The study concluded that JA signaling appeared to mediate long-distance information transmission. It was also noted that the systemic transcriptional response had significant overlap with local herbivory and wounding responses. Therefore, it can be concluded that JA signaling might be common pathway for both abiotic and biotic stress signals.

Fungicidal or herbicidal stresses

Azoxystrobin and fenpropimorph are two fungicides used against powdery mildew and rust diseases in wheat (*T. aestivum* L). In contrast to the fungicides which directly affect pathogen metabolism, BTH provides resistance against wheat pathogens by activating SAR in the host plant. The effects of these agrochemicals on gene expression were analyzed in greenhouse grown spring wheat by using a microarray containing 600 barley cDNA clones (Pasquer *et al.* 2005). BTH treatment caused similar changes that were observed after treatment with fenpropimorph and azoxystrobin demonstrating the activation of a defense reaction. The results of the same experiments performed under field conditions gave dramatically different results with none of the genes showing differential expression after treatment (Pasquer *et al.* 2005). The defense genes were observed to be expressed at a high level before application of the agrochemicals. It was concluded that environmental conditions drastically affected the response to agrochemicals.

It is known that the surfactant application together with herbicides improves the performance of the herbicides. In order to understand how this effect occurs at molecular level NUL1026 surfactant applied *A. thaliana* plant gene expression was analyzed using ATH1 GeneChips (Madhou *et al.* 2006). After 1 h, 196 genes were found to be significantly altered when plants were treated with the surfactant. Altered genes included metabolism, physiological processes, transport, protein metabolism, response to stimulus and transcription related genes. The up-regulation of genes encoding enzymes involved in the JA biosynthesis pathway and also the 1-aminocyclopropane-1-carboxylate synthase gene for ET production indicated that treatment of surfactant NUL1026 affected the expression of a number of genes involved in the detoxification and signaling pathways.

The changes induced by three herbicides [2,4-dichlorophenoxyacetic acid (2,4-D), cinidon-ethyl and tribenuron-methyl] on the wheat transcriptome were studied at different application intervals using cDNA microarrays (Pasquer *et al.* 2006). Under controlled and field conditions 2,4-D induced genes of the phenylpropanoid pathway and cinidon-ethyl triggered peroxidase and defense-related gene expression but the up-regulation was weaker under field conditions. The same genes were up-regulated in the field as under controlled conditions. The up-regulation due to tribenuron-methyl was observed not immediately but only after 1 week of treatment.

BTH is a plant activator that takes role in activating SA signaling pathway upon diseases. Microarray analysis of rice treated with BTH revealed the presence of BTH- and SA-inducible WRKY TF genes (Shimono *et al.* 2007). Two defense-related genes, encoding a GST and a cytochrome P450, were found to be regulated downstream of *WRKY45*. The study showed that *WRKY45* is a component of BTH-induced and SA-mediated defense signaling in rice.

EXPRESSION PROFILING UNDER ABIOTIC STRESSES

All abiotic stresses are important environmental factors that reduce plant growth and yield. Plants respond and adapt to these stresses in order to survive. Signaling pathways are induced in response to environmental stresses; therefore recent studies have focused on molecular and genetic bases of these pathways involving various components. The products of stress-inducible genes which could be directly protecting against these stresses include the enzymes responsible for the synthesis of various osmoprotectants like late embryogenesis abundant (LEA) proteins, antifreeze proteins, chaperones; and detoxification enzymes. Another group of gene products involved in gene expression and signal transduction pathways includes TFs, protein kinases and enzymes involved in phosphoinositide metabolism and 3',5'-cyclic guanyl monophosphate (cGMP), nitric oxide (NO) and Ca^{2+} homeostasis. Stress responses and the signaling pathways that are either common or specific to the response and crosstalk among various transduction pathways under abiotic stresses in regulation of metabolism are reviewed previously (Seki *et al.* 2003; Kaur and Gupta 2005). Different abiotic stresses induce a range of physiological and biochemical responses in plants. Many transformation studies were performed to understand cellular and molecular responses under these stresses and to obtain osmotic stress tolerant plants (Öktem *et al.* 2006). Recently, a number of stress-inducible genes have been identified using microarray analysis in various plant species, such as *Arabidopsis* and rice. Microarray technology employing cDNAs or oligonucleotides is a powerful tool for analyzing gene

expression profiles of plants exposed to abiotic stresses such as drought, high salinity, or cold, or to ABA treatment (Yamaguchi-Shinozaki and Shinozaki 2006).

Full-length cDNAs were employed for the correct annotation of genomic sequences and for the functional analysis of genes and their products. *Arabidopsis* full-length cDNA microarrays were used for monitoring expression profiles of drought- and/or cold-inducible genes and for the discovery of target genes of stress-related TFs (Seki *et al.* 2001a). 155,144 RIKEN *Arabidopsis* full-length (RAFL) cDNA clones were isolated. The 3'-end ESTs of all 155,144 RAFL cDNAs were clustered into 14,668 non-redundant cDNA groups, about 60% of predicted genes (Seki *et al.* 2004). cDNA microarray analysis has been developed for quantitative analysis of global and simultaneous analysis of expression profiles of genes under various stress- and hormone-treatment conditions and in various mutants and transgenic plants.

Signaling molecules and hormones involved in abiotic stress

Studies on plant "signalome" – the identification of all signaling components in messenger-mediated transduction pathways, analysis of their function and regulation, and crosstalk among these components – might help in understanding plant cell responses to diverse signals. Accumulating evidence suggests that cGMP, NO and Ca^{2+} serves as messengers in many normal growth and developmental process and in plant responses to biotic and abiotic stresses (**Fig. 2**). Numerous signals have been shown to induce transient elevation of these molecules in plants. Functional genomics approaches such as reverse genetics, microarray analyses and proteomics might permit functional analysis of various components in signaling and also enable identification of complex networks of interactions. Role of Ca^{2+} in signaling has been reviewed previously (Reddy 2001). Relative expression of Ca^{2+}-dependent protein kinases (*CDPK*s) had been analyzed by using GeneChip rice genome array during three vegetative stages, six stages of panicle and five stages of seed development along with three abiotic stress conditions (cold, salt and desiccation) given to seedling. Thirty-one *CDPK* genes were found to be expressed in at least one of the experimental stages studied. Six *CDPK* genes were found to be induced while the expression of one gene was down-regulated under stress conditions. The differential expression of *CDPK* genes during reproductive development and stress is suggestive of common elements between reproduction and stress (Ray *et al.* 2007).

In many plant species, cGMP has been reported as a second messenger. Physiological processes where cGMP signaling has been observed to play a role include expression of defense-related genes and salt or osmotic stress. A transcriptomics approach was used to identify putative targets for cGMP signaling. Root exposure to 10 µM cGMP induced changes in transcripts related with metabolism, gene transcription, signaling and defense. It was also found that exposure to cGMP was found to modulate influx and efflux of the monovalent cations Na^+ and K^+ (Maathuis 2006a).

ABA is important in seed maturation, seed dormancy, stomatal closure, and stress response. An *Arabidopsis* ABA-hypersensitive mutant, *ahg2-1*, that showed ABA hypersensitivity not only in germination, but also at later developmental stages was analyzed. It was found that *ahg2-1* accumulated more endogenous ABA in seeds. Microarray experiments revealed increase in expressions of ABA-, SA- and stress-inducible genes in *ahg2-1* plants. Therefore it was suggested that the *ahg2-1* mutation affects responses to both ABA and various stresses. Analyses of *ahg2-1* mutation suggested that the mutation reduced poly(A)-specific ribonuclease (AtPARN) production. On the other hand, *AtPARN* expression was increased when exposed to ABA, high salinity and osmotic stress (Nishimura *et al.* 2005).

Several ABA-hypersensitive *A. thaliana* mutants, named *ahg1-1* and *ahg3-1* were analyzed. Map-based cloning of *AHG1* revealed that *ahg1-1* has a nonsense mutation in a gene encoding a novel PP2C. The *ahg3-1* mutant has a point mutation in the *AtPP2CA* gene, which encodes another PP2C. After 4 days of normal growth wild-type, *ahg1-1* and *ahg3-1* seeds were incubated for 2 days on media containing ABA. Microarray experiments using ATH1 Gene Chips revealed that many seed-specific and ABA-inducible genes were highly expressed in *ahg1-1* and *ahg3-1* mutants compared to wild-type (Nishimura *et al.* 2007). In another study, it was also shown that the peroxidase 1 gene promoter was ABA up-regulated 4-fold within 1 day of exposure to ABA and its expression was lateral root specific (Yu *et al.* 2007).

An oligonucleotide microarray was used for transcriptomic analysis of *Physcomitrella* treated with ABA, or subjected to osmotic, salt and drought stress. In protonemal tissue, 130 genes were induced by dehydration, 56 genes by ABA, but only 10 and 8 genes by osmotic and salt stress, respectively. Fifty-one genes were induced by more than one treatment. Seventy-six genes, principally encoding chloroplast proteins, were drought down-regulated (Cuming *et al.* 2007).

Receptor-like kinase1 (RPK1), a Leu-rich repeat (LRR) receptor kinase in the plasma membrane, is up-regulated by ABA in *A. thaliana*. Repression of *RPK1* expression in *Arabidopsis* decreased sensitivity to ABA during germination, growth, and stomatal closure; microarray and RNA gel analysis showed that many ABA-inducible genes were down-regulated in these plants. It was also proposed that *RPK1* is involved in the main ABA signaling pathway and in early ABA perception in *Arabidopsis* (Osakabe *et al.* 2005).

In another study, microarray analysis showed that ABA- and stress-inducible genes were up-regulated in the *RD26*-overexpressed plants and repressed in the *RD26*-repressed plants (Fujita *et al.* 2004). *A. thaliana RD26* cDNA, isolated from dehydrated plants, encodes a NAC protein. Expression of the *RD26* gene was induced not only by drought but also by ABA and high salinity. Moreover, transgenic plants overexpressing *RD26* were highly sensitive to ABA, while *RD26*-repressed plants were insensitive. The results of the study indicated that *RD26* functions as a transcriptional activator in ABA-inducible gene expression under abiotic stress in plants.

To detect the possible ABA related signal transduction pathways, investigators tried to isolate ABA-regulated genes in ABA-treated (for 2, 4, 8 and 12 h) rice seedlings through cDNA macroarray technology. Of 6,144 cDNA clones tested, 37 differential clones showing induction or suppression for at least one time, were isolated. Of them, 30 and 7 were up- or down-regulated, respectively. In addition, some clones were further shown to be regulated by other plant growth regulators like auxin and brassinosteroid, which indicated the complex crosstalk between plant hormones (Lin *et al.* 2003).

DNA microarray experiments revealed that catalytic subunit of PP2A (PP2Ac-2) is negatively involved in ABA responses through regulation of ABA-dependent gene expression. Moreover, the results obtained indicated that ABA antagonistically regulates *PP2Ac-2* expression and PP2Ac-2 activity thus allowing plant sensitivity to the hormone to be reset after induction. Phenotypic, genetic and gene expression data strongly suggested that PP2Ac-2 is a negative regulator of the ABA pathway (Pernas *et al.* 2007).

Nitric oxide (NO) is emerging as an important signaling molecule with diverse physiological functions in plants. Changes in gene expression in response to 0.1 mM and 1.0 mM sodium nitroprusside, a donor of NO, were studied in *Arabidopsis* using the whole genome ATH1 microarray (Parani *et al.* 2004). Most of the changes in 342 up-regulated and 80 down-regulated genes were specific to NO treatment. After treatment with NO scavenger, 2-(4-carboxyphenyl]-4,4,5,5-tetramethylimidazoline-1-oxy-3-oxide (c-PTIO), a reverse trend was reported. Genes encoding disease-resis-

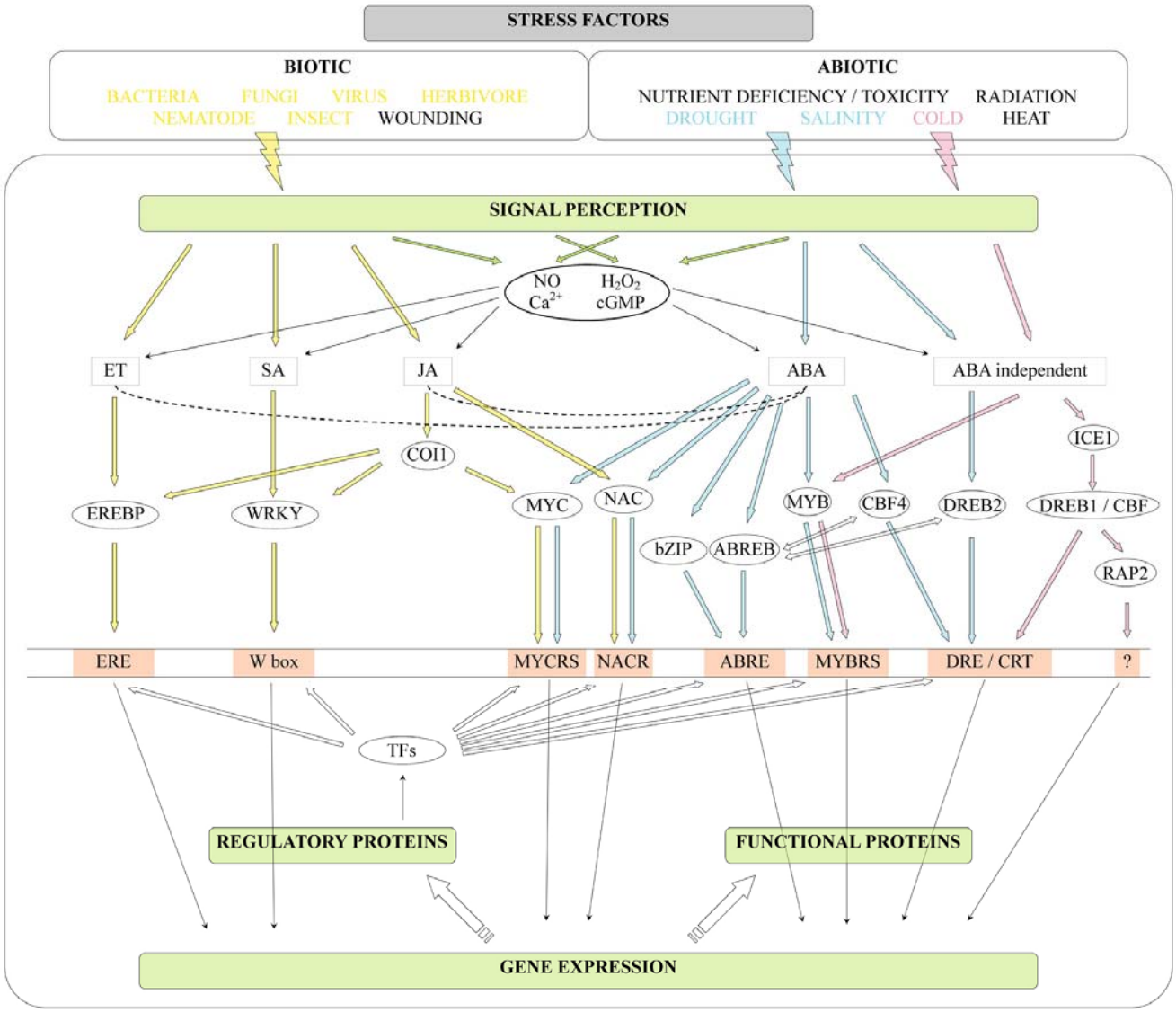

Fig. 2 Simplified model of crosstalk between regulatory network of gene expression in response to biotic and abiotic stresses. Signal perception under biotic (i.e. infection, invasion or attack by bacteria, fungi, virus, herbivore, nematode or insect, or wounding) or abiotic (i.e., drought, salinity, cold, heat, nutrient deficiency / toxicity or radiation) stresses leads to generation of various signaling molecules like nitric oxide (NO), hydrogen peroxide (H_2O_2), calcium (Ca^{2+}) or 3',5'-cyclic guanyl monophosphate (cGMP), which are presented in a big oval in the figure. These signaling molecules or perception of stress regulate various cellular signaling or response pathways involving abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), ethylene (ET) and others. These pathways regulate various transcription factors (TFs) which in turn control stress-inducible gene expression and which are shown in small ovals in the figure. Such transcription factors include EREBP, WRKY, COI1, MYC, NAC, bZIP, ABREB, MYB, CBF4, DREB2, DREB1/CBF, ICE1, RAP2 and many more. Binding of transcription factors to corresponding *cis*-acting elements like ERE, W box, MYCRS, NACR, ABRE, MYBRS, DRE/CRT and many more initiates stress-responsive gene expression. Such *cis*-acting elements on the genome are indicated in pink rectangular boxes in the figure. Stress-responsive transcription leads to expression of genes of functional or regulatory proteins which in turn might start cascades of regulation by transcription factors as late responses to environmental stresses. Such late and adaptive responses, which are shown in the lower part of the figure, might involve possible crosstalk between regulatory networks. Dashed lines indicate possible antagonistic relation between ABA and JA or ET signaling pathways. The open double-headed arrows show possible crosstalk between regulatory networks. Solid arrows yellow-, blue- and purple-in-color present the main transcription cascades involved in responses to biotic, drought/salinity and cold stresses, respectively. Many kinases and phosphatases, which might also provide nodes in crosstalk of various networks of cellular signaling or response pathways, are not shown in the figure.

tance proteins, WRKY proteins, TFs, zinc finger proteins, GSTs, ABC transporters, kinases and biosynthetic genes of ET, JA, lignin and alkaloids were up-regulated. Approximately 2% of the genes in *Arabidopsis* responded to NO treatment, of which 10% were TFs. NO might also influence the signal transduction network of plant as indicated by the transcriptional activation of several protein kinases, including a MAPK (Parani *et al.* 2004).

It was reported that multiple phosphatidylinositol (PtdI) pathway-related gene families were involved in plant cellular responses to many environmental factors. Through an analysis of the *A. thaliana* genome, 82 polypeptides were identified as being involved in PtdI signaling. 79 mRNA clones were amplified and used for DNA chip generation. Results of expression profile analysis of multiple tissues showed that many PtdI pathway-related genes were differentially expressed under experimental conditions like treatment with hormones (auxin, cytokinin, gibberellin, ABA and brassinosteroid) or environmental factors (temperature, Ca^{2+}, Na^{+}, drought, SA and JA) (Lin *et al.* 2004).

Salinity stress mediated by NaCl or $NaHCO_3$

Genomics studies are focused on gene expression analysis following exposure of plants to high salinity, using salt-shock experiments to mimic stresses that affect hydration and ion homeostasis. Comparative analysis was employed to identify functional isoforms and genetic orthologs of

stress-regulated genes common to various organisms and higher plants (Bohnert *et al.* 2001).

Exposure to high levels of NaCl not only affects plant water relations but also creates ionic stress in the form of cellular accumulation of Cl^- and, in particular, Na^+ ions. Salt stress also changes the homeostasis of other ions such as Ca^{2+}, K^+, and NO_3^-. Therefore salinity requires insights into how transport and compartmentation of these nutrients is affected. Maathuis (2006b) gathered the literature and public databases of many genomics studies in the context of cation membrane transport and salinity. Transcriptomics might help identify important transcripts and relevant associations between physiological processes. Such analyses identified (i) vascular K^+ circulation, (ii) root shoot translocation of Ca^{2+}, and (iii) transition metal homeostasis as potentially important aspects of the plant response to salt stress (Maathuis 2006b).

Analyses of complete transcriptomes suggest that systems like synthesis of osmolytes and ion transporters and regulation of transcriptional and translational machineries have distinct roles in salt-stress response. In particular, induction of transcripts of specific TFs, RNA-binding proteins, ribosomal genes, and translation initiation and elongation factors has been reported to be important during salt stress (Sahi *et al.* 2006).

When microarray expression profiles of wild type plants, a T-DNA insertion knockout mutant of *AtNHX1* (*nhx1*), and a rescued line (*NHX1::nhx1*) exposed to both short (12 h and 48 h) and long (one and two weeks) durations of a non-lethal salt stress were investigated, 147 transcripts showed both salt responsiveness and a significant influence of *AtNHX1*. Fifty-seven of these genes showed differential regulation across all salt treatments, while the rest were regulated as a result of a particular duration. Transcripts encoding proteins involved in metabolic and energy processes were mostly down-regulated (Sottosanto *et al.* 2007).

A macroarray containing 384 genes related to stress responses was used to compare root gene expression during salt stress in *M. truncatula* genotypes (108-R and Jemalong A17). Homolog of *COLD-REGULATEDA1* gene and a TFIIIA-related TF, *MtZpt2-1*, known to regulate the former gene, were identified in tolerant genotype Jemalong A17. Two MtZpt2 TFs (*MtZpt2-1* and *MtZpt2-2*) showed increased expression in roots when compared to 108-R (de Lorenzo *et al.* 2007).

The ET receptor gene *NTHK1* from tobacco which is salt-inducible was introduced into *Arabidopsis* plants. Most (87 out of 90) of the differentially expressed genes in microarray analyses were down-regulated in the *NTHK1* overexpressing line and only 3 genes were up-regulated, implying that overexpression of *NTHK1* might inhibit expression of some genes during salt treatment (He *et al.* 2005). Approximately one-third of these differentially regulated genes were reported to have regulatory roles in signal transduction. From these putative regulatory genes, one NAC-type TF gene, which was salt-inducible was identified. This gene was named as *AtNAC2*, following an auxin-inducible gene *NAC1* from *Arabidopsis* and further analyzed (He *et al.* 2005).

Genes of salt cress (*Thellungiella halophila*) have a high sequence identity (90%-95% at cDNA level) to genes of its close relative, *Arabidopsis*. To compare the differences in the regulation of salt tolerance between salt cress and *Arabidopsis*, Taji *et al.* (2004) analyzed the gene expression profiles in salt cress by using a full-length *Arabidopsis* cDNA microarray. In salt cress, only a few genes were induced by 250 mM NaCl stress in contrast to *Arabidopsis*. Notably a large number of known abiotic- and biotic-stress inducible genes, including *Fe-SOD*, *P5CS*, *PDF1.2*, *AtNCED*, *P-protein*, *β-glucosidase*, and *SOS1*, were expressed in salt cress at high levels even in the absence of stress. Stress tolerance of salt cress might be due to constitutive overexpression of many genes that function in stress tolerance and that are stress inducible in *Arabidopsis* (Taji *et al.* 2004).

Gong *et al.* (2005) used a microarray platform, developed for *Arabidopsis*, with more than 25,000 oligonucleotides of 70-mer for *Thellungiella* transcript profiling. Microarray profiling and intensity analysis, qRT-PCR, and metabolite profiles defined genes and pathways that showed common and differential responses to salinity stress in the two species. 60% of regulated genes distinguished *Thellungiella* from *Arabidopsis*. Analysis of the differences showed that *Arabidopsis* exhibited a global defense strategy that required bulk protein synthesis, while *Thellungiella* induced genes functioning in protein folding, post-translational modification and protein redistribution (Gong *et al.* 2005).

Expression profiles of *Tamarix androssowii* in response to $NaHCO_3$ stress were investigated and nearly 400 among 2,455 high quality ESTs were found to be involved in salt-tolerance. Among them, metallothionein-like protein and germin-like protein were the most abundant transcripts, and account for 2.44 and 1.91% of total ESTs, respectively. Ninety-six unique genes were selected for small cDNA microarray analysis. It was found that 6 were down-regulated and 3 up-regulated significantly upon $NaHCO_3$ stress (Wang *et al.* 2006b).

The microarray analysis in burma mangrove identified 6 major co-expression clusters that support the interpretation of an adaptive process to high-salinity environment (Miyama and Hanagata 2007).

Gene expression profiles in *Puccinellia tenuiflora* exposed to saline-alkali, $NaHCO_3$-induced stress, were investigated using a cDNA microarray. In total, 158 differentially expressed genes were identified, and 93, 56, 21 and 71 genes were differentially expressed with $NaHCO_3$ stress for 6, 12, 24 and 48 h, respectively. These differentially expressed genes were categorized as putative novel (32%), photosynthesis (16%), unknown (15%), metabolism (13%) and defense genes (9%). The other differentially expressed genes were involved in a variety of functional areas, such as transport, transcriptional regulation, and protein synthesis (Wang *et al.* 2007a).

cDNA microarrays containing 1,067 clones of *P. tenuiflora* were constructed to investigate gene expression patterns resulting from saline-alkali ($NaHCO_3$) stress. A total of 95 transcripts were differentially regulated under the conditions studied, and 38, 35, 25 and 49 genes were differentially expressed with $NaHCO_3$ stress for 6, 12, 24 and 48 h, respectively. Among these, approximately 40% were putative novel or functionally unknown genes, and the remainder function in photosynthesis, cell rescue, defense, transport, metabolism, transcription regulation and protein destination (Wang *et al.* 2007b).

Expression patterns of 460 non-redundant salt-responsive genes in barley under osmotic versus salt stress using cDNA microarrays with northern blot and RT-PCR analyses were compared to find genes and pathways that respond to changes in osmotic potential under salt stress. 11 genes were found to be regulated in an identical manner under salt stress. It was suggested that during the initial phase under salt stress, several of the cellular responses were mediated by changes in osmotic potential (Ueda *et al.* 2004).

Transcripts of *Populus euphratica* significantly up-regulated by salt stress included ionic and osmotic homeostasis elements, metabolism regulators and the photosynthesis-activating enzyme Rubisco activase and photorespiration-related glycolate oxidase. Several photosynthesis-related transcripts were down-regulated in response to 72 h of salt stress but were up-regulated after long-term recovery (48 h). Sucrose synthase, ABC transporter, calmodulin, Pop3 peptide and aquaporin appeared to be actively involved in the process of plant recovery from salt stress (Gu *et al.* 2004).

Microarray profiling of 150 mM NaCl-treated *Arabidopsis* roots revealed dynamic changes in transcript abundance for at least 20% of the genome, including hundreds of TFs, kinases/phosphatases, hormone-related genes, and effectors of homeostasis (Jiang and Deyholos 2006).

A total of 201 non-redundant genes that were differentially expressed upon 30 min of severe salt stress were iden-

tified in early stage tomato seedlings using microarray analysis (Ouyang *et al.* 2007).

Activities of membrane transporters are critical under salt stress. Maathuis *et al.* (2003) designed an oligonucleotide microarray representing 1,096 *Arabidopsis* transporter genes and analyzed the root transporter transcriptome over a 96-h period with respect to 80 mM NaCl, K^+ starvation and Ca^{2+} starvation. Results showed that cation stress led to changes in transcript level of many genes across most transporter gene families. Analysis of transcriptionally modulated genes across all functional groups of transporters revealed families such as V-type ATPases and aquaporins that responded to all treatments, and families – which included putative non-selective cation channels for the NaCl treatment and metal transporters for Ca^{2+} starvation conditions – that responded to specific ionic environments (Maathuis *et al.* 2003)

Response of the maize root transcriptome was monitored after imposition of 150 mM NaCl stress during 72 h (Wang *et al.* 2003). The analysis identified 916 ESTs representing genes whose RNA levels were significantly changed at various time points, corresponding to 11% of the ESTs printed. Clustering of regulated transcripts based on the timing and duration of changes suggested a structured succession of induction and repression for salt responsive genes in multiple signal and response cascades. Within this framework, 16 signaling molecules, including 6 protein kinases, 2 PPs and 8 TFs, were regulated with distinct expression patterns by high salinity (Wang *et al.* 2003).

Gene expression profiles of rice (cv. 'Nipponbare') seedlings subjected to salt stress (130 mM NaC1) were analyzed. Transcripts of Mn-SOD, Cu/Zn-SOD, cytosolic and stromal ascorbate peroxidase (Apx), glutathione reductase and Cat were regulated, whereas expression of thylakoid-bound Apx and Cat were down-regulated. The levels of the compatible solute proline and of transcripts of its biosynthetic gene, *P5CS*, were strongly increased by salt stress. Among 149 genes whose expression was altered at all the times assayed (3, 4 and 6 days) during salt stress; there were 47 annotated novel genes and 76 unknown genes (Kim *et al.* 2007b).

GeneChip wheat arrays were used to identify differentially expressed genes in roots and leaves of five wheat germplasm lines under salt stress at electrical conductivity of 30 dS/m. In leaves dehydrin, LEA, lipid transfer proteins, various TFs, cytochrome P450 genes were found to be up-regulated. In roots, on the other hand, nodulin, wound-induced proteins, O-methyltransferases were found to be up-regulated where peroxidases were down-regulated (Mott and Wang 2007).

Chilling, cold stress and cold acclimation

A large number of studies have used a transcriptional profiling approach to identify genes in *Arabidopsis* that respond at the level of transcript abundance to cold (4°C) or chilling (13°C) temperatures. Results have shown that plants respond to low temperatures by altering mRNA levels of a large number of genes belonging to different independent pathways. The qualitative and quantitative difference in transcriptional response to chilling and cold suggests that plants might have different molecular mechanisms to acclimate to different types of low-temperature stresses (Zhu and Provart 2003).

The dehydration-responsive element (DRE)/C-repeat (CRT), a *cis*-acting element, is involved in osmotic stress- and cold stress-inducible gene expression (**Fig. 2**). TFs that bind to the DRE/CRT were isolated and named DRE-binding protein 1 (*DREB1*)/CRT-binding factor (*CBF*) and *DREB2*. The *DREB1A*/*CBF3*, *DREB1B*/*CBF1* and *DREB1C*/*CBF2* regulons are involved in cold stress-responsive gene expression, whereas, the *DREB2* regulon is involved in osmotic stress-responsive gene expression (Nakashima and Yamaguchi-Shinozaki 2006). Homologous genes of *DREB1*/*CBF* have been found in many other plant species including tomato and rice, which are unable to undergo cold acclimation. Thus, it is apparent that the *DREB1*/*CBF* regulon is ubiquitous within higher plants. Current research endeavors are focusing to identify additional TFs that are associated with stress response. The ultimate goal of regulon biotechnology is the control of signal transduction networks, a manipulation which in turn is expected to improve stress tolerance in plants (Nakashima and Yamaguchi-Shinozaki 2006). Structure and role of *DREB*s in plant stress signaling and tolerance and the present status of their deployment in developing stress tolerant transgenic plants have been reviewed (Agarwal *et al.* 2006).

Many of the known cold-regulated genes are under the control of a primary master regulator, *DREB1*/*CBF*, but it is not likely to be the sole master regulator. In considering the origin of freezing tolerance in higher plants, it has been suggested that freezing tolerance likely arose by adopting drought tolerance mechanisms. This may explain why many genes responsive to cold stress are also responsive to drought and/or other osmotic stresses (Guy 2003).

The *CBF* cold response pathway includes action of three TFs, *CBF1*, *2* and *3* that are rapidly induced in response to low temperature followed by expression of the *CBF*-targeted genes that act in concert to increase plant-freezing tolerance. Transcriptome profiling analysis and mutagenesis experiments indicated that additional cold response pathways exist and may have important roles in life at low temperature. ATH1 GeneChip was used in order to define cold responsive and *CBF2* regulated genes (Vogel *et al.* 2005). A total of 514 genes were placed in the core set of cold-responsive genes. Eighty-five cold-induced genes and eight cold-repressed genes were reported to be regulated by *CBF2*. An additional nine cold-induced genes and 15 cold-repressed genes were assigned to a regulon controlled by *ZAT12*. Of the 25 core cold-induced genes that were most highly up-regulated (induced over 15-fold), 19 genes were induced by *CBF2* and another two genes were regulated by both *CBF2* and *ZAT12* (Vogel *et al.* 2005).

Microarray and RT-PCR analyses with transgenic plants constitutively expressing *DREB2C* revealed that *DREB2C* regulates expression of several heat stress-inducible genes that contain DRE/CRT elements in their promoters. From these data, it was concluded that *DREB2C* is a regulator of heat stress tolerance in *Arabidopsis* (Lim *et al*. 2007).

Transgenic overexpression of a barley gene, *HvCBF4*, in rice resulted in an increase in tolerance to drought, high-salinity and low-temperature stresses without stunting growth. Using the 60K rice whole genome microarray, 15 rice genes were identified that were activated by *HvCBF4*. When compared with 12 target rice genes of *CBF3*/*DREB1A*, 5 genes were common to both *HvCBF4* and *CBF3*/*DREB1A* (Oh *et al.* 2007).

Zhu *et al.* (2004) reported a stress response screen using *Arabidopsis* plants carrying the firefly luciferase gene under the control of stress-responsive *RD29A* promoter. They identified a mutant, *hos9-1* (for high expression of osmotically responsive genes), in which the reporter construct was activated by low temperature, but not by ABA or salinity stress. Response of *CBF* genes were not altered by the *hos9-1* mutation. Correspondingly, microarray analysis showed that none of the genes affected by the *hos9-1* mutation were controlled by the *CBF* family. The study concluded that *HOS9* is a putative homeodomain TF and important for a part of freezing tolerance, by affecting the activity of genes independent of the *CBF* pathway (Zhu *et al.* 2004).

cDNA microarray approach was used to monitor the expression profile of rice under cold stress and 328 cold-regulated genes were identified. Among them, *OsMYB3R-2* was further analyzed and indicated to be a master switch in stress tolerance (Dai *et al.* 2007). The *OsMYB4* rice gene encodes a MYB TF involved in cold acclimation. Its constitutive expression in *A. thaliana* results in improved tolerance to abiotic and biotic stresses. Microarray analysis to compare the transcriptome profile of wild type and trans-

genic *Arabidopsis* lines identified 254 and 83 up- and down-regulated genes, respectively (Vannini *et al.* 2006). *OsMYB4* up-regulated 254 genes, 22% of which encode proteins involved in gene expression regulation and signal transduction, suggesting an upstream role of *MYB4* in stress response.

Many temperate plant species such as *A. thaliana* are able to increase their freezing tolerance when exposed to low, nonfreezing temperatures in a process called cold acclimation. Hannah *et al.* (2005) presented a comprehensive analysis of the genome-wide changes of gene expression in response to 14 days of cold acclimation in *Arabidopsis*, and validated these data by comparing datasets obtained for two whole-genome microarrays composed of either 25- or 50-mer oligonucleotides. All data were integrated into a database containing the cold responsiveness of 22,043 genes as a function of time of exposure (Hannah *et al.* 2005).

Hwang *et al.* (2005) tried to characterize cold-regulated transcripts in the hot pepper (*C. annuum*), using a 3.1 K cDNA microarray. They isolated a total of 317 cold-inducible genes and used 42 up-regulated and 3 down-regulated genes for further analysis. Among the up-regulated cold-stress genes, were a variety of TFs, including: a family of 4 EREBP (designated *CaEREBP-C1* to *C4*) genes, a bZIP protein (*CaBZ1*), *RVA1*, Ring domain protein, *HSF1*, and the WRKY (*CaWRKY1*) protein. Among the 45 genes 19 genes appeared to be simultaneously regulated by salt stress. These genes included: *CaEREBP-C3*, *CaBZ1*, putative *trans*-activator factor, *NtPRp27*, malate dehydrogenase, putative auxin-repressed protein, SAR8.2 protein precursor, LEA protein 5 (*LEA5*), DNAJ protein homologue, xyloglucanendo-1,4-β-D-gucanase precursor, PR10, and the putative non-specific lipid transfer protein StnsLTP (Hwang *et al.* 2005).

In species such as wheat, for which large scale mutant screening and transgenic studies are not currently practical, transcriptome comparison by microarray analysis is an essential approach to identify key genes providing tolerance to environmental stresses such as low temperature. Gene expression during cold acclimation was compared in 2 cultivars with significant differences in freezing tolerance using a microarray constructed with PCR amplified cDNA inserts from 1,184 wheat ESTs that represent 947 genes (Gulick *et al.* 2005). Among 300 cold-regulated genes, 65 were regulated differently between the 2 cultivars for at least 1 time point. These included genes that encode potential regulatory and metabolism related proteins, including protein kinases, putative TFs, Ca^{2+}-binding proteins, a Golgi localized protein, an inorganic pyrophosphatase, a cell wall associated hydrolase, and proteins involved in photosynthesis.

A 5,740 feature cDNA amplicon microarray that was enriched for signal transduction and regulatory genes was constructed to compare changes in gene expression in a highly cold-tolerant winter wheat cultivar CDC Clair and a less tolerant spring cultivar, Quantum. Changes in gene expression using a 5,740 feature cDNA amplicon microarray over a time course of 14 days detected over 450 genes that were regulated by cold treatment and were differentially regulated between spring and winter cultivars, of these 130 are signaling or regulatory gene candidates, including: TFs, protein kinases, ubiquitin ligases and GTP, RNA and Ca^{2+}-binding proteins (Monroy *et al.* 2007).

In a study investigating gene networks controlling tolerance to cold stress with ATH1 GeneChips, 939 cold-regulated genes with 655 up-regulated and 284 down-regulated expressions were determined. A large number of early cold-responsive genes encode TFs and many genes involved in chromatin level and posttranscriptional regulation. A number of genes important for the biosynthesis or signaling of plant hormones, such as ABA, gibberellic acid, and auxin, are regulated by cold stress. The cold-responsive transcriptomes of the wild type and inducer of CBF expression 1 (*ice1*), a mutant defective in an upstream TF required for chilling and freezing tolerance were compared. The transcript levels of many cold-responsive genes were altered in the *ice1* mutant not only during cold stress but also before cold treatments. This study provides a global picture of the *Arabidopsis* cold-responsive transcriptome and its control by *ICE1* (Lee *et al.* 2005).

The microarray and Northern blot results revealed that 39 genes had a significantly differential expression level in the *StEREBP* transgenic plants. Of 39 genes, 34 and 5 genes were found to be up- and down-regulated, respectively. The genes for HSP90, a lichenase precursor, PR-1, a hexose transporter, dehydrin, peroxidase calreticulin, tyramine hydroxycinnamoyl transferase, the RD22 protein and the receptor protein kinase-related protein appeared to be up-regulated by *StEREBP*. However, the genes for the fruit ripening protein, the major-latex like protein and secretory peroxidase appeared to be down-regulated by *StEREBP* (Hwang *et al.* 2004).

Gene expression in *Thlaspi arvense* leaf tissue during the very early stages of cold acclimation (or cold stress) was assayed at three time points (1, 4 and 24 h) and compared to an untreated control using whole genome *Arabidopsis* microarrays containing 70-mer oligonucleotides. This analysis highlights some of the difficulties and benefits of using cross-species microarray analysis. The data suggested that *T. arvense* responds in a similar fashion to cold stress as the model plant *A. thaliana*. However, quantitative differences in the level and timing of expression of a number of genes were identified (Sharma *et al.* 2007).

Polyamines play pivotal roles in plant defense to environmental stresses (Kuznetsov and Shevyakova 2007; Pang *et al.* 2007). Kasukabe *et al.* (2004) cloned spermidine synthase cDNA from *Cucurbita ficifolia* and the gene was introduced to *A. thaliana* under the control of the CaMV35S promoter. As compared with the wild-type plants, the T2 and T3 transgenic plants exhibited a significant increase in spermidine synthase activity and spermidine content in leaves together with enhanced tolerance to various stresses including chilling, freezing, salinity, hyperosmosis, drought, and paraquat toxicity. A cDNA microarray analysis revealed that several genes including those for stress-responsive TFs such as DREB and stress-protective proteins like rd29A were more abundantly transcribed in the transgenics than in the wild type under chilling stress (5°C). The results suggested an important role for spermidine as a signaling regulator in stress signaling pathways (Kasukabe *et al.* 2004).

About 900 EST clones from cDNA library of cold acclimatized leaves of barley cv. 'Nure' were arrayed, and gene expression analyses of cold acclimatized plants were investigated. Many of the up- or down-regulated genes had no assigned functions. These genes were suggested to be novel cold-regulated genes (Faccioli *et al.* 2002).

Using the biotinylated CAP trapper method, Seki *et al.* (2001b) constructed full-length *Arabidopsis* cDNA libraries from plants in different conditions, such as drought and cold, or unstressed plants, and at various developmental stages from germination to mature seed. cDNA microarray using 1,300 cDNAs was used to determine drought- and cold-inducible genes and target genes of *DREB1A*/*CBF3*. In total, 44 and 19 cDNAs for drought- and cold-inducible genes, respectively, were isolated. Among them 40 were novel stress-inducible genes. Twelve genes were identified as targets of *DREB1A*, and six of them were identified as novel (Seki *et al.* 2001b).

AP2/EREBP TFs play functionally important roles in plant growth and development, especially in hormonal regulation and in response to environmental stress. Expression profile results provide strong support for a role for AP2/EREBP family members in development and in response to environmental stimuli (Feng *et al.* 2005).

Cytosolic Apx1 is a key H_2O_2 removal enzyme in plants. Microarray analysis of *Apx1*-deficient plants revealed that the expression of two zinc finger proteins (*Zat12* and *Zat7*) and a WRKY TF (*WRKY25*) were elevated in knock-out *Apx1* plants grown under controlled conditions (Rizhsky *et al.* 2004).

AtNUP160 was shown to encode a putative homolog of the animal nucleoporin Nup160. Microarray analysis revealed that a number of other genes important for plant cold tolerance were also affected in the *atnup160-1* mutants. It was suggested that *Arabidopsis AtNUP160* is critical for the nucleocytoplasmic transport of mRNAs and required for cold stress tolerance (Dong *et al.* 2006).

The transcriptional profiles of low temperature-grown sunflower plants (15 and 7°C) were compared with those grown under standard conditions (25°C). 108 cDNA clones were shown to be differentially expressed between the low temperature-grown plants and controls. About 90% of these genes were found to be down-regulated and involved in the metabolism of carbohydrate and energy, protein synthesis, signal transduction, and transport function. It was stated that only 4 genes can be considered as differentially expressed suggesting that similar genetic programs underlie the response of sunflower plants to these temperature regimes (Hewezi *et al.* 2006).

A total of 70 cold-responsive genes in *Lolium perenne* were up- or down-regulated with a minimal of 2-fold difference. Some of these genes were defined as putative candidates for genes involved in vernalization induced flowering. Three of the up-regulated genes were indicated as homologous to members of the MADS box, CONSTANS-like and JUMONJI families of TFs (Ciannamea *et al.* 2006).

Microarray analysis of transcript abundance in shoot tips of Cabernet Sauvignon grapevines reported no significant differences in transcript abundance between salinity and PEG before 24 h. It was stated that osmotic stress affected more protein synthesis and cell cycle transcripts, whereas chilling affected more Ca^{2+}-signaling transcripts, indicating that chilling has more complex Ca^{2+}-signaling. The concentrations and transporter transcripts of several anions including nitrate, sulfate, and phosphate were found to be increased with time (Tattersall *et al.* 2007).

Transcription factor genes involved in abiotic stress

TFs are important in regulating plant responses to environmental stress (**Fig. 2**). Chen *et al.* (2002) used microarray profiles to deduce functions of 402 genes encoding known and putative *Arabidopsis* TFs under 81 different developmental stages and stress conditions. The expression of 74 genes responsive to bacterial pathogen infection was reduced or abolished in mutants that have defects in SA, JA, or ET signaling. Therefore, the regulation of these genes might be mediated at least partly by these plant hormones and TF genes might be involved in the regulation of additional downstream responses mediated by these hormones (Chen *et al.* 2002).

NAC-type TF *OsNAC6* is induced by abiotic stresses, including cold, drought and high salinity and biotic stresses like wounding and blast disease. Microarray analysis revealed that many genes that are inducible by abiotic and biotic stresses were up-regulated in rice plants overexpressing *OsNAC6* (Nakashima *et al.* 2007).

Heat stress and heat shock transcription factors

In order to assess specific functional roles of plant heat shock TFs (HSF) Busch *et al.* (2005) conducted a transcriptome analysis of *A. thaliana hsfA1a/hsfA1b* double knock out mutants and wild-type plants. Heat stress had a severe impact on the transcriptome of mutant and wild-type plants. Approximately 11% of all monitored genes of the wild type showed a significant effect upon heat stress treatment. Gene expression profiles revealed a number of *HsfA1a/1b*-regulated genes for functions including protein biosynthesis and processing, signaling, metabolism and transport (Busch *et al.* 2005).

Microarray analyses with ATH1 arrays confirmed that the genomic responses to photoperiodic and thermal induction differ in *Arabidopsis* plants. Thermal and the photoperiodic shifts affected a small number of heat shock genes. From the genes highly induced in the thermal samples was *At3g12580,* one of the 14 *HSP70* genes encoded in the genome (Balasubramanian *et al.* 2006).

Microarray analysis of *HsfA2*-overexpressing transgenic *Arabidopsis* plants (*El2Ω::HsfA2*) under unstressed conditions revealed HS stress-inducible genes and other stress-responsive genes. In *El2Ω*::*HsfA2* plants, 56 genes were up-regulated more than 6-fold compared with wild-type plants (Ogawa *et al.* 2007).

Stress related genes were equally or more dominantly up-regulated in the seedlings exposed to high temperatures compared with the panicles in barley seedlings. In contrast, certain genes associated with histones, DNA replication initiation, mitochondria, and ribosomes were specifically repressed in the exposed panicles (Oshino *et al.* 2007).

Drought stress

In a recent review, progress resulting from analysis of gene expression during the drought-stress response in plants as well as progress in elucidating the functions of genes implicated in the stress response and/or stress tolerance is summarized (Shinozaki and Yamaguchi-Shinozaki 2007). Analysis of dehydration-inducible genes should help not only to understand the molecular mechanisms of stress responses in higher plants, but also to improve the stress tolerance of crops by genetic manipulation (Öktem *et al.* 2006).

Translational regulation based on polysomal and non-polysomal RNA hybridizations was investigated for over 2,000 genes using 8.2K GeneChip in leaves of *Arabidopsis* under moderate dehydration stress. The level of each mRNA in polysomes ranged between 23 and 97% in non-stressed leaves and was significantly reduced for a large portion of the genes (71%) in response to dehydration. In response to water-deficit stress 40% of the dehydration-inducible mRNAs with 2-fold or greater increase in abundance showed impaired ribosome loading. Many mRNAs that encode proteins of similar biological function displayed similar translational regulation (Kawaguchi *et al.* 2004).

Many aquaporins (AQPs) acting as water channels play important roles in plant water relations. cDNA microarrays specifically designed for AQPs were used for determination of expression patterns of all 35 *Arabidopsis* AQPs in leaves, roots and flowers. No AQP isoform were determined to be leaf specific. Plasma membrane intrinsic protein (PIP) transcripts were generally down-regulated upon gradual drought stress in leaves, with the exception of *AtPIP1;4* and *AtPIP2;5. AtPIP2;6* was constitutively expressed and not significantly affected by the drought stress (Alexandersson *et al.* 2005).

Genome wide changes in gene expression in roots and shoots at 3 and 27h post-treatment were monitored in the drought tolerant *S. bicolor*, under high salinity (150 mM NaCl), osmotic stress (20% PEG) or ABA (125 μM). Expression of 2,200 genes was altered in response to dehydration, high salinity or ABA. Osmotic stress inducible sorghum genes identified for the first time included a β-expansin expressed in shoots, actin depolymerization factor, inositol-3-phosphate synthase, a non-C4 NADP-malic enzyme, oleosin, and three genes homologous to 9-*cis*-epoxycarotenoid dioxygenase that may be involved in ABA biosynthesis (Buchanan *et al.* 2005).

300 unique ESTs were subjected to microarray analysis to study differential gene expression between leaves of well-watered wheat plants and plants subjected to water deficit stress. Overall, 30% of the genes were significantly up-regulated and 18% were significantly down-regulated under water deficit stress (Way *et al.* 2005).

Protein phosphorylation/dephosphorylation are major signaling events induced by osmotic stress in higher plants. *Arabidopsis* 2 Oligo Microarray (Agilent) was used to compare transcription profiles of transgenic plants containing *SRK2C* gene which is an osmotic-stress-activated protein kinase. Microarray analysis revealed that drought tolerance

of transgenics coincided with up-regulation of many stress-responsive genes, like *RD29A*, *COR15A*, and *DREB1A*/*CBF3* (Umezawa *et al.* 2004).

A total of 55 dehydration-inducible cDNAs from *Xerophyta humilis* which can protect itself from dehydration stress were identified. Dehydration-up-regulated cDNAs included a large number of genes encoding LEA proteins, dehydrins and desiccation-related proteins. Novel dehydration-up-regulated genes included cDNAs encoding a putative chloroplast RNA-binding protein and a protein containing SNF2/helicase domains (Collett *et al.* 2004).

Analysis of transcript profiles of loblolly pine (*Pinus taeda*) with microarray containing 2,173 cDNAs indicated that there are distinct patterns of expression related to the two levels of drought stress. Genes encoding HSPs, LEA proteins, enzymes from the aromatic acid and flavonoid biosynthetic pathways, and from C metabolism showed distinctive responses associated with acclimation (Watkinson *et al.* 2003).

Relationship of rehydration-, proline- and water-treatment-inducible genes was shown with a cDNA microarray containing 7,000 *Arabidopsis* full-length cDNAs. Among the 152 rehydration-inducible genes, 58 genes contained the ACTCAT sequence involved in proline- and hypoosmolarity-inducible gene expression in their promoter regions, and therefore it was suggested that ACTCAT sequence is a major *cis*-acting element involved in rehydration-inducible gene expression (Oono *et al.* 2003).

The early post-pollination phase of maize (*Zea mays*) development is particularly sensitive to water deficit stress. Using cDNA microarrays it was shown that 9 days after pollination, transcriptional profiles of placenta and endosperm differed considerably under water stress. In placenta, 79 genes, mainly by up-regulation whereas in endosperm, 56 genes, mainly by down-regulation, were significantly altered. Only 9 of the stress-regulated genes were common to both tissues. In placenta, the largest class of up-regulated genes contained the ones encoding HSPs, chaperonins, and major intrinsic proteins. In contrast, in endosperm, genes in cell division and growth category represented a large class of down-regulated genes (Yu and Setter 2003).

The mechanisms of the response to dehydration in the reproductive organs of maize, during meiosis in the tassels and floret formation in the ears were investigated using oligo microarrays. It was stated that the majority of changes were organ specific after 7 days of stress with only 74 transcripts co-regulated in two organs. Numbers of differentially expressed genes were 1,513 and 202 for tassels and ears, respectively. The most notable might function in carbohydrate metabolism, particular in sucrose, trehalose and raffinose metabolism, and in cell wall metabolism in the tassels (Zhuang *et al.* 2007).

It was reported that flowering remains a susceptible developmental period to abiotic stress in elite maize hybrids and yield losses are associated with abnormal floral development and impaired ear growth. It was also shown that genes within the starch biosynthetic pathway are coordinately regulated under stress. Moreover, gene expressions in some tissues were reported to be more responsive to stress than other tissues (Zinselmeier *et al.* 2002).

Potential functions of approximately 130 genes of *A. thaliana* that have been shown to be up-regulated under water-deficit are tabulated by Bray (2002). These point out signaling events, detoxification and other functions involved in the cellular response to water-deficit stress.

Expression profile analysis of 1,947 UniESTs from the subtracted cDNA libraries of foxtail millet (*Setaria italica*) seedlings were reported using a cDNA microarray. The results showed that dehydration stress up-regulated 95 and 57 ESTs in roots and shoots of seedlings, respectively and down-regulated 10 and 27 ESTs in roots and shoots, respectively (Zhang *et al.* 2007b).

Fewer genes (n = 64) were reported to be responsive to water deficit conditions in roots of *Phaseolus vulgaris*, the more drought sensitive species, compared with *P. acutifolius* (n = 488) using slides printed with 5,200 cDNAs from libraries of *Phaseolus* spp. Only 25 genes were common to both species. Most of the responsive genes in *P. vulgaris* were stress responsive, while the largest functional class in *P. acutifolius* was populated with unannotated or novel genes (Micheletto *et al.* 2007).

Water stress responses in two moderately drought-tolerant native Andean potato clones, SA2563 and Sullu were analyzed under field conditions using the TIGR 10K microarray (Schafleitner *et al.* 2007). Gene expression profiling revealed 1,713 significantly differentially expressed genes with 186 up-regulated in both clones. Each clone induced a specific gene set as an addition to commonly regulated genes. The traits for tolerance included osmotic adjustment, changes in carbohydrate metabolism, membrane modifications and cell rescue mechanisms, such as detoxification of oxygen radicals and protein stabilization. Many of the up-regulated genes have been identified previously in laboratory studies on model plants using shock treatments, and report of Schafleitner *et al.* (2007) confirmed the importance of these genes under field conditions.

High water use efficiency or transpiration efficiency (TE) in wheat is a desirable physiological trait for increasing grain yield under water-limited environments. Microarray analysis of approximately 16,000 unique wheat ESTs revealed 93 genes that were differentially expressed between wheat lines with high and low TE levels. Moreover, 20% them were responsive to drought stress. Several growth-related regulatory genes, which were down-regulated by drought, were expressed at high levels in the high TE lines. Some of these differentially expressed genes might be candidates for use as expression quantitative trait loci (eQTLs) for TE (Xue *et al.* 2006).

To better understand microRNA function, Zhao *et al.* (2007) have used an oligonucleotide microarray to monitor rice microRNA expression profile under drought stress. Two drought-induced microRNAs were identified. Furthermore, miR-169g was confirmed as the only member induced by drought among the miR-169 family and the induction of miR-169g was more prominent in roots than in shoots.

A sunflower cDNA microarray containing about 800 clones was employed to study gene expression profiles in leaves and embryos of drought-tolerant and -sensitive genotypes subjected to water-deficit stress under field conditions. 409 differentially expressed genes were identified among genotypes, water treatment and organs. Changes in qualitative but not quantitative mRNA expression indicated the difference between two genotypes. Comparison of expression levels in organs revealed 82 cDNA clones showing organ-specific variation. Genes related to amino acids and carbohydrates metabolisms, and signal transduction were induced in embryos and repressed in leaves (Roche *et al.* 2007).

Nutrient requirements, deficiency or toxicity

The transcriptomes of two plant species, *Thlaspi caerulescens*, a zinc (Zn) hyperaccumulator, and *Thlaspi arvense*, a nonhyperaccumulator, were profiled using *A. thaliana* ATH1 arrays (Hammond *et al.* 2006). Approximately 5,000 genes were differentially expressed in the shoots of *T. caerulescens* compared with *T. arvense*, including genes involved in Zn transport and compartmentalization.

Transcriptome studies identifying genes that respond to nitrate within minutes, use of an *Arabidopsis* nitrate reductase-null mutant in microarray studies and use of new bioinformatics tools to perform comparative studies of multiple transcriptome responses provided a detailed picture of nitrate responses in plants (Gutierrez *et al.* 2007a).

Gene expression analysis with *Arabidopsis* whole genome microarray revealed that mild N stress triggered only a small set of genes significantly different at the transcriptional level, which are largely involved in various stress responses. Severe N stress resulted in more pronounced res-

ponses, involving a large number of genes in many different biological processes. Differentially expressed genes were also identified in response to short-and long-term N availability increases (Bi *et al.* 2007).

Evidence for interactions between C and N that include genes involved in metabolic pathways, protein degradation and auxin signaling was determined. Moreover, a qualitative multi-network model of the *Arabidopsis* metabolic and regulatory molecular network, including 6,176 genes, 1,459 metabolites and 230,900 interactions among them was constructed (Gutierrez *et al.* 2007b).

In total, 198 genes of rice (*O. sativa* L.) were shown to have a unique expression response in leaves to nitrate-and ammonium treatment. Most of these genes for which function is known were involved in signal transduction, plant stress resistance, transcriptional regulation, and basic metabolism (Zhu *et al.* 2006).

Very little is known about nutrient sensing and signaling in plants. K^+ and Pi are important macronutrients for crops but are often deficient in the field. Recent advances in discovering molecular responses of plants to K^+ and Pi deficiency by microarray experiments are reviewed previously (Amtmann *et al.* 2006). Previous studies provide not only a comprehensive picture of adaptive mechanisms, but also a large number of transcriptional markers that can be used to identify upstream components of K^+ and Pi signaling pathways.

Lian *et al.* (2006) analyzed the expression profiles of an indica rice cultivar Minghui 63 at seedling stage after 20 min, 1 and 2 h under low N stress, using a microarray of 11,494 rice ESTs representing 10,422 unique genes. 115 and 358 ESTs showed up- and down-regulation, respectively. Rapid down regulation of the genes involved in photosynthesis and energy metabolism under low N stress was reported (Lian *et al.* 2006).

The analysis using 22,810 genes revealed a coordinated induction and suppression of 612 and 254 Pi-responsive genes, respectively. These genes was found as involved in various metabolic pathways, ion transport, signal transduction, transcriptional regulation, and other processes related to growth and development (Misson *et al.* 2005).

Using microarrays, Hammond *et al.* (2003) identified genes whose expression changed more than 2.5-fold in shoots of plants growing hydroponically when Pi, but not N or K^+, was withheld from the nutrient solution. A literature survey indicated that the expression of many of these "late" genes responded specifically to Pi starvation. The expression of *SQD1*, a gene involved in the synthesis of sulfolipids, responded specifically to Pi starvation and was increased 100 h after withdrawing Pi (Hammond *et al.* 2003).

Microarray analysis revealed that more than 1,800 of the 6,172 genes present in the array of *Arabidopsis* in response to phosphate (Pi) starvation were regulated by 2-fold or more within 72 h from the onset of Pi starvation. Many genes for photosynthesis and N assimilation were down-regulated. More than 100 genes each for TFs and cell-signaling proteins were regulated in response to Pi starvation, implying major regulatory changes in cellular growth and development. A significant fraction of those regulatory genes exhibited distinct or even contrasting expression in leaves and roots in response to Pi starvation, supporting the idea that distinct Pi starvation response strategies are used for different plant organs in response to a shortage of Pi in the growth medium (Wu *et al.* 2003).

Based on the changes of gene expression of rice roots under Pi treatment, the up-regulation of some genes due to Pi deficiency was confirmed. Some metabolic changes namely: (1) acceleration of C supply for organic acid synthesis through glycolysis; (2) alteration of lipid metabolism; (3) rearrangement of compounds for cell wall; and (4) changes of gene expression related to the response for metallic elements such as aluminum (Al), iron (Fe) and Zn were indicated to be related to Pi deficiency (Wasaki *et al.* 2003a).

A novel rice gene was isolated by microarray analysis and designated as *OsPI1* (*Oryza sativa* Pi-limitation Inducible gene 1). Induction of *OsPI1* gene by Pi starvation in both shoots and roots was reported. Moreover, when Pi was supplied to Pi-deficient plants, the abundance of *OsPI1* transcripts rapidly decreased (Wasaki *et al.* 2003b).

Transcriptomic analyses indicated that the *OsPI1* gene was the most significant down-regulated gene following Pi re-supply to Pi-deficient plants. Many starch metabolism-related genes, as well as several genes for Pi-liberating enzymes, were up-regulated by Pi-treatment in leaf tissues. mRNAs for glucanases were also induced by Pi re-supply. Most of the genes up-regulated by Pi-treatment were down-regulated by Pi re-supply, suggesting that their responses were specific to Pi (Wasaki *et al.* 2006).

Iron (Fe) is an essential nutrient for plants and crucial for a variety of cellular functions. In most soils Fe is present in large quantities, but mainly in forms that are not available to plants. Progress towards an integrative picture of how Fe is sensed and acquired was reviewed previously (Schmidt 2003).

Colangelo and Guerinot (2004) reported the identification of the essential gene Fe-deficiency Induced TF 1 (*FIT1*), which encodes a putative TF that regulates Fe uptake responses in *A. thaliana*. Microarray analysis with ATH1 arrays in the roots of a T-DNA insertion line, *fit1-1*, plants grown under Fe-sufficient and Fe-deficient conditions showed that expression of many (72 of 179) Fe-regulated genes was dependent on *FIT1*. It was demonstrated that *FIT1* regulates Fe(III) chelate reductase FRO2 at the level of mRNA accumulation (Colangelo and Guerinot 2004).

Thimm *et al.* (2001) identified a set of genes induced including several encoding cytochrome P450-like proteins and two encoding zinc finger proteins in *Arabidopsis* under Fe deficiency. A chip representing 8,987 rice clones was used to analyze genes responding to Fe deficiency in barley roots (Negishi *et al.* 2002). The *OsNAS1* gene and a zinc finger protein were identified in this study. Wintz *et al.* (2003) employed *Arabidopsis* genome array containing 8,300 genes to dissect novel transporters involved in metal homeostasis under copper, Zn and Fe deficiencies.

Microarray comparison identified 4 cDNAs that were under-expressed by a 2-fold or greater difference in the Fe inefficient plant compared to the Fe efficient soybean plant (O'Rourke *et al.* 2007).

Although responses to Fe deficiency in graminaceous plants, such as increased production and secretion of metal chelators, mugineic acid family phytosiderophores (MAs), have been described, the gene regulation mechanisms related to these responses are largely unknown. Studies of the genes involved in the methionine cycle using microarray glass slides containing 8987 rice ESTs showed that the transcripts of these genes were increased in both Zn-deficient and Fe-deficient barley roots, probably allowing the plant to meet its demand for methionine, a precursor in the synthesis of MAs (Suzuki *et al.* 2006).

In rice, overexpression of *OsIRO2*, Fe-deficiency-inducible basic helix-loop-helix TF, resulted in increased MAs secretion, whereas repression of *OsIRO2* resulted in lower MAs secretion and hypersensitivity to Fe deficiency. Microarray analysis demonstrated that *OsIRO2* regulates 59 Fe-deficiency-induced genes in roots. Some of these genes, including 2 TFs up-regulated by Fe deficiency, possessed the *OsIRO2* binding sequence in their upstream regions. *OsIRO2* possesses a homologous sequence of the Fe-deficiency-responsive *cis*-acting elements in its upstream region (Ogo *et al.* 2007).

A point mutation leading to loss of function in a gene encoding nicotianamine aminotransferase (NAAT1) was identified in rice *naat1* mutant. Accumulation of nicotianamine, the substrate for NAAT1, failure to absorb Fe(III) efficiently and failure to produce deoxymugineic acid were observed in mutant. Microarray analysis was employed to show that the expression of genes involved in Fe(II) acquisition were stimulated in the *naat1* mutant. It was concluded that disruption of deoxymugineic acid biosynthesis can

stimulate Fe(II) acquisition and increase Fe accumulation in rice (Cheng *et al.* 2007).

A. thaliana GeneChips were used in order to identify genes with a potential involvement in cellular metal – Zn and cadmium (Cd) – homeostasis in the shoots (Becher *et al.* 2004) and roots (Weber *et al.* 2004a) of *A. halleri* which is a naturally selected Zn- and Cd-tolerant Zn hyperaccumulator. Compared to *A. thaliana*, transcript abundance of several genes was found to be substantially higher in shoots of *A. halleri* after 4 days of exposure to low as well as high Zn concentrations in the hydroponic culture medium. The identified candidate genes encode proteins closely related to the following *A. thaliana* proteins: AtZIP6, a putative cellular Zn uptake system and member of the Zn-regulated transporter (ZRT)-iron regulated transporter (IRT)-like protein (ZIP)-family of metal transporters, the putative P-type metal ATPase AtHMA3, the cation diffusion facilitator ZAT/ AtCDF1, and the nicotianamine synthase AtNAS3 (Becher *et al.* 2004). The two genes showing highest expression in *A. halleri* roots relative to *A. thaliana* roots under control conditions encode a nicotianamine synthase and a putative Zn uptake system (Weber *et al.* 2004a).

To elucidate the network of interactions under sulfur deficiency, Nikiforova *et al.* (2003) have investigated transcriptomes of *Arabidopsis* plants subjected to 6, 10 and 13 days of sulfur depletion. Among the 1,507 sulfur-responsive clones, 632 genes responded specifically to sulfur deficiency by significant overexpression. Genes of the sulfur assimilation pathway were altered in expression. Furthermore, genes involved in flavonoid, auxin, and jasmonate biosynthesis pathways were up-regulated under conditions of sulfur deficiency (Nikiforova *et al.* 2003).

Data mining in global profiles under abiotic stress

Annotations of probes, representing uncharacterized genes on a microarray, provide useful and suggestive information since they are frequently based on sequence similarity to a known protein or EST in another organism. Based on datasets of publicly available microarray, a candidate gene could be queried against existing expression profiles to find its transcriptional response to various environmental stresses. Comparison of expression patterns across samples might help associate a specific trait and changes in gene expression (Rensink and Buell 2005; Clarke and Zhu 2006).

In a recent study, global co-expression analyses of datasets from 1,310 publicly available ATH1 arrays were performed to associate genes of unknown function with regulatory networks and biological processes (Horan *et al.* 2008). In analysis of differentially regulated genes, a large set of abiotic stress-responsive genes including 104 genes of unknown function responding to a wide range of abiotic stresses and 206 responding to specific stress treatments were identified. Wohlbach *et al.* (2008) created AtMega Cluster, large-scale summary of expression data, from expression levels reported in publicly available datasets of *Arabidopsis* tissues grown under a wide variety of conditions and expression levels in *athk1* mutants. Hierarchical clustering in AtMegaCluster was used to identify a group of genes co-expressed with *ATHK1*. It was found that *ATHK1* is transcriptionally co-regulated with several *Arabidopsis* response regulators.

Co-expression of *Arabidopsis* genes, encoding enzymes of secondary metabolism pathways were investigated using publicly available sets of microarray data, generated by ATH1 GeneChips under a wide range of different stress and developmental conditions. Hierarchical clustering revealed that major enzymes of each pathway displayed a clear co-expression throughout all the conditions studied. Such data mining approaches combined with sequence information allow drawing precise hypotheses on the function of uncharacterized genes (Gachon *et al.* 2005).

Expression of specific genes from three different experiments (Kreps *et al.* 2002; Seki *et al.* 2002; Kawaguchi *et al.* 2004) was compared to understand changes in gene expression in response to water-deficit stress. A relatively small set of genes that were commonly induced (27 genes) or repressed (3 genes) were determined. The induced genes fell into different functional categories like, metabolism, transport, signaling, transcription, and hydrophilic proteins. The 3 commonly repressed genes supported a frequently observed response to water-deficit stress, decreased growth (Bray 2004).

Global expression profiles from *A. thaliana* roots and shoots under nine abiotic stress conditions (cold, osmotic stress, salt, drought, genotoxic stress, ultraviolet light, oxidative stress, wounding, and high temperature) and at six different time points of stress exposure (0.5, 1, 3, 6, 12, and 24 h) were compared. In roots, correlations between responses to different stresses peaked after 1 h of stress exposure, while in shoots, correlations increased after 6 h. Stress responses at the transcriptional level were time and organ dependent. A total of 67 genes were indicated as displaying a significant pattern of expression under all nine stress treatments. Analysis of the gene set identified at early to middle (1-6 h) time points of stress exposure indicated that cell rescue/defense/virulence, energy, and metabolism functional classes were over-represented, suggesting novel insights on the basis of multiple stress tolerance in *Arabidopsis* (Swindell 2006).

To estimate the specificity of ROS-driven transcript expression, transcriptome data, obtained by exogenous application of various oxidative stress-causing agents and from a mutant and transgenic plants, in which the activity of an individual antioxidant enzyme (Cat, cytosolic Apx, and Cu/Zn-SOD) was disturbed, were compared (Gadjev *et al.* 2006). Overall, 8,056, 5,312, and 3,925 transcripts showed at least a 3-, 4-, or 5- fold change in expression, respectively. Moreover, several transcripts were identified as general oxidative stress response markers because of their 5-fold up-regulation in most experiments. Gadjev *et al.* (2006) also investigated the expression of all annotated TFs and suggested new candidate regulatory transcripts that might be responsible for modulating the specific transcriptomic responses triggered by different ROS (Gadjev *et al.* 2006).

Carbon dioxide and ozone stress

The consequences of increasing atmospheric carbon dioxide (CO_2) for long-term adaptation of plants remain uncertain, with few studies undertaken at the molecular or genetic level. A transcriptomic analysis was conducted following 6 yr exposure of *Populus* to elevated CO_2 in a FACE (free-air CO_2 enrichment) experiment. Gene expression was observed to be regulated upon elevated CO_2 but the response was dependent on the developmental stage. Elevated CO_2 resulted in up-regulation of differentially regulated genes in young leaves, whereas in semi-mature leaves down-regulation was the main response (Taylor *et al.* 2005). A similar response dependence on developmental age was observed in soybean (*Glycine max*) leaves under elevated CO_2 (Ainsworth *et al.* 2006). Differential regulations of 1,146 transcripts between growing and fully expanded leaves were reported. Transcripts for ribosomal proteins, cell cycle, and cell wall loosening, necessary for cytoplasmic growth, were highly expressed in growing leaves. CO_2-responsive genes suggested induction of respiratory breakdown of carbohydrates, which might provide energy and biochemical precursors for leaf expansion and growth under elevated CO_2 (Ainsworth *et al.* 2006).

Transcript profiles of *A. thaliana* grown under elevated CO_2 or ozone (O_3) were investigated using a microarray containing nearly 26,000 DNA probes, in order to find determinants of plant performance influenced by atmospheric changes. Furthermore most significant changes in gene expression were observed between plants grown in growth chambers and in FACE under ambient field conditions. Regulated transcripts were reported to be in categories such as chaperones and general defense reactions, altered metabolic functions, redox control, energy provision, protein turnover,

signaling and transcription (Miyazaki *et al.* 2004).

Changes in expression of a set of genes were determined in *Arabidopsis* to detect and discriminate between plants stressed by 0.2 ppm O_3 for 24 h, drought for 5 h, or wounding by punching rosette leaves several times with a bundle of needles. Discrimination was done by a cDNA microarray containing a small and adequate number of cDNAs for the detection of specific stress-inducible genes (Matsuyama *et al.* 2002).

Arabidopsis plants exposed to purified air or 150 ppb O_3, for 8 h per day during 2 days were used to elucidate the response to O_3 stress. HSPs, GSTs and genes involved in cell wall stiffening and microbial defense were reported to be O_3 responsive. Moreover, inductions of genes involved in SA biosynthesis, PCD and senescence were reported (D'Haese *et al.* 2006).

Cellular responses in the tolerant *A. thaliana* genotype Col-0 exposed to O_3 (300 ppb) for 6 h were investigated using ATH1 GeneChip microarrays. New genes like reticuline oxidase were reported to be involved in O_3 response. The transcript levels of several WRKY genes were increased upon O_3 treatment and the W-box was the *cis*-element over-represented in the promoter region of up-regulated genes (Tosti *et al.* 2006).

Hydrogen peroxide stress

In plants, exposure to various abiotic and biotic stresses results in accumulation of H_2O_2 and oxidative stress. In a transcriptome analysis performed in order to determine cellular responses to H_2O_2, it was revealed that 175 ESTs were differentially regulated in *Arabidopsis* under oxidative stress with induction of 113 and repression of 62. A large proportion of these ESTs had predicted functions in cell rescue and defense processes (Desikan *et al.* 2001).

H_2O_2 is accepted as a key regulator in stress and PCD responses, but knowledge on signaling pathways leading from H_2O_2 to PCD in plants is limited. In a review (Gechev and Hille 2005), complexity of the H_2O_2 network and studies directed to unravel this network via identification of key regulatory mutants and whole genome microarray analysis of H_2O_2-induced cell death were summarized. A novel link between H_2O_2 and sphingolipids, two signals that might interplay and regulate PCD were also presented (Gechev and Hille 2005).

Reduction in Cat activity and endogenous accumulation of H_2O_2 which eventually triggered cell death were observed upon exposure to the Cat inhibitor aminotriazole (AT). Microarray analysis of *Arabidopsis* with a microarray representing 21,500 genes and subsequent comparison with other PCD-related expression studies revealed a set of new H_2O_2-responsive genes that were highly regulated in a common fashion during different types of PCD. These included an oxoglutarate-dependent dioxygenase and various oxidoreductases, the TFs *Zat11*, *WRKY75* and *NAM*, and proteasomal components (Gechev *et al.* 2005).

Senescence and programmed cell death

The mechanisms by which plants control senescence and the processes involved were reviewed in a genomics approach previously (Buchanan-Wollaston *et al.* 2003). More than 1,400 genes that showed relative changes in expression during 3 stages of leaf development (mature green, early senescence, and mid senescence) were identified using 8.2K *Arabidopsis* GeneChip arrays (Buchanan-Wollaston *et al.* 2003).

By monitoring the gene expression patterns at chosen time points during dark-induced leaf senescence, thousands of up- or down-regulated genes were identified. An association of GRAS, bZIP, WRKY, NAC, and C2H2 TF families with leaf senescence was reported (Lin and Wu 2004).

UV and gamma radiation

Microarray technology was used to identify genes, which are responding after exposure to UV-C radiation and to other agents causing genotoxic stress. Global changes in gene expression were investigated in *Arabidopsis* plants challenged with UV-C, bleomycin and xylanase, all leading to elevated homologous recombination frequencies. Genes specifically involved in the dynamic response to UV were determined by comparing expression profiles (Molinier *et al.* 2005).

Gene expression in various organs of maize at several UV-B fluence rates and exposure times was investigated to understand the processes of UV-B acclimation that result in altered plant morphology and physiology. After 8 h of high UV-B, the abundance of 347 transcripts was significantly altered with 285 up-regulated and 80 down-regulated. More transcript changes were observed in directly exposed than in shielded organs, and in adult compared to seedling tissues. It was indicated that the response to UV-B was very rapid, as some transcript levels were altered within 1 h of exposure. Most of the UV-B regulated genes were organ-specific (Casati and Walbot 2004).

Expression responses of 241 genes to UV-B in field-grown plants of *N. longiflora* were examined using a microarray enriched in wound- and insect-responsive sequences. Expression of approximately 20% of the sequences represented on the array regulated differentially. It was found that the expression responses to UV-B had similarities with those elicited by *M. sexta* herbivory. The most obvious similarities were down-regulation of several photosynthesis-related genes, and up-regulation of genes involved in fatty acid metabolism and oxylipin biosynthesis such as hydroperoxide lyase, α-dioxygenase, 13-LOX, and allene oxide synthase. Genes encoding a WRKY TF, a ferredoxin-dependent glutamate-synthase, and several other insect-responsive genes of unknown function were also similarly regulated by UV-B and insect herbivory treatments (Izaguirre *et al.* 2003).

Gene expression profiling indicated that UV-induced morphogenesis was associated with changes in phytohormone (auxins, brassinosteroids and gibberellins) homeostasis and the cell wall. It was also reported that acclimation to low, chronic dose rates of UV-B is distinct from that to acute, stress-inducing UV-B dose rates (Hectors *et al.* 2007).

To investigate transcriptomic profile of ionizing radiation-responsive genes in *Arabidopsis* plants, ATH1 microarrays were employed. Most remarkable changes were observed 9 days after irradiation and a total of 2,165 and 1,735 genes were identified as gamma-ray inducible and repressible, respectively. Comparison of the control and irradiated groups identified 354 differentially expressed genes as significant (Kim *et al.* 2007c).

Heavy metal accumulation and metal stress

In order to determine the influence of salts of two heavy metals – lead (Pb) and Cd – on plants, analysis of global gene expression was performed after exposure to 50 μM of Cd and Pb. The analysis revealed 65 and 338 up- and down-regulated genes by Cd and 19 and 76 by Pb, respectively. The greater number of genes regulated by Cd reflects generally higher genome instability of plants as well as higher uptake as compared to Pb. Half of the genes that changed their expression in Pb-treated plants also changed their expression under Cd treatment (Kovalchuk *et al.* 2005).

Since *A. thaliana* is a nontolerant plant to a large number of toxic compounds, it is a suitable model to study regulation of genes involved in response to heavy metals. It was found that ABC transporters were differentially regulated after Cd treatments and was suggested that some plant ABC transporters might be transporting glutathione-Cd or phytochelatins-Cd complexes into subcellular compartments or outside of the cell (Bovet *et al.* 2005).

When transcriptional regulation in response to Cd treat-

ment was investigated in roots and leaves of *Arabidopsis*, using whole genome CATMA microarray containing nearly 24,600 independent probe sets, it was demonstrated that there exists a regulatory network which differentially modulates gene expression in a tissue-specific manner. Responses observed in roots included the induction of genes involved in sulfur assimilation-reduction and glutathione metabolism. Therefore it was suggested that in order to cope with Cd, plants activate the sulfur assimilation pathway by increasing transcription of related genes to provide an enhanced supply of glutathione for phytochelatin biosynthesis. On the other hand, in leaves an early induction of several genes encoding enzymes involved in the biosynthesis of phenylpropanoids was reported (Herbette *et al.* 2006).

Three categories of genes were identified from transcriptome changes upon Cd and Cu exposure in roots of *A. thaliana* and the Cd-hypertolerant metallophyte *A. halleri*. These were: (1) common responses conserved across species; (2) metallophyte-specific responses representing candidate genes for Cd hypertolerance; and (3) specific responses to Cd (Weber *et al.* 2006).

Results from microarray experiments were used to identify genes from *A. thaliana* that were induced in response to one but not other heavy metals. *Arabidopsis* plants containing the promoter of one of the Ni-inducible genes (*AHB1*)::β-glucuronidase (GUS) transgene showed reporter gene activity when they were grown on media containing Ni but not when grown on media containing Cd, Cu, Zn, or without added metals. Thus, transgenic models might serve as biomonitors of bioavailable heavy metal contamination in soils and sediments (Krizek *et al.* 2003).

When transcript profiles of roots of *A. thaliana* and metal hyperaccumulator *T. caerulescens* plants grown under deficient, sufficient, and excess supply of Zn were examined, a total of 608 Zn-responsive genes with at least a 3-fold difference in expression level were detected in *A. thaliana* and 352 in *T. caerulescens* in response to changes in Zn supply. Only 14% of these genes were also Zn responsive in *A. thaliana*. When comparing *A. thaliana* with *T. caerulescens* at each Zn exposure, more than 2,200 genes were significantly differentially expressed. Many genes with a different expression between *A. thaliana* and *T. caerulescens* appeared to function in metal homeostasis, in abiotic stress response, and in lignin biosynthesis (van de Mortel *et al.* 2006).

Crosstalk in response or tolerance to abiotic and biotic stresses

Cell signaling integrates independent stimuli using connections between biochemical pathways. The sensory apparatus can be represented as a network, and the connections between pathways are termed crosstalk (**Fig. 2**). Several examples of crosstalk in plant biology were described previously and network models allowing genetic data to be integrated into the logical network of connections deduced from DNA microarray data were suggested (Genoud and Metraux 1999).

Twenty-six genes were detected to be up-regulated during three abiotic stresses (cold, salt and desiccation) in rice and of these, 14 genes were expressed specifically during the stress conditions analyzed while 12 were also up-regulated during reproductive development, suggesting that some components of the stress response pathways are also involved in reproduction (Agarwal *et al.* 2007).

The transcriptional change of more than 2-fold was observed for 109, 210 and 386 genes in chickpea after drought, cold and high-salinity treatments, respectively. Among these, 2, 15 and 30 genes were consensually differentially expressed between tolerant and susceptible genotypes studied for drought, cold and high-salinity, respectively (Mantri *et al.* 2007).

Expression patterns of 49 cytochrome P450 genes were analyzed by microarrays under various treatments, such as hormones (SA, JA, ET, ABA), pathogen-inoculation (*Alternaria brassicicola*, *A. alternata*), paraquat, rose bengal, UV stress (UV-C), heavy metal stress ($CuSO_4$), mechanical wounding, drought, high salinity and low temperature. Expression of 29 cytochrome P450 genes was induced by various treatments. Inoculation with *A. brassicicola* and *A. alternata* as biotic stresses increased transcript levels of 12 and 5 genes in *Arabidopsis* plants, respectively. Moreover, induction of some of the genes also by abiotic stresses suggested crosstalk between abiotic and biotic stresses. It was also stated that most cytochrome P450 genes induced by both abiotic and biotic stresses contained the recognition sites of MYB and MYC, ACGT-core sequence, TGA-box and W-box for WRKY TFs in their promoters. These *cis*-acting elements are known to participate in the regulation of plant defense (Narusaka *et al.* 2004).

To identify genes of potential importance to cold, salt, and drought tolerance, global expression profiling was performed on *Arabidopsis* plants subjected to stress treatments of 4°C, 100 mM NaCl, or 200 mM mannitol, respectively. Combined results from all 3 stresses identified 2,409 genes with a greater than 2-fold change compared to control. This suggested that about 30% of the transcriptome is sensitive to regulation by common stress conditions. It was also pointed out that the majority of changes were stimulus and tissue specific. The gene with the largest induction under all 3 stress treatments was *At5g52310* (*LTI*/*COR78*), with induction levels in roots greater than 250-fold for cold, 40-fold for mannitol, and 57-fold for NaCl. A stress response was observed for 306 (68%) of the known circadian controlled genes (Kreps *et al.* 2002).

When rice seedlings were subjected to different abiotic stress conditions, 43 F-box protein-encoding genes have been found to be differentially expressed and several of them were found to be influenced by light (Jain *et al.* 2007).

It was reported that the initial transcriptional stress response of *Arabidopsis* under heat, cold, drought, salt, high osmolarity, UV-B light and wounding stress might comprise a set of core environmental stress response genes which, by adjustment of the energy balance, could have a crucial function in responses to these stresses (Kilian *et al.* 2007).

A total of 312 genes regulated by *ESK1* showed greater overlap with sets of genes regulated by salt, osmotic and ABA treatments than with genes regulated by cold acclimation or by the TFs *CBF3* and *ICE1*, which have been shown to control genetic pathways for freezing tolerance (Xin *et al.* 2007).

The expression profiles of 1,545 genes were investigated in sugarcane subjected to drought, Pi starvation, herbivory and N-2-fixing endophytic bacteria. 179 genes with different expression levels were identified as differentially expressed in at least one of the treatments analyzed (Rocha *et al.* 2007).

Stress-induced, transcriptional alterations of underlying effector gene families, which encode enzymes acting in secondary metabolism and defense reactions, were investigated using a DNA array. It comprised complete sets of genes encoding 109 secondary product glycosyltransferases and 63 glutathione-utilizing enzymes along with 62 cytochrome P450 monooxygenases and 26 ABC transporters. Their expression levels were monitored in different organs of unstressed plants and in shoots in response to herbicides, UV-B radiation, endogenous stress hormones, and pathogen infection. A principal component analysis based on the transcription of these effector gene families defined distinct responses and crosstalk. MeJA and ET treatments were separated from a group combining reponses towards two sulfonylurea herbicides, salicylate and an avirulent strain of *Pseudomonas syringae* pv. tomato. The responses to the herbicide bromoxynil and UV-B radiation were distinct from both groups. Moreover, these analyses pointed out individual effector genes indicating their role in these stress responses. Small groups of induced effector genes indicate common defense strategies. Furthermore, homologous members within branches of these effector gene families displayed differential expression patterns either in both or-

gans or during stress responses suggesting their non-redundant functions (Glombitza *et al.* 2004).

A full-length cDNA microarray containing approximately 7,000 independent, full-length *Arabidopsis* cDNAs was prepared to analyze the expression profiles of genes under drought, cold and high-salinity stress conditions over time. The transcripts of 53, 277 and 194 genes increased after cold, drought and high-salinity treatments, respectively, more than 5-fold compared to control and 22 stress-inducible genes that responded to all 3 stresses were identified. *DREB1A* was one of the genes whose expression peaked at 2 h after cold treatment. Among the drought, cold or high-salinity stress-inducible genes identified, 40 TF genes (corresponding to approximately 11% of all stress-inducible genes identified) were determined, and it was suggested that various transcriptional regulatory mechanisms function in the drought, cold or high-salinity stress signal transduction pathways (Seki *et al.* 2002).

An activation-tagged allele of activated disease resistance 1 (*ADR1*) has previously been shown to convey broad spectrum disease resistance. It was also shown that either constitutive or conditional enhanced expression of *ADR1* conferred significant drought tolerance. On the other hand, it was reported that cross-tolerance was not a characteristic of *adr1* plants; rather they showed increased sensitivity to thermal and salinity stress. Hence, *ADR1*-activated signaling may antagonize some stress responses. Microarray analyses of plants containing a conditional adr1 allele demonstrated that a significant number of the up-regulated genes had been previously implicated in responses to dehydration. Therefore, it might be concluded that biotic and abiotic signaling pathways might share multiple nodes and their outputs may have significant functional overlap (Chini *et al.* 2004).

Transgenic applications for transcriptome analysis

Examples of how full-genome expression profiling can contribute to the understanding of complex stress responses and the identification and evaluation of novel transgenes that could hold the key to the development of commercially viable and sustainable crop plants were outlined previously (Denby and Gehring 2005).

To understand the stress response of rice in comparison with that of *Arabidopsis*, Oh *et al.* (2005) developed transgenic rice plants that constitutively expressed *CBF3*/*DREB1A* and *ABF3*, *Arabidopsis* genes that function in ABA-independent and ABA-dependent stress-response pathways, respectively. *CBF3* in transgenic rice elevated tolerance to drought and high salinity, and produced relatively low levels of tolerance to low-temperature exposure. The data were in direct contrast to *CBF3* in *Arabidopsis*, which is known to function primarily to enhance freezing tolerance. *ABF3* in transgenic rice increased tolerance to drought stress alone. It was reported that 12 and 7 target genes were activated in transgenic rice plants by *CBF3* and *ABF3*, respectively. The target genes together with 13 and 27 additional genes were induced further upon exposure to drought stress, consequently making the transgenic plants more tolerant to stress conditions (Oh *et al.* 2005).

The ectopic overexpression of pepper *CaPIF1* (*C. annuum* Pathogenesis Induced Factor), which encodes a plant-specific C2H2 zinc finger protein, in tomato resulted in a massive change in gene expression: of a total of 8700 genes on the microarray. Among these genes, 110 were up- or down-regulated, without exhibiting any visual morphological abnormality. It was reported that *CaPIF1* turned on genes involved in metabolic pathways, and stress and defense responses. It was also suggested that the up-regulation of the genes might increase tolerance to cold stress and pathogen attack. The tolerance levels of transgenic plants to cold stress and the bacterial pathogen *Pseudomonas syringae* pv. tomato DC 3000 were correlated with *CaPIF1* expression levels. These results suggested that *CaPIF1* confers increased tolerance to biotic and abiotic stresses (Seong *et al.* 2007).

StEREBP1 induced expression of several GCC box- and/or DRE- containing stress response genes was shown in *StEREBP1*-overexpressing transgenic potato plants using TIGR 10K potato chip. In addition, overexpression of *StEREBP1* enhanced tolerance to cold and salt stress in transgenic potato plants. Overall it was suggested that *StEREBP1* is a functional TF that might be involved in abiotic stress responses in plants (Lee *et al.* 2007b).

DNA topoisomerase 6 (TOP6) belongs to a novel family of type II DNA topoisomerases. Overexpression of *OsTOP6A3* and *OsTOP6B* in transgenic *Arabidopsis* plants conferred reduced sensitivity to the stress hormone, ABA, and tolerance to high salinity and dehydration. Based on microarray analysis with ATH1 arrays, it was revealed that a large number of genes were regulated differentially in 10-day-old transgenic plants. Therefore, it was proposed hat TOP6 genes play a crucial role in stress adaptation of plants by altering gene expression (Jain *et al.* 2006).

Microarray analyses of rice transformed with *OsMADS26:GR* (glucocorticoid receptor) fusion construct showed that biosynthesis genes for jasmonate, ET, and ROS, as well as putative downstream targets involved in the stress-related processes, were up-regulated in *OsMADS26*-overexpressing plants (Lee *et al.* 2008). At least 1.5-fold differences in expression of 301 genes and 2-fold differences in expression of 48 genes were reported.

Endoplasmic reticulum stress and unfolded protein response

Eukaryotic cells respond to the accumulation of unfolded proteins in the endoplasmic reticulum (ER). In this case, so-called unfolded protein response (UPR) genes are induced. Kamauchi *et al.* (2005) determined the transcriptional expression of *A. thaliana* UPR genes by fluid microarray analysis of tunicamycin-treated plantlets and identified 215 up-regulated and 17 down-regulated genes. Reanalyses of these genes with DNA microarrays revealed 36 up-regulated and 2 down-regulated genes which were indicated as UPR genes. Among them, the up-regulated genes were related to protein degradation, regulation of translation, and apoptosis. It was concluded that plant cells appeared to have a strategy for overcoming ER stress through enhancement of protein folding activity, degradation of unfolded proteins, and regulation of apoptosis (Kamauchi *et al.* 2005).

When the effect of ER stress on gene expression was investigated, it was found that expressions of 26 genes were increased in *Arabidopsis*. Among them, transcriptional activations of at least 9 whose products act in the ER were confirmed by promoter analyses (Noh *et al.* 2003).

Other environmental stress-related microarray analyses

2,4,6-trinitrotoluene (TNT) is a nitro-substituted xenobiotic explosive that is toxic to plants and animals. Expression analysis of *Arabidopsis* exposed to to TNT at low and high concentrations (1 and 10 μM) revealed that a total of 52 genes were significantly up-regulated, and 47 genes were down-regulated at a 1.7-fold cut-off. A large number of these genes had predicted functions in cell defense and detoxification. Moreover, conserved motifs were identified in the promoter region of co-regulated genes, some of which were defined as novel *cis*-regulatory elements (Mentewab *et al.* 2005).

Plant root growth is affected by both gravity and mechanical stimulation. Whole-genome microarray analysis of *Arabidopsis* root apices after gravity reorientation and mechanical stimulation was carried out in order to determine the transcriptional responses. Transcript levels of 22,744 genes in a time course during the first hour after either stimulus were monitored (Kimbrough *et al.* 2004). Rapid, transient changes in the relative abundance of specific

transcripts were observed in response to gravity or mechanical stimulation, and the changes revealed clusters of coordinated events. Transcriptional regulation was observed in the root apices within less than 2 min after either stimulus.

Callus cultures of *A. thaliana* were exposed to altered *g*-forces (1-10 *g*) by centrifugation. Exposure to approximately 5 *g* and higher for 1 h were indicated to alter transcript levels with a shift from starch synthesis to starch degradation and an increase in rates of anaplerosis. Microarray analysis was performed with samples exposed to 7 *g* for 1 h, in order to determine *g*-related effects on gene expression. Transcripts of more than 200 genes were significantly increased (Martzivanou and Hampp 2003). Transcripts coding for enzymes of major pathways formed the largest group (25%), followed by gene products involved in cellular organization and cell wall formation/rearrangement (17%), signaling, phosphorylation/dephosphorylation (12%), proteolysis and transport (10% each), hormone synthesis and related events (8%), defense (4%), stress-response (2%), and gravity-sensing (2%). It was stated that although, many of the alterations were part of a general stress response, some changes related to the synthesis/rearrangement of cell wall components might be more hyper-*g*-specific.

Trehalose exists in most living organisms and functions as a storage carbohydrate and as an osmoprotectant in yeast, fungi, and bacteria. On the other hand, exogenous trehalose is toxic to higher plants. Microarray analysis revealed that expression levels of 91 transcripts were regulated differentially in *Arabidopsis* seedlings under 1-6 h of trehalose (30 mM) treatment (Bae *et al.* 2005). The exogenous trehalose treatment altered transcript levels of TFs, cell wall modification, N metabolism, and stress-related, defense-related, and fatty acid biosynthesis genes. It was found that many of the transcripts altered by exogenous trehalose treatment were associated with the ET and MeJA-signaling pathways.

There is limited information on the acclimation process of plant cells to acid stress. Gene expression profiles of the cells of *Synechocystis* sp. PCC 6803 treated at pH 8 (control) and pH 3 for 0.5, 1, 2 or 4 h were compared (Ohta *et al.* 2005). It was found that among the 32 up-regulated genes, expressions of *slr0967* and *sll0939* kept-increasing until 4 h under the acid stress and increased by 7 to 16-fold after the 4 h treatment, suggesting important roles for products of these two genes in the acid acclimation process.

Malondialdehyde (MDA) originates from fatty acids containing more than two methylene-linked double bonds; therefore, tri-unsaturated fatty acids are the *in vivo* source of up to 75% of MDA. A molecular proof to this hypothesis was provided by a microarray analysis of *Arabidopsis* plants exposed to low levels of MDA (Weber *et al.* 2004b). A high number of genes including those functioning in abiotic/environmental stresses were up-regulated whereas none of the PR genes represented on the array responded to MDA. Overall it was concluded that changes in the concentration/localization of unbound MDA *in vivo* might strongly affect stress-related transcription.

CONCLUSION

Microarray studies have provided important information on transcriptomes of plants to investigate stress responsive genes under various stresses. Further genomics, proteomics and metabolomics studies are necessary to enlighten whole cellular processes related with biotic and abiotic stress tolerance in plants and to understand how the components such as genes, proteins and metabolites work together to comprise functioning plant cells.

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