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Plant microarray for gene expression profiling and their application

Mingzhu Wu[1], Ang Chen[2], Zhong Wang[1], Jianfeng Zhang[1], Chen Wang[1], Feng Li[1], Pan Wei[1], Ran Wang[1], Zhaopeng Luo[1], Chunyang Wei[1], Fucheng Lin[1], Jun Yang[1]*

[1]China Tobacco Gene Research Center of Zhengzhou Tobacco Research Institute CNTC, Zhengzhou 450001, China; [2] School of life sciences, Xiamen University, Fujian China, 361102

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Microarray can parallel quantification of large numbers of genes and promises to provide detailed insight into cellular processes involved in the regulation of gene expression. In plants, microarray for gene expression profiling should provide an important way for understanding of gene functions and signaling networks that operate plants growth and development, respond to biotic and abiotic stresses, important agronomic characters. This review focuses on the application of microarray for gene expression profiling in plants. Moreover, development and application of tobacco microarray is also summarized. This review will provide useful information for better application of plant microarray in studies of gene function and regulation mechanism.

Keywords: plant microarray, gene function, regulation mechanism, tobacco microarray

Introduction

Gene chips, also known as microarray, are a molecular biological technology based on hybridization theory and have been developed in the 1990s. Fodor *et al.* (1991, 1993) initially put forward the concept of biochip by combining planographic printing, semiconductor technology, confocal laser techniques, synthesis of oligonucleotides, fluorescent labeling, and computer analysis methods. Biochips share some features in common with microelectronics and micro-electromechanical systems, and can process many biological samples at the same time. Microarray is one type of biochip. In microarrays, a large number of unique nucleotide probes are arrayed on various

*Corresponding author: e-mail address: yangjun@ztri.com.cn

solid supports (including nylon membranes, glass slides, and plastic sheets, among others). DNA that hybridizes to these probes is then radioactively or fluorescently labeled and then the strength of the hybridization signals is scanned by using laser scanning or confocal laser fluorescence microscopy techniques (Cheung *et al*., 1999; Zhu, 2003). The signal values measured are then analyzed with a variety of computational methods, and biologically relevant information about these genes in different samples or tissues is obtained (Stears *et al.*, 2003).

The development of microarray realizes the possibility for parallel analysis of expression of thousands of genes. Because microarrays only needs few samples, and have important features like automation, high through-put, miniaturization of volume. Microarray for expression profiling has been widely used in the analysis of gene expression in model organisms (Walker *et al*., 2004; Son *et al*., 2005; Xia *et al*., 2007). And the use of microarrays could greatly promote the development of functional genomics and systems biology studies.

1 Research progress in plant microarray

The study of microarray in plant genes started late, but with the development of genomics and molecular biology, the application of high through-put sequencing techniques in plant gene studies and the fact that more and more genomic sequences and functional genes have been discovered, the number of probes on the chip is also increasing and the coverage is expanding. Meanwhile, with the development of chip technology, the types of gene chip are increasing. Plant microarrays are developing from the single cDNA chip into various types such as Oligo microarray, DNA methylation microarray, Single Nucleotide Polymorphism (SNP) chip and MiRNA microarray.

Oligo microarray is the most widely used gene chip in plant studies and includes genome oligo microarray and mRNA oligo microarray, which are used to study changes in gene expression on the levels of genome and mRNA respectively. At present genome oligo microarray almost covers model plants, important field crops and economic crops, such as Arabidopsis (Richards et al., 2012), rice (Jung *et al*., 2013), barley (Kwasniewski *et al*., 2012), wheat (Quijano *et al*., 2014), corn (Allardyce *et al*., 2013), tobacco (Edwards *et al*., 2010), soybean (Le *et al*., 2012), tomato (Martínez-Andújar *et al*., 2012) and alfalfa (Friesen *et al*., 2010) etc. Using rice as an example, in recent years a large amount of genome data has been obtained for rice and these data have been used to design various chips with different specifications, including BGI/Yale 60K chip (Ma *et al.*, 2005), Agilent 44K chip (Shimono *et al*., 2007), NSF 45K chip (Jung *et al*., 2008) and Affymetrix 57K chip (Li *et al*., 2007),

etc. Among these chips, the number of probes in Affymetrix 57K chip is about 57000 and this chip can detect about 50000 genes at the same time and detect the expression of genes in the whole genome. At present Oligo Microarray is widely used in studies on plant growth and development, biotic and abiotic

stresses, discovery of important agronomic characters, discovery of new genes and construction of gene regulatory network.

Application of microarray for gene expression profiling

Plant microarray	No. of genes, transcripts or EST	Key references
Affymetix Rice Genome Array	49824 transcripts	Jung *et al*., 2013
Affymetix Arabidopsis ATH1 Genome Array	24,000 genes	Richards *et al*., 2012
Affymetix Barley Genome Array	400,000 EST	Kwasniewski *et al*., 2012
Affymetix Wheat Genome Array	55,052 transcripts	Quijano *et al*., 2014
Affymetix Maize Genome Array	13,339 genes, 14850 transcripts	Allardyce *et al*., 2013
Affymetix Tomato Genome Array	9,200 transcripts	Martínez-Andújar *et al.*, 2012
Affymetix Soybean Genome Array	60,800 transcripts	Le *et al*., 2012
Agilent Tobacco Oligo Microarray	42,034 genes and transcripts	Edwards *et al*., 2010
Affymetix Medicago Genome Array	58,232 transcripts	Friesen *et al*., 2010

2.1 plant growth and development

Microarrays are widely used for gene expression profiling in plant growth and development (Lan *et al*., 2004; Wang *et al*., 2010; Richards *et al*., 2012; Redman *et al*., 2004; Clouse *et al*., 2011). Richards *et al*. (2012) assessed genome-wide gene expression patterns throughout the Arabidopsis life cycle, and it was found that accession and flowering status (vegetative versus flowering) were strong components of transcriptional variation in this plant (Richards *et al*., 2012). A rice cDNA microarray was used to analyze the pollination and fertilization developmental stages. 253 genes was found

exhibiting differential expression during pollination and fertilization, and about 70% of these could be assigned a putative function (Lan *et al*., 2004). Wang *et al.* (2010) used 190 rice microarrays to evaluate gene expression patterns in 39 tissues collected throughout the life cycle of rice. 69% of the expressed genes showed significantly variable expression levels among tissues/organs. Among these genes, 5.2% of the expressed genes showed tissue-specific expression, 22.7% of the transcripts exhibited constitutive expression, with 19 genes that had high and stable expression in all tissues.

Auxin and Brassinosteroids (BRs) both play important role in plant growth and development. A total of 222 genes were significantly up-regulated and 103 genes were significantly down-regulated by exposure to IAA in Arabidopsis; most of the up-regulated genes were transcription factors and protein kinases, and over one-third of the auxin-regulated genes had no known function (Redman *et al*., 2004). BRs activated a whole signal transduction pathway through activation of the expression of two transcription factors, BZR1 and BES1 (Clouse *et al*., 2011). Sun *et al.* (2010) combined transcript profiling and chromatin-immunoprecipitation microarray (ChIP-chip) experiments and found 953 BR-regulated BZR1 target (BRBT) genes. The BRBT target genes revealed numerous molecular links between the BR-signaling pathway and downstream components involved in developmental and physiological processes. The application of ChIP-chip in studies of Arabidopsis treated with BR revealed that 50 genes were directly regulated by BES1. These genes regulated by BES1 were related to BR responses, interactions with other hormones, and light signal transduction pathways. Further studies showed that BES1 inhibited the development of chloroplasts through inhibition of the transcription factors GLK1 and GLK (Yu *et al*., 2011).

2.2 plant biotic stress and response action

Previous studies have shown that genes were confirmed to participate in signal transduction, protein synthesis, modification, degradation and secondary metabolism in response to plant pests stress by using microarrays (Smith and Boyko, 2007; Voelckel *et al*., 2004; Boyko *et al*., 2006). It was found that the caldesmon gene is induced when wheat infested with *D. noxia* and Arabidopsis infested with *M. persicae* by using microarray. When wheat infested with D. noxia and tobacco infested with *M. nicotianae*, expression level of glutamate synthase gene was found significantly up-regulated (Smith and Boyko, 2007).

Aphid damage influenced gene expression profiles in tobacco, wheat, and sorghum. Genes related to the synthesis of chlorophyll and photosystem proteins were found to be highly up-regulated, which may compensate for the loss of chlorophyll caused by aphids (Voelckel *et al*., 2004; Boyko *et al*., 2006).

Systemic acquired resistance (SAR) in plants refers to the defense response activated by invasion of pathogenic microbes. Maleck *et al*. (2000) used Arabidopsis microarrays to detect changes in gene expression under fourteen different conditions. The results show that SAR was induced or inhibited, and 26 combinatorial regulation defense genes were identified (Maleck *et al*., 2000). The gene expression profiles of Arabidopsis treated with the pathogenic fungus Alternaria brassicicola, salicylic acid, methyl jasmonate, and ethylene were analyzed using microarrays. There were 169 genes found to be induced by the various treatments, and a cooperative regulatory mechanism of defense existed among different treatments (Schenk *et al*., 2000).

In addition to the detection of changes in gene expression after inoculation of pathogenic bacteria and fungus, microarrays are also one of the important tools that used in detecting plant virus currently. Lee *et al.* (2003) used a plant virus cDNA chip to detect four species of selected cucurbit-infecting tobamoviruses for the first time, and the viral gene chip was able to successfully detect the target viruses specifically. Subsequently, microarrays able to detec six potato viruses in both single and mixed infections were developed (Bystricka *et al*., 2005). Later, a microarray able to detect 10 common viruses in both single and mixed infections appeared, including cucumber mosaic virus, tomato wilt virus, tobacco mosaic virus, and tomato mosaic virus, etc. (Tiberini *et al*. 2014). Nicolaisen *et al.* (2011) reported a kind of microarray that can detect 52 viruses simultaneously. Compared with other methods such as electron microscopy, enzyme linked immunosorbent assay (ELISA), and polymerase chain reaction (PCR), microarrays can detect one or mixed viruses infections at the same time, with the advantages of high accuracy, fewer samples, and easier protocols (Boonham *et al*., 2007; Agindotan and Perry, 2007).

2.3 plant abiotic stress and response action

When plants suffer abiotic stresses such as high salinity, drought, cold damage, and heavy metal toxicity, the expression of some genes in plants will change significantly (Walia *et al*., 2006; Wang *et al*., 2011; Brini *et al*., 2011; Lee *et al*., 2005; Huang *et al.,* 2014). Barley is a salt-tolerant crop species with important economic value in arid and semi-arid regions of the world. Microarrays were used to detect the early responses of barely seedling in gene

expression following exposure to salinity stress, it was found that genes related to jasmonic acid synthesis and responses to jasmonic acid played important roles in the response to salinity, and a large number of abiotic stress (such as heat, drought, and low temperature) related genes were also found to be responsive to salinity stress (Walia *et al*., 2006). Rice is highly sensitive to drought stress, and there were 5284 genes that found differentially expressed under drought stress by using microarrays. A total of 261 differentially expressed transcription factor genes were found to respond to drought stress, and a cis-element containing a special CGCG box was identified in the upstream region of 55 common induced genes (Wang *et al*., 2011). Transgenic Arabidopsis plants overexpressing the wheat dehydrin DHN-5 showed enhanced tolerance to osmotic stress, Transcription profiling analysis by using Arabidopsis ATH1 microarrays showed that genes related to ABA response (such as RD29B)was significantly up-regulated (Brini *et al*., 2011). Lee *et al*. (2005) used Arabidopsis microarrays to analyze genome transcript expression profiles in response to cold stress and discovered 939 cold-regulated genes. Many genes involved in the biosynthesis or signaling of plant hormones such as abscisic acid, gibberellic acid, and auxin are regulated by cold stress; these hormones are of potential importance in coordinating cold tolerance with growth and development (Lee *et al*., 2005).

Phosphorus is one of the essential elements for plant growth. A total of 254 genes in Arabidopsis were found to be Pi-responsive by using microarray, some of these genes were involved in various metabolic pathways such as ion transport, signal transduction, and transcriptional regulation (Misson *et al*., 2005). Chromium (VI) is the most toxic form of chromium. Rice roots exposed to chromium (VI) for long-term and short-term periods were analyzed with rice microarrays. Long-term and Short-term Cr(VI) exposure regulated different gene expression, Long-term Cr(VI)-regulated genes included those related to cytokinin signalling, the ubiquitin-proteasome system and DNA repair. Short-term Cr(VI) exposure up-regulated genes related to mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) (Huang *et al*., 2014). Glutathione (GSH) plays an important role in plants for adaption to various abiotic stress conditions. The expressions of 453 genes were found significantly changed when Arabidopsis seedlings were exposed to 5 mM GSH by using microarrays. GSH regulates adaptability to the environment through up-regulating defense response genes and down-regulating growth and development response genes expression (Hacham *et al*., 2014).

2.4 Important agronomic characters analyze by using microarray

At present, the plant traits of high yield, high quality, and stress resistance need to be improved in agricultural production. Thus, it is very important to study the molecular mechanisms affecting different aspects of plant development, such as plant morphology, fertility, seed formation, and the regulation of starch metabolism. These important agronomic traits are controlled by multiple genes, but using routine molecular biology techniques cannot analysis multiple genes simultaneously, this makes it difficult to further understand the processes underlying these important crop traits. Microarrays provide a way of studying such complex agronomic traits. Huang *et al*. (2014) mapped 75 differentially expressed genes in two QTL intervals in rape that are associated with the number of pods in the main inflorescence by using microarray and chromosome mapping technology. Microarays were also used to detect changes of the transcriptome profiles during papaya maturation. 414 genes related to this process were identified, including transcription factors of MADS, NAC and AP2/ERF gene family (Fabi *et al*., 2012). By combining a suppression subtractive hybridization (SSH) library and a cNDA chip, a total of 279 different expression clones in a Ponkan mandarin seedless mutant were identified. Further analysis showed that the transcription level of a gene encoding a protein related to male sterility was highly up-regulated and that the expression levels ofmany transcription factors were repressed in the seedless mutant compared to the wild type (Qiu *et al*., 2012). Yano *et al.* (2012) identified 45 QTL candidate genes related to rice seedling vigor by using microarrays, and finally confirmed that OsGA20ox1 was the target gene in regulating rice seeding vigor. Cold stress resistance is also controlled by QTLs. A study that combined microarrays with QTL mapping discovered 4 genes in rice that respond to cold stress. Overexpressing one of these genes significantly enhanced the resistance of rice seedlings to low temperature (Liu *et al*., 2013).

2.5 Discover new genes and construct genes expression network

A microarray study in Arabidopsis of WRKY transcription factors responding to jasmonic acid treatment discovered that 30% of WRKY transcription factors (22 out of 72 WRKY) responded to JA treatment, including 6 new WRKY genes (AtWRKY7, AtWRKY20, AtWRKY26, AtWRKY45, AtWRKY48, and AtWRKY72) that had never been implicated in particular physiological functions (Schluttenhofer *et al*., 2014).

In Arabidopsis, microarrays have been used to analyze the expression of genes exposed to drought, high salinity, ABA, and cold stresses. These studies showed that more than half of the drought-induced genes were also induced by high salinity and ABA, and only 10% of the drought-induced genes were also induced by cold stress, suggesting that there is very likely an interactive network that exists among the signal pathways for plant responses to drought, high salinity and ABA (Seki *et al*., 2001; Seki *et al*., 2002a; Seki *et al.*, 2002b). Rabbani *et al*. (2003) used a rice cDNA chip to study rice treated by drought, high salinity, and ABA stresses, and discovered that more than 98% of the salt stress induced genes and 100% of the ABA-induced genes can were induced by drought stress. These studies demonstrated that a general signal control system or an interactive signal network may exist in plant responses to drought, high salinity and ABA stresses.

3 Research progress in tobacco microarray

Tobacco is one of the most important cash crops in the world; it is also an important model plant that has been widely used in studies of plant developmental biology, physiology, biochemistry, and genetics. Tobacco is an allopolyploid species and that is generally thought to have originated from chromosome doubling after interspecific hybridization between N. tomentosiformis (T-genome) and N. sylvestris (S-genome) (Clarkson *et al*., 2005; Lim *et al*., 2004). The genome of Nicotiana tabacum is large (4.5Gbp) and contains a large number of repetitive sequences (Arumuganathan and Earle, 1991; Kenton *et al*., 1993; Zimmerman and Goldberg, 1977).

The Affymetrix and Agilent companies have developed high-density tobacco microarrays for commercialization. The Tobacco Gene Expression Microarray from Agilent (product No.: G2519F) consists of 43,803 probes that were designed mainly based on the TIGR (The Institute for Genomic Research) and Unigenes in the NCBI database. Affymetrix has produced two kinds of tobacco microarrays. One is the expression profile microarray funded by Advanced Technologies (Cambridge) Ltd. in 2010; the probesets for this chip were based on the EST data obtained from the proprietary data and public database entries (40642 unigenes in total). The other tobacco microarray designed by Affymetrix is the exon microarray funded by Philip Morris International R&D in 2012. This chip contains 1,089,368 probes (covering a total of 272,342 exons, with 4 probes for each exon), which are from American TGI methylation filtering GSS sequence and EST data in the public databases. These two kinds of tobacco microarray designed by Affymetrix have not yet been sold as directory chips.

The China Tobacco Genome Project has finished sequencing the complete genomes of Nicotiana tomentosiformis, Nicotiana sylvestris, and the Nicotiana tabacum. Our group has first designed a tobacco tiling microarray based on the whole genome sequences of Nicotiana tomentosiformis, Nicotiana sylvestris, and the EST sequences and transcriptome sequencing data of Nicotiana tabacum. This microarray is an authorized production using the Affymetrix Whole-Transcript Expression Analysis method. We have further cooperated with Affymetrix in designing the tobacco genome microarray (WT, whole transcript) based on the newest predicted genes from the whole genome of *Nicotiana tabacum*. So far, these two tobacco gene microarrays have been used in studies of gene expression profiles of *Nicotiana tabacum*. We are committed to characterizing the expression patterns of genes in the major development stages, tissues, and organs in Hongda tobacco. Further, we expect to identify functional genes related to tobacco growth, development, stress resistance, disease resistance, and quality. All these efforts will lay the foundation for the genetic improvement of tobacco.

4 Conclusion and future perspectives

Microarrays and their attendant protocols and data analysis methods are well established and largely standardized technologies; they can presently be relied on for highly accurate data acquisition and analysis. Therefore microarrays are powerful tools available to researchers for the transcription profiling at the whole genome scale. They can be used to detect differentially expressed genes in throughout the course of plant growth and development, as well as in studies seeking to evaluate gene expression patterns when plants are exposed to biotic and abiotic stresses. These types of expression profiles can contribute significantly to the discovery of new functions of genes. Microarrays are a critically important tool in the broader effort to characterize the functions of each gene in the various metabolic and regulatory pathways in plants and will be of great utility in helping to reveal whole gene regulatory networks.

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