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REVIEW

Plant–Pathogen Interactions: What Microarray Tells About It?

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Abstract Plant defense responses are mediated by elementary regulatory proteins that affect expression of thousands of genes. Over the last decade, microarray technology has played a key role in deciphering the underlying networks of gene regulation in plants that lead to a wide variety of defence responses. Microarray is an important tool to quantify and profile the expression of thousands of genes simultaneously, with two main aims: (1) gene discovery and (2) global expression profiling. Several microarray technologies are currently in use; most include a glass slide platform with spotted cDNA or oligonucleotides. Till date, microarray technology has been used in the identification of regulatory genes, end-point defence genes, to understand the signal transduction processes underlying disease resistance and its intimate links to other physiological pathways. Microarray technology can be used for in-depth, simultaneous profiling of host/pathogen genes as the disease progresses from infection to resistance/susceptibility at different developmental stages of the host, which can be done in different environments, for clearer understanding of the processes involved. A thorough knowledge of plant disease resistance using successful combination of microarray and other high throughput techniques, as well as biochemical, genetic, and cell biological experiments is needed for practical application to secure and stabilize yield of many crop plants. This review starts with a brief introduction to microarray technology, followed by the basics of plant–pathogen interaction, the use of DNA microarrays over the last decade to unravel the mysteries of plant–pathogen interaction, and ends with the future prospects of this technology.

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Abbreviations

EST	Expressed sequence tag
RT-PCR	Reverse transcriptase polymerase chain reaction
MeV	MultiExperiment Viewer
EDGE	Extraction of differential gene expression
FiRe	Find Regulon
ROS	Reactive oxygen species
SA	Salicylic acid
NO	Nitric oxide
JA	Jasmonic acid
SAR	Systemic acquired resistance
ISR	Induced systemic resistance
PR	Pathogenesis-related
GR	Glucocorticord receptor
Dex	Dexamethasone
NPR	Nonexpressor of pathogenesis related genes
MJ	Methyl jasmonate
TSWV	Tomato spotted wilt virus
HR	Hypersensitive response
DRG	Differentially regulated genes
HSP	Heat shock protein
PEBV	Pea early browning virus
CELO	Chicken embryo lethal orphan
PAMP	Pathogen-associated molecular patterns
DAMP	Danger-associated molecular patterns
PTI	PAMPs-triggered immunity
ETI	Effector-triggered immunity

ORMV Oilseed rape mosaic virus
MGED Microarray Gene Expression Data Society

Introduction

The interactions between plants and pathogens are complex [1, 2]. At the onset of plant pathogen interaction, plants develop two strategies to detect and defend pathogen attack. One strategy involves the generation of pathogen-associated molecular patterns (PAMPs) and danger-associated molecular patterns (DAMPs) while the other involves recognition by pathogen effectors, resulting in PAMPs-triggered immunity (PTI) and effector-triggered immunity (ETI), respectively [1, 2]. As a consequence, the plant switches on downstream signaling pathways and produces antimicrobial compounds to kill the pathogen and maintain homeostasis [1–4]. This very precisely controlled complex process involves a number of genes and a number of signaling pathways [5]. It is this complexity of plant–pathogen interactions, which makes it very difficult to discern, which anatomical features, metabolites, and signaling pathways are activated: traditional biochemical and genetic experimental methods are inadequate tools for the task. Nowadays, the field of genomics provides powerful tools to investigate these critical factors. Transcript profiling techniques allow the simultaneous examination of thousands of genes, and are used to study changes in gene expression that are transcriptionally regulated [6]. DNA microarray is among the most common of profiling tools, and is becoming more and more advanced with the availability of the genomic and EST sequences of plants simultaneous with the advancement in the computational biology tools. It helps in the study of defense mechanism of plants after pathogen attack, in the identification of pathogenesis-related genes and also to understand the interactions between different signaling pathways [7–9]. This review begins with concise information of microarray technology and the basics of plant–pathogen interaction and focuses mainly on the use of DNA microarrays over the last decade to unravel the mysteries of plant–pathogen interaction at the transcript level, ending with the future prospects of this technology.

DNA Microarray

Microarray technology provides a suitable platform to measure the expression levels of thousands of genes in a sample in a single experiment, thereby creating an expression profile or "transcriptome" for the sample under study to create a global picture of cellular function [10, 11]. Although there are many protocols available for DNA microarray, the basic technique involves extraction of mRNA from two biological samples, a control sample and the other an experimental. The isolated mRNAs are converted to cDNA by reverse transcriptase polymerase chain reaction (RT-PCR). Each of the two cDNA pools is fluorescently labeled by two different fluorochromes, mixed together and hybridized for a period of time to a large number of gene sequences placed as individual spots on a microarray slide [11]. After hybridization, the excess cDNA is washed off. Hybridization results are analyzed by determining the relative intensity of fluorescence at each gene spot with a laser scanner. Spots that fluoresce predominately with one label or the other indicate a gene that is differentially upregulated or downregulated in the sample under the conditions of the study [11].

There are two basic types of microarray:

cDNA Microarray

The spotted arrays are created by the deposition of concentrated solution of double-stranded DNA onto a solid support, using robotic pins [11, 12].

Oligonucleotide Microarray

Oligonucleotides are shorter sequences; usually 16–20 bp in length. Specific oligonucleotides synthesized in a predetermined spatial orientation on a solid surface using a technique called photolithography generate oligonucleotide arrays. Affeymatrix, the pioneer of this technology, have come up with a variety of commercially available arrays representing different organisms [13]. Sometimes the oligonucleotides are deposited onto glass slides by spotting or using miniature devices similar to ink jet printers. The oligonucleotides density that can be achieved on such arrays is quite high, with recent arrays representing 12,000 sequences at 16–20 oligomers per sequence for a total of 192,000–240,000 oligonucleotides per chip.

Many free and commercial software packages are now available to analyze microarray data sets, although it is still difficult to find a single complete software package that answers all functional-genomics questions. As the field is still young, when developing a bioinformatics analysis pipeline, it is more important to have a good understanding of both the biology involved and the analytical techniques rather than having the right software. Although many bioinformatics companies sell software that assists in microarray analysis, there are several freely available software packages that can be used to perform the analytical techniques. Only the important softwares are listed in Table 1.

Table 1 List of important free softwares available for microarray data analysis

Software name	Functions performed	Source
TM4 (MeV)	MultiExperiment Viewer (MeV) is a Java application designed to allow the analysis of microarray data to identify patterns of gene expression and differentially expressed genes	http://www.tm4.org/
EDGE	EDGE (Extraction of Differential Gene Expression) is an open source, point-and-click software program for the significant analysis of DNA microarray experiments. EDGE can perform both standard and time course differential expression analysis	http://faculty.washington.edu/jstorey/edge
R	R is a language and environment for statistical computing and graphics	http://cran.at.r-project.org/
CYBER-T	Web interface for *t* test, regularized *t* test, etc.	http://visitor.ics.uci.edu/genex/cybert/
FiRe	FiRe (Find Regulons) is an Excel® macro that quickly survey microarray data by establishing lists of "interesting" candidate genes that follow a given pattern of mRNA accumulation. Genes are selected depending on their fold-change ratios over different experimental conditions	http://www.unifr.ch/plantbio/FiRe/FiRe_2.2.xls
Cluster, TreeView	Standard for hierarchical clustering and viewing dendrograms and also creates self-organizing maps and performs principal components analysis	http://rana.lbl.gov/EisenSoftware
GeneCluster2.0	This software is used for constructing self-organizing maps. The latest version now also finds nearest neighbors and performs other supervised methods. Written in Java, this program can essentially run under any computer operating system	http://www.genome.wi.mit.edu/cancer/software/genecluster2
MultiExpression Viewer	Creates self-organizing maps and performs hierarchical clustering, as well as finding principal components. This package also includes a component for support vector machines, but at present offers little for documentation. The software is written in Java, and a license for the source code of the software is also available	http://www.tigr.org/software
MAExplorer	Performs many aspects of microarray processing, including the raw image analysis. It contains few analytical techniques, including hierarchical clustering. The software is written in Java, and the source code is freely available for modification	http://maexplorer.sourceforge.net/
RELNET	Creates relevance networks. The software is written in Java, and a license for the source code is also available	http://www.chip.org/relnet

Plant–Pathogen Interaction

Plant–pathogen interactions have been studied comprehensively over the years from both the plant and the pathogen perspectives. In each type of host–pathogen interaction, precise communication occurs between the plant (host) and the invading pathogen [1, 14, 15]. Plants serve as host for vast numbers of parasites such as pathogenic fungi, oomycetes, bacteria, viruses, nematodes, and insects [16]. During compatible interactions, the plant is unable to mount an effective anti-infectious defense response, allowing the pathogen to complete its life cycle [16]. In incompatible interaction, the plant triggers a series of complex defense responses against pathogenic interaction [14] to prevent pathogen growth in the plant. In these interactions, pathogen activity aims at colonizing the host and utilizing its resources while the plant adapts itself to detect the presence of pathogen and to respond with antimicrobial defense and other stress response [9].

Generally, there are two types of defenses induced in plants interacting with pathogens; local and systemic defense responses [14, 17]. Hypersensitive response (HR) is a type of local response that plants build up rapidly against the pathogen leading to active production of

reactive oxygen species (ROS) and localized cell death [14]. Hypersensitive response fails in the case when the virulent pathogen is necrotrophic, i.e., obtains nutrient from dead cells [17]. The important features of the local response are pathogen recognition, amplification of pathogenesis related (PR) proteins, and expression of the genes related to plant defense response [17].

A systematic or long-term response elevates the level of salicylic acid (SA), nitric oxide (NO), ethylene, jasmonic acid (JA), calcium and other ion fluxes and also protein kinases, which in-turn activates many downstream processes [9, 18, 19]. Systemic host responses are of two subtypes; systemic acquired resistance (SAR) and induced systemic resistance (ISR) and they share two components: elevated production of certain antimicrobial compounds and ability of defense activation machinery so that antimicrobial responses are activated more strongly in response to subsequent infection [20, 21].

DNA Microarrays to Study Plant–Pathogen Interaction

Over the last decade, microarray technology has proven to be an essential tool for discovery of genes related to plant defense and for giving comprehensive picture of global expression profiles in plants upon attack by pathogens. Using microarray, researchers have gained novel informations about plant–pathogen interactions.

Maleck et al. [22] have applied microarray technology to provide a comprehensive description of the SAR genes from *Arabidopsis thaliana*. They constructed microarray chip with 10,000 expressed sequence tags (ESTs) representing 7,000 genes (30% of all *Arabidopsis* genes). Gene expression changes of 14 different conditions related to SAR generated by chemical or biological means were examined including the study with plant mutants. Comparison of the gene expression profile of all the 14 experiments resulted in the identification of 413 ESTs (approximately 300 genes, many of which are novel) that appeared to be associated with SAR. Using different clustering algorithms, groups of genes with common regulation patterns (regulons) were derived [22]. The regulon containing PR-1, a reliable marker gene for SAR in *A. thaliana*, contains known PR genes and novel genes that functions during SAR and disease resistance. The induction of PR-1 is under the control of NPR1 [Nonexpressor of pathogenesis-related (PR) genes 1] protein which interacts with members of the TGA family of basic leucine zipper (TGA-bZIP) transcription factors. The promoter of the Arabidopsis PR-1 gene contains a binding site for the TGA-bZIP factors (the sequence TGACG) that serves as the positive cis acting element for SAR induction [23]. Thus, it was expected that all genes of the PR-1 regulon would contain a TGA-bZIP binding site in their promoters. However, Maleck et al. [22] found that TGA-bZIP recognition site is not present in each and every PR-1 regulon. With the aid of microarray analysis Maleck et al. identified a common promoter element called W box (WRKY factor binding site, the sequence TTGAC); a major sequence element in the promoters of genes co-regulated with PR-1. The analysis with DNA microarray showed that the PR-1 gene is regulated by three transcription factors; a TGA-bZIP factor, an unknown transcription factor that activate the transcription, and a WRKY factor that represses the transcription. WRKY factor could act together with other types of transcription factors to achieve precise regulation of gene expression during SAR. Maleck et al. [22] proposed that PR-1 regulon genes may be co-repressed by WRKY factors and during SAR these genes would be de-repressed. This microarray analysis results extend expression profiling to define regulatory networks and gene discovery in plants.

A path-breaking finding that induction of protein secretory pathway is required for SAR was carried out by Wang et al. [24] utilizing microarray, based primarily on the aforementioned findings. To identify additional NPR1 target genes, Wang et al. [25] used the 35S::NPR1-GR transgenic line generated in the npr1-3 mutant where nuclear translocation of NPR1-GR (GR, glucocorticoid receptor) required not only SA but also dexamethasone (Dex). Treatment of 35S::NPR1-GR plants first with SA and then with Dex specifically activated NPR1 target genes [24]. Using Affymetrix GeneChips (8200 genes), they identified putative NPR1 primary target genes by comparing transcriptional profiles of NPR1 and NPR1/35S::NPR1-GR that were both treated with SA and then Dex. Induced genes clearly fell into two categories; one group contained genes known to be involved in defense, including several PR genes, while the other group encoded members of the protein secretory pathway (most of which are endoplasmic reticulum localized proteins) [24]. For the first time, Wang et al. [24] provided genetic evidence that during SAR, there is a massive buildup of PR proteins in vacuoles and the apoplast and to ensure proper folding, modification, and transport of these PR proteins, a coordinated upregulation in the protein secretory machinery is required.

Gene expression profiling by microarray analysis has demonstrated a substantial crosstalk between different defence signaling pathways. Expression profiling of 2,375 selected genes were carried out by cDNA microarray in *A. thaliana* after inoculation with an incompatible fungal pathogen *Alternaria brassicicola,* or treatment with the defense-related signaling molecules including ethylene, methyl jasmonate (MJ), and salicylic acid (SA) [26]. Differential expression of 705 mRNAs was observed in

response to one or more of the treatments, including known and putative defense-related genes and 106 genes with no previously described function or homology. In leaf tissue inoculated with *A. brassicicola*, 168 mRNAs were upregulated, whereas 39 mRNAs were downregulated. After treatment with ethylene, MJ, and SA, the number of mRNAs that were highly upregulated (>2.5-fold) were 55, 221, and 192, respectively. A coordinated defense response was observed, including 169 mRNAs regulated by multiple treatments/defense pathways. The highest number of differentially expressed genes was found after treatments with SA and MJ. Moreover, 50% of the genes induced by ethylene treatment were also induced by MJ treatment. These results demonstrated that a substantial network of regulatory interactions exists and that significant interaction occurs among the different defense signaling pathways, especially between the SA and MJ pathways, which were previously believed to act in an antagonistic mode. Salzman et al. [27] conducted a large-scale study of gene expression in sorghum in response to the signaling compounds SA, MJ, and the ethylene precursor aminocyclopropane carboxylic acid using a microarray containing 12,982 nonredundant elements. Numerous gene clusters were identified in which expression was correlated with particular signaling compound and tissue combinations. Many genes previously identified in defense response responded to the treatments, including numerous pathogenesis-related genes and most members of the phenylpropanoid pathway, and several other genes that may represent novel activities or pathways. Genes of the octadecanoic acid pathway of jasmonic acid (JA) synthesis were induced by SA as well as by MJ. Measurement of JA content confirmed that increased SA could lead to increased endogenous JA production. Comparison of responses to SA, MJ, and combined SA + MJ revealed patterns of one-way and mutual antagonisms, as well as synergistic effects on regulation of some genes [27]. This shows that crosstalk and fine-tuning of different defence pathways are vital for enabling the plant to build up appropriate defence responses without draining energy resources to unsustainable levels. The discovery of regulatory defense signaling networks by microarrays has demonstrated that ultimately genes and their products, and not pathways are controlled by signaling [27].

The microarray profiling has also been used to examine gene expression of the biotrophic fungus *Blumeria graminis* f. sp. *hordei* during infection on barley [28, 29]. With the help of published cDNA sequences [30], the microarray containing 2,027 unigenes was used to study *Blumeria*–barley interaction. In this study, the mRNA extracts were used from four developmental stages prior to penetration on the host by the pathogen, and four stages thereafter. Contrasting expression patterns of genes encoding enzymes in various primary metabolic pathways were observed. At the onset of infection, lipid catabolism genes were highly upregulated. As the infection progressed, the expression of these genes gradually decreased implying that lipids are dominant carbon storage source for germination of fungal spores. This result matches with previous findings in other fungal pathogens that intact lipid catabolic pathways are required for germination and fungal pathogenicity [31–34]. The results and conclusions from these studies help in understanding the primary metabolism of the hosts during infection.

Global gene expression analyses during plant defence responses have identified new physiological processes involved in induced defence responses. Scheideler et al. [35] used cDNA arrays comprising 13,000 unique ESTs from Arabidopsis leaves after infection with the bacterial biotrophic pathogen *Pseudomonas syringe*. They observed expression change from housekeeping to defence metabolism, showing an increased demand for energy and biosynthetic capacity in plants fighting off a pathogen attack [35]. Differential regulation patterns were observed on the genes encoding enzymes in glycolysis, the Krebs cycle, the pentose phosphate pathway, the biosynthesis of aromatic amino acids, phenylpropanoids, and ethylene [35]. Furthermore, the results showed potentially important changes in areas of metabolism, such as the glyoxylate metabolism, hitherto not suspected to be components of plant defense. Likewise, genes for the β-oxidation pathway of fatty acids in Arabidopsis were upregulated in both local and systemic tissue when plants were inoculated with the incompatible fungus *A. brassicicola* [26]. Apart from fatty acid metabolism, this pathway is also important for the synthesis of JA during plant defence, an essential contributor for resistance against this necrotrophic pathogen [2].

Expression profiling is highly cell-type-specific and results are affected by the question, whether whole organs (e.g., leaves) have been used for RNA isolation (as done in the majority of studies), or whether cells have been isolated from specific organs and used for this purpose. In case of whole organs, expression profiles for particular genes get leveled out across different cell and tissue types. To overcome this problem, Gjetting et al. [36] for the first time microextracted mRNA from *B. graminis* f. sp. *hordei*-infected cells, papilla-containing penetration-resistant cells, and unattacked cells of barley leaves 18 h after inoculation and carried out cDNA array analysis. They used Gatersleben barley PGRC1 10,000 cDNA arrays (10 K array) for this purpose [37]. Gjetting et al. successfully obtained separate gene expression profiles for specific mildew-resistant and -infected barley cells. Analysis of the differentially expressed genes showed that 46 genes were upregulated only in samples from infected cells, 98 genes were upregulated only in resistant cell samples, and 54

genes were upregulated in both infected and resistant cell samples [36]. The clear separation between control, resistant, and infected samples indicated that (i) a large number of genes were induced or repressed and (ii) affected genes displayed large changes in expression. For the first time, Gjetting et al. identified candidate genes specifically regulated in infected host cells during haustorium formation and establishment of biotrophy. Catoni et al. [38] performed a comparative analysis of expression profiling in shoots and roots of tomato systemically infected by tomato spotted wilt virus (TSWV). Tom2 12K oligonucleotide-based tomato array (available from Boyce Thompson Institute for Plant Research) was used for this purpose. Microarray analysis of 14 days post-inoculated roots and shoots revealed that the number of genes regulated in shoots is approximately twice that regulated in roots. In the shoots, genes related to defense and signal transduction were induced, while genes related to primary, secondary, as well as amino acid metabolism were repressed [38]. On the contrary, in roots, expression of genes involved in signal transduction, primary metabolism, and amino acid metabolism (except for those involved in synthesis of secondary compounds) were unaltered by TSWV infection. Also, in roots, genes involved in biotic stress were induced and those associated to the response to abiotic stress were repressed. All these results indicate organ-specific transcriptional responses, although the virus was present in similar concentration in both the organs [38].

Non-host resistance, a rarely studied defence phenomenon, was believed to be genetically complex of the fact that activation of any specific defense component may not be sufficient to render a plant resistance reaction. Microarray experiments played a key role in delineating the molecular mechanism of non-host resistance. Zellerhof et al. [39] studied the transcriptional responses of one particular genotype of barley (*Hordeum vulgare* subsp. *vulgare* 'Ingrid') to three different pairs of adapted (host) and non-adapted (non-host) isolates of fungal pathogens, which belong to the genera *Blumeria* (powdery mildew), *Puccinia* (rust), and *Magnaporthe* (blast). They used the barley PGRC1 array carrying 10,000 spotted cDNAs [37]. Non-host resistance against each of these pathogens was associated with changes in transcript abundance of distinct sets of non-host-specific genes, although general (not non-host-associated) transcriptional responses to the different pathogens overlapped considerably [39]. The powdery mildew- and blast-induced differences in transcript abundance between host and non-host interactions were significantly correlated with differences between a near-isogenic pair of barley lines that carry either the Mlo wild-type allele or the mutated Mlo5 allele, which mediates basal resistance to powdery mildew [39]. Moreover, they found similar patterns of overrepresented and underrepresented functional categories of genes during the interactions of barley with the different host or non-host pathogens. Their results suggest that non-host resistance and basal host defense of barley are functionally related and that non-host resistance to different fungal pathogens is associated with more robust regulation of complex but largely non-overlapping sets of pathogen-responsive genes involved in similar metabolic or signaling pathways. Zhou et al. [40] studied the molecular mechanisms underlying hypersensitive response (HR) of rice to its bacterial pathogen, *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*) mediated by a non-host maize R gene *Rxo1*, using a microarray experiment and a pair of transgenic (9804-*Rxo1*) and non-transgenic (9804) rice lines. Affymetrix Genechips® Rice Genome Array chips, which contain 51,279 transcripts from two rice cultivars was used for this experiment. They detected 2,450 and 1,950 differentially regulated genes (DRGs) in 9804-*Rxo1* and 9804 using stringent statistical conditions. The difference between 9804-*Rxo1* and 9804 in expression patterns of these up- or downregulated genes was very striking [40]. Of the 1,239 and 963 upregulated genes in 9804-*Rxo1* and 9804 induced by *Xoc*, only 143 genes were in common between the transgenic line and its recipient. Similarly, of the 1,211 and 987 downregulated genes in 9804-*Rxo1* and 9804 induced by *Xoc*, 83 genes were commonly repressed in both the transgenic line and its recipient [40]. In particular, 107 genes were regulated in opposite directions between 9804-*Rxo1* and 9804, including 61 genes upregulated in 9804-*Rxo1* but downregulated in 9804 and 46 genes down-regulated in 9804-*Rxo1* but upregulated in 9804, respectively [40]. Analysis of all the DRGs indicated that *Rxo1* appeared to function in the very early step of the interaction between rice and *Xoc*, and could specifically activate large numbers of genes involved in signaling pathways leading to HR and some basal defensive pathways such as SA and ET pathways. In the former case, Rxo1 appeared to differ from the typical host R genes in that it could lead to HR without activating NDR1 (non-race-specific disease resistance 1) [40]. This study explored the molecular mechanism of the non-host resistance of rice mediated by *Rxo1* and provided useful information to understand the evolution of plant resistance genes.

Microarray technology not only identifies the signal transduction pathways induced by the pathogen, but also identifies genes that are specifically induced by the pathogen to support the infection process, namely the host factors used by viruses. Senthil et al. [41] constructed EST microarray derived from potato cDNA libraries to analyze expression profile in *Nicotiana benthamiana* to the biotic stress induced by Impatiens necrotic spot virus (INSV); a plant virus that replicates in the host cytoplasm. The

Table 2 A summary of important defense-related experiments using DNA microarrays

Host plant	Interacting pathogen	No. of genes arrayed in microarray chip	No. of genes induced/ repressed	Reference no.
A. thaliana	*Alternaria brassicicola*	2,375	100	[26]
A. thaliana	Phytophthora infestans	11,000	54	[50]
A. thaliana	*Pseudomonas syringae*	8,000	2338	[51]
A. thaliana	Tobacco mosaic virus	10,000	68	[52]
A. thaliana	*Blumeria graminis* f. sp. hordei	11,500	89	[53]
A. thaliana	Cucumber mosaic virus	*Arabidopsis* whole genome	444	[54]
A. thaliana	*Erysiphe cichoracearum*	11500	14	[53]
A. thaliana	Aphid (*Myzus persicae*)	*Arabidopsis* whole genome	2181	[55]
A. thaliana	Cabbage aphid (*Brevicoryne brassicae*)	26,604	1133	[56]
A. thaliana	Plum pox virus	22,810	7151	[57]
Arachis hypogaea (Peanut)	*Cercosporidium personatum* (Leaf spot disease)	384	121	[58]
Brassica napus (Canola)	*Sclerotinia sclerotiorum*	26000	2233	[59]
B. napus	*Alternaria brassicicola*	2,375	75	[60]
Glycine max L.	*Phytophthora sojae*	4,896	1009	[61]
G. max L.	*Pseudomonas syringae*	27,648	3897	[62]
G. max	*Phakopsora pachyrhizi* (Rust)	37,500	5107	[63]
G. max	Soybean mosaic virus	18613	446	[64, 65]
G. max	*Popillia japonica* (Japanese beetle)	35,000	3062	[66]
G. max	*Bradyrhizobium japonicum*	36,760	6555	[67]
G. max cv. Dowling	*Aphis glycines* cv. Williams 82	18,000	140	[68]
Hordeum vulgare	*Blumeria graminis* (Powdery mildew)	3,128	311	[69]
H. vulgare	*Polymyxa graminis Polymyxa betae*	14,000	13	[70]
		14,000	20	
H. vulgare	*Rhopalosiphum padi* (Aphid)	21,439	497	[71]
Hordeum vulgare (barley)	*Puccinia hordei*	15,000	1,410	[72]
Lolium multiflorum Lam (Italian ryegrass)	*Xanthomonas translucens* pv. *graminis*	9,990	158	[73]
Lens esculentum	*Pseudomonas syringae*	500	156	[74]
Lycopersicon esculentum L.	*X. campestris* pv. *vesicatoria*	1,152	426	[75]
Manihot esculenta L. (Cassava)	*X. axonopodis* pv. *manihotis*	5,700	199	[76]
Nicotiana attenuate	*Manduca sexta*	11,243	754	[77, 78]
Nicotiana benthamiana	Enveloped viruses	15,264	4165	[41]
Picea sitchensis (Sitka spruce)	*Choristoneura occidentalis* (Spruce budworms)	5,500	3490	[79]
P. sitchensis	*Pissodes strobe* (White pine weevils)	5,500	2382	[79]
P. sitchensis	*Mechnical wounding*	5,500	3089	[79]
Populus trichocarpa x *deltoides* (Hybrid poplar)	*Malacosoma disstria* (Forest tent caterpillars)	15,496	1728	[80]
P. trichocarpa x *P. deltoides*	*M. laricipopulina* (Rust)	28,000	1055	[81]
Solanum nigrum	*Manduca sexta*	11,243	754	[77]
Solanum tuberosum L.	*Phytophthora infestans*	7,680	643	[82]
S. tuberosum L.	*Leptinotarsa decemlineata* (Colorado potato beetle)	11,421	127	[83]
S. tuberosum L.	Potato virus Y	10,000	2132	[84]
Triticum aestivum	*Powdery mildew*	3,128	311	[69, 85]
Vitis vinifera L. (Grape.)	*Uncinula necator* (Powdery mildew) and *Plasmopara viticola* (Downy mildew)	2,712	121	[86]

microarray analysis revealed that INSV-induced expression of small heat-shock proteins genes to high levels (HSP18, HSP20, HSP70). Earlier reports (with different techniques) involving potyviruses and tobamoviruses [42–44] supported the finding that induced expression of HSPs are associated with plant virus replication. Activating HSPs, which have been shown to play a direct role in viral transcription complexes [45], is a specific viral function ensuring proper synthesis of viral proteins and virions. Carr et al. [46] showed that the expression of HSP101 and HSP70 was independent of the SA and JA defense signaling pathways in *A. thaliana* during Oilseed rape mosaic virus (ORMV) infection, confirming that ORMV activates the expression of HSP. RNA1 of Pea early browning virus (PEBV) alone was responsible for the induction of HSP70 expression in pea cotyledons [44]. Several significant microarray experiments has been carried out [47–49], providing information about the plant genes that are modulated by viruses.

Till date, hundreds of microarray experiments have been successfully carried out in the area of molecular plant–microbe interaction, focusing mainly on the mechanisms controlling plant disease resistance, crosstalk among the signaling pathways involved, and the strategies used by the pathogens to suppress the defense. However, as space is limited, it is not possible to discuss all these interactions; Table 2 gives a summary of the important experiments involving plant–pathogen interaction using DNA microarrays. Biological experimenters should interpret microarray data carefully as different laboratories use different platforms and different algorithms to decide up- or down-regulation of transcripts. Microarray data should be validated by secondary methods such as Northern hybridization or real time PCR. In majority of the examples described in this review, the microarray data were confirmed either by Northern hybridization method or by Real time PCR method. Absence of a unified “language” for exchange of microarray data between different laboratories prompted the “Microarray Gene Expression Data Society” (MGED) to develop guidelines for the publication of DNA microarray data [87]. MGED also develop a Microarray Markup Language to provide a standard platform for submitting and analyzing the microarray expression data generated by different laboratories around the world [87].

Future Prospects

With the experiments of plant–pathogen interaction completed to date, we can truly consider microarray as a mature platform for gene expression analysis in plant–pathogen interaction. Till date, microarray technology has been used in the identification of regulatory genes, end-point defence genes, to understand the role of particular transcription factor, as well as to understand the signal transduction processes underlying disease resistance and its intimate links to other physiological pathways. The gene expression profiling can be used as a tool for the study of effect of starvation and stress condition. Sequencing projects will help in the construction of the ESTs and give better understanding about the results. In future, microarray technology can have its fruitful application with more in-depth studies on simultaneous profiling of plant/pathogen gene expression and on the influence of multiple environmental factors on plants. The detailed information regarding the plant defense system will be known with more microarray experiments. Microarray containing the full complement of *Arabidopsis* genes will provide a more complete analysis. Similarly, the microarray experiments developed for crop plants will provide important information. Recently, direct sequencing of transcripts by high-throughput sequencing technologies (RNA-Seq) has become an additional alternative to microarrays. RNA-Seq does not depend on genome annotation for prior probe selection and avoids biases introduced during hybridization of microarrays [88]. On the other hand, RNA-Seq poses novel algorithmic and logistic challenges, and current wet-lab RNA-Seq strategies require lengthy library preparation procedures [88]. Therefore, RNA-Seq is the method of choice in projects using non-model organisms and for transcript discovery and genome annotation [88]. Because of their robust sample processing and analysis pipelines, microarrays are the choice for projects that involve large numbers of samples for profiling transcripts in model organisms with well-annotated genomes [88]. A symbiotic relationship between microarray technology and high-throughput sequencing in the future will enable new questions to be addressed in the area of plant–pathogen interaction.

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