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Comparative microarray data analysis of *Arabidopsis* genome during interaction with a mutualistic and a pathogenic bacteria

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Abstract

Plants are in continuous interaction with both mutualistic and pathogenic microorganisms, particularly in the rhizosphere. Arabidopsis has served as an excellent model plant in a variety of experiments to determine the details and nature of such relationships. Studies involving transcriptome profiling of *Arabidopsis thaliana* in response to pathogenic and beneficial bacterial infection are available, each focusing primarily on defense related and plant growth promotion related genetic component respectively. In an attempt to decipher the difference in responses of plants to these two types of bacteria, we resorted to genome wide comparative analysis both when it was exposed to a foe and a friend. Publically accessible web based array data emanating from Arabidopsis responses to *Pseudomonas syringae* pv. tomato DC 3000 (Pst) a virulent pathogen that causes disease on tomato and Arabidopsis and *Burkholderia phytofirmans* Ps JN, a growth promoting rhizobacteria were used for the comparative approach using bioinformatics tools including GEO 2R, TAIR etc. The results, although, contained regulated genes common in both treatments, the differentially regulated genes unique to each data set predominated the common genes. The results clearly indicated that different sets of Arabidopsis genes were regulated when treated with pathogenic and mutualistic bacteria. Differences were also evident at pathways, cellular processes and the molecular function level. The findings call for a comprehensive and detailed analysis of those genes showing a dissimilar trend as far as changes in their expression pattern is concerned.

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Introduction

Plants do not live on an island isolated from other living creatures rather they are in continuous interaction with their neighboring breathing partners particularly the microorganisms. On spatial basis the relationships between the plants and microbes could either be found in the phylosphere or rhizosphere. Still nature of the association provides another pivot for classification. On such basis the interactions may result in pathogenic, mutualistic or neutral relationships (Singh *et al.,* 2004). The pathogenesis hampers growth and development of plants mainly through production of phytotoxins, contesting for nutrients and limiting or inhibiting the beneficial impacts of other microorganisms. Neutralism, on the other hand, brings no harm or benefit to the interacting partners, while mutualism unlike pathogenesis ends in benefits to both plants and the microbes. The diverse and complex plant associated microbes are, therefore sometimes, referred to as second plant genome, which are not only of prime importance for higher crop yields but also from view point of environment.

Irrespective of the nature of the microbe, the interaction brings about changes in the expression pattern of the genes of host plant. These changes in turn decide not only the survival fate of host but also of the microorganism, besides determining the type of association. A plethora of research work therefore looks, among others, to focus on the inherent capabilities of the plant to cater pathogen attack. Similarly the underlying host genetic components in a mutualistic scenario are fairly well investigated particularly in case of Rhizobia-Legume symbiosis. However, another class of beneficial bacteria viz Plant Growth Promoting Bacteria (PGPB) has attained little attention compared to Rhizobia and pathogenic bacteria. Understanding biotic environment of the plant and probing its effects on the host is hence important both in terms of sustainable disease management and increased crop productivity.

In a plant pathogen paradigm, the host tries to circumvent the attacking microbe by restricting its growth; however, such attempts are not apparent when exposed to a beneficial microorganism. These observations fully support the notion that plants have the ability to discriminate between a foe and a friend. How the plants differentiate between the two is largely undefined till recently. Comparing gene expression alterations upon exposure to a beneficial and a pathogenic one might hint towards solving the puzzle.

Plant genetic research gained a real boast upon completion and annotation of the *Arabidopsis thaliana* genome (Arabidopsis, 2000). One of the featured achievements made possible after the said genome sequencing was to look at the whole genome expression profile patterns particularly under biotic stress conditions. Such profiling efforts ultimately lead to unveil gene functions, their categorization and placement into different biological networks (Dupl'áková *et al.,* 2007).

Gene expression analysis technologies revealing expression levels of individual genes are in vogue for quite some time. Although accurate and reliable, the techniques are unsuited and impractical when dealing with thousands of genes. DNA microarray presents solution to this enigma by facilitating primarily global expression and Single Nucleotide Polymorphism (SNP) analysis (Heller, 2002). The analysis has thus opened new vistas of research helping in identifying, new genes of plant involved in interaction with microbes, co-regulated genes and even to reveal interactions between different signaling pathways (Harmer and Kay, 2000; Kazan *et al.,* 2001).

Pseudomonas syringae, a common plant pathogen with a wide host range, cause disease symptoms ranging from leaf spots to stem cankers (Hirano and Upper 2000). For studying the plant pathogen interaction, *P. syringae* pv. tomato (Pst) strain DC 3000 and *Arabidopsis thaliana* are considered model system. This pathogenic strain causes necrotic lesions in susceptible tomato and Arabidopsis plants (Katagiri *et al.,* 2002; Whalen *et al.,* 1991).

Unlike *P. syringae*, *Burkholderia phytofirmans* Ps JNP is known for its growth promoting effects on different crops particularly Tomato, Potato and Grapes (Compant *et al.,* 2005; Nowak *et al.,* 2002; Sessitsch *et al.,* 2005) beside enhancing resistance to low levels of pathogen (Ait Barka *et al.,* 2002).

Transcriptome profiling data concerning responses of plants genetic components upon challenge by pathogenic as well as mutualistic microbe is available; however, bulk of such studies target the plant pathogen interactions (Ditt *et al.,* 2006; Drogue *et al.,* 2014; Ghannam *et al.,* 2016; Gupta *et al.,* 2016; Postnikova and Nemchinov, 2012; Poupin María Josefina *et al.,* 2013a; Van Loon, 2007). Such interactions are not confined to plant-bacteria rather it encompass fungi; viruses etc. As far as investigations involving transcription level responses of plants upon their contact with beneficial microbes are concerned (Poupin María Josefina *et al.,* 2013a; Wang Y. *et al.,* 2005b; Wise *et al.,* 2007), its number is increasing, indicating importance of mutualism.

The availability of plant omics data from both pathogenic and mutualistic interaction perspective, and the realization that their comparative bioinformatics analysis has seldom been carried out, provided basis for undertaking such analysis. We hypothesized that the study would be helpful in revealing unique responses of plant genetic components in each of the above mentioned scenario

Utilizing the already published available microarray data emanating from exposure of *Arabidopsis thaliana* to *P. syringae* (Thilmony *et al.,* 2006*)* and *B. phytofirmans* (Poupin MJ. *et al.,* 2013b) we have tried to figure out the Arabidopsis genetic components whose expression levels have been altered upon inoculation of the said bacteria. A comparative genomic approach was then adopted to unfold the similarities and differences in the expression profile of plant when associated with a pathogenic or a beneficial microorganism. The analysis might help in deciphering the complexities of infection and mutualism.

Materials and methods

Sources of the present study

The array data used for comparison in this study pertain to two different works. In the first one , effects of a Plant Growth Promoting Bacteria (PGPB) on Arabidopsis thaliana were investigated (Poupin M. J. *et al.,* 2013b). The second publication highlighted the transcriptional response of Arabidopsis to a pathogenic bacteria *Pseudomonas syringae* tomato DC3000 (Thilmony *et al.,* 2006).

Both the array data were accessed through Gene Expression Omnibus (GEO), a repository at the National Center for Biotechnology Information (NCBI). GEO not only archives but also distributes freely, among others, the gene expression data generated by DNA microarray technology (Barrett and Edgar 2006).

Normalization and statistical analysis of Microarray data

GEO2R is a publically accessible web based tool (www.ncbi.nlm.nih.gov/geo/geo2r) designed to compare two or more set of samples in order to underline differentially expressed genes in given experimental conditions. GEO2R itself relies for array data analysis on Geoquery and LIMMA (Linear Model for Microarray Analysis) R packages from the Bioconductor, a R language program based open source software for genomic data analysis (Davis and Meltzer 2007, Smyth 2004).

Using GEO2R for the array analysis, we first pasted the GEO accession numbers of the microarray experiments mentioned above. As per instructions contained in the GEO2R, we defined groups as treated and control. Benjamini and Hochberg false discovery rate method (Benjamini and Hochberg, 1995) was used for multiple-testing corrections. The list of differentially expressed genes (P value ≤ 0.05) thus obtained for each experiment was then put to comparison with each other.

Mapman

MAPMAN is in use to functionally categorize sets of genes in a microarray data since 2004 (Thimm *et al.,* 2004). This tool puts thousands of Arabidopsis genes into a set of hierarchical functional categories (bins, subbins individual enzyme). The first tier of the said division is termed bin which, among others, includes categories like signaling, stress, secondary metabolism, hormone metabolism DNA, RNA, protein etc. The list of genes with altered expression values in each experiment were loaded on the MAPMAN tool to for further functional classification.

The Arabidopsis Information Resource (TAIR)

The Arabidopsis Information Resource (TAIR) www.arabidopsis.org/index.jsp is a widely used genome database and information resource for the scientific community involved in Arabidopsis research (Lamesch *et al.,* 2012). TAIR mainly focuses on integration of information from different data sources to abreast the research community with a comprehensive view of each Arabidopsis gene. One such attempt is to functionally annotate genes by collecting information about describing a gene's biological identity, molecular function, subcellular location etc. We, therefore, used this function of TAIR to describe the subcellular location of the differentially expressed genes in the two microarray data under investigation.

Results

To chalk out differences and similarities in *Arabidopsis thaliana* genetic components upon challenge by a Plant Growth Promoting Bacteria (PGPB) and a pathogen separately, the already published array data for the two interactions was analyzed.

The web based available microarray data in the Gene Express Omnibus (GEO) for *Arabidopsis thaliana* upon challenge by a Plant Growth-Promoting Bacterium *Burkholderia phytofirmans* Ps JN (Poupin MJ. *et al.,* 2013b) and plant pathogen *Pseudomonas syringae* pv. tomato DC3000 (Thilmony *et al.,* 2006) were explored primarily with the GEO2R tool.

Approximately two hundred and eight (208) Arabidopsis genes were found differentially regulated (p value 0.05) after the PGPR inoculation. Eighty three of these transcripts were found induced while the remaining exhibited repressed expression when compared to the control.

Similar analysis was performed to observe changes in Arabidopsis transcriptome upon challenge by the pathogenic bacteria *P. syringae* pv. tomato DC 3000. Out of total seven hundred sixty one genes (761) exhibiting altered mRNA expression levels, three hundred and ninety three (393) were up regulated while three hundred and sixty eight (368) were down regulated.

In order to decipher changes in the plant genome emanating specifically either in its interaction with a PGPB or pathogen, analyzed data from both arrays were put to further scrutiny using various bioinformatics tools.

Genes with alike and different regulation trend

Venny is an interactive tool for comparing data lists and visualizing them in the form of venn diagram (www.bioinfogp.cnb.csic.es/tools/venny). Utilizing Venny, we tried to figure out the genetic factors common to both array experiments. Such comparison between the lists of Arabidopsis regulated genes after interaction with a pathogenic and a beneficial bacterium revealed very few i.e. twenty five genes common to both lists. Further decrease in the number of common genetic factors was observed when induced/repressed genes in both data sets were put to comparison with like regulation trend genes. As opposed to 25, only three and four genes respectively for up-regulated vs upregulated and down-regulated vs downregulated trend were observed with alike regulation pattern (Fig. 1). Otherwise most of the transcripts showed unique regulation trend.

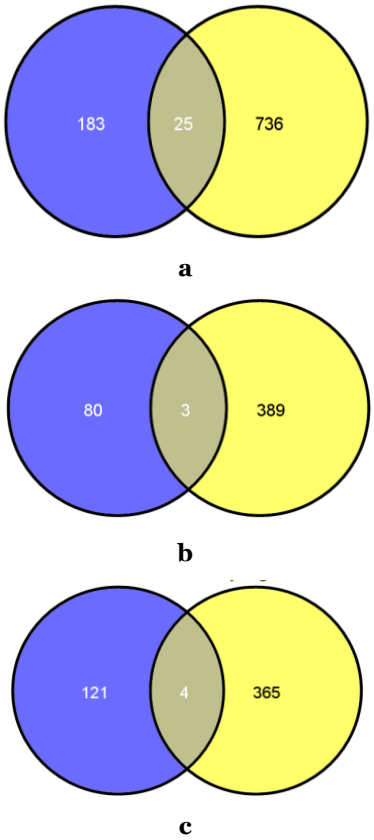


Fig. 1. Venn diagram showing a) Total number of differentially regulated genes b) Up regulated genes c) Down regulated genes in Arabidopsis interaction with a PGPB (blue) and a pathogen (yellow).

In an attempt to cluster the genes differentially expressed in both arrays in different pathways, we resorted to MAPMAN, a widely used microarray data analysis tool. However, no clear cut classification seen owing to the divergent processes these commonly regulated genes were involved in. For instance among the highly regulated genes, At1g73830 is a putative BHLH transcription factor which encodes the brassinosteroid signaling component BEE3 (BR-ENHANCED EXPRESSION 3). At 5g44680, on the other hand is a putative methyladenine glycosylase involved in the DNA repair. Both of these genes were found induced in the Arabidopsis interaction with the pathogen and repressed in the mutualistic scenario. Among the highly induced after pathogen exposure were a putative membrane protein of unknown function (At 5g66650) and a Toll-Interleukin-Resistance (TIR) domain-containing protein involved in the innate immune response (At 1g72900).

The number of genes falling in different MAPMAN bins is never the less illustrated in the table 1 which clearly shows the divergence.

Table 1. Number of differentially expressed genes common to both arrays and their placement in different MAPMAN bins.

Category	Elements
Major CHO metabolism	1
Hormone metabolism	2
Stress	1
Misc.	4
RNA	5
DNA	1
Sigalling	2
Transport	1
Not assigned	7

Besides the divergent pathways, the direction of regulation of these commonly regulated genes was quite opposite in one array data to the other, meaning thereby that transcripts repressed in pathogenic interaction were induced in the symbiotic scenario and vice versa. The heat map given in Fig. 2. Clearly illustrates this dichotomy.

Functional Categorization of Differentially regulated Genes

The regulated genes in the two microarray data were functionally categorized using microarray data analysis tool MAPMAN (Thimm *et al.*, 2004). For each of the array data set, MAPMAN based classification was carried out which were further compared to each other to underline the highly representative pathways in each case (Fig. 3).

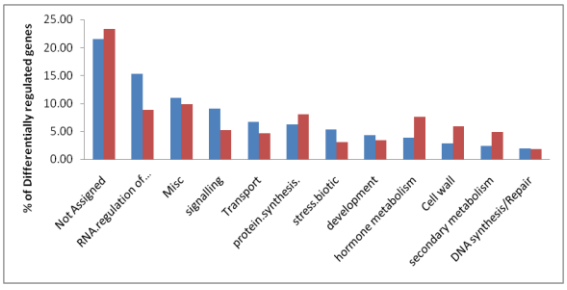
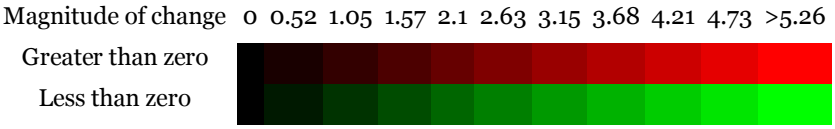


Fig. 3. Comparative sketch of differential regulation trend of genes falling in different MAPMAN bins. Red bars represent Arabidopsis (*P. syringae)* and blue Arabidopsis (*B. phytofirmans)* interaction.



Common genes	P. syringae	PGPR
At2g34620	-2.6	1.6
At5g44680	-3.1	1.4
At1g73830	-4.2	1.3
At1g35180	-3	1.3
At1g34640	-2.3	0.8
At1g58440	-1.7	0.5
At5g66650	4.9	-0.8
At2g29480	2.9	-0.8
At1g33110	2.4	-1.1
At1g69260	2.4	-1.1
At4g16690	2.4	-1.2
At2g46270	1.8	-1.2
At1g12240	2.2	-1.4
At2g29490	2.8	-1.5
At1g72900	3.1	-1.7
At1g06180	1.9	-1.8
At1g05680	3.1	-2.3
At5g54130	1.7	-2.5
At2g41800	2.8	0.9
At2g36080	1.4	0.8
At1g24625	2	0.7
At2g36970	-1.7	-1.2
At2g04795	-1.7	-1.4
At2g15020	-1.7	-1.8
At1g35140	-5.2	-1.9

Fig. 2. Differential regulation trend of genes common to mutualistic and pathogenic interaction. The heat maps generation resource was www.bbc.botany.utoronto.ca. The color scale represents log2 fold change.

Bulk of entries in both cases pertained to the not assigned bin. In relative terms, the classes significantly highly represented in the plant- PGPR array include, RNA regulation of transcription, Signaling and stress. Likewise, in a plant pathogen context, the highly representative bins were Cell wall, Secondary metabolism and Hormone metabolism.

RNA regulation of transcription

Expression levels of about 32 transcripts (>15% of the regulated genes) were found altered upon inoculation of Arabidopsis with *B. phytofirmans*. Nineteen of these genes depicted down regulation while the rest up-regulation trend. Looking at the sub bin level revealed that neither of the transcription factor (TF) family manifested all genes regulated in the single direction i.e. either induced or repressed. Rather a mix pattern was observed. For instance there were four TFs belonging to Basic Helix Loop Helix class (BHLH), three of them were repressed while one was induced. Similar findings were noticed for other TF classes. Pertinent to note that although the number of genes (67) with altered transcript levels was higher in the RNA bin as far as

Arabidopsis-pathogen array results are concerned, but its percentage to the total number of differentially regulated genes was only 8.8% which is quite less in relation to 15% observed in the array experiment.

At the sub bin level, most of the TF in the mutualistic association were related to C2H2 zinc finger family, C2C2(Zn) CO-like, Constans-like zinc finger family and Basic Helix-Loop-Helix family. However, different TF families like MYB domain transcription factor family, .AP2/EREBP, APETALA2/Ethylene-responsive element binding protein family, Basic Helix-Loop-Helix family and Homeobox transcription factor family dominated in plant pathogen interaction.

Signaling

Out of the total regulated genes, 9% and 5.3% belonged to the signaling category when Arabidopsis transcriptome was analyzed after challenge by a PGPR and pathogen respectively. Further scrutiny revealed that most of the genes are involved in calcium signaling and Receptor kinases leucine rich repeat class. Interestingly all elements in the calcium signaling were down regulated except at2g41090 upon infection of *B. phytofirmans* while all up regulated except at1g62480 when challenged by *P. syringae*. All LRR receptor kinases were, on the other hand, highly induced in the later interaction.

Stress biotic

In the comparative array analysis, the mutualism brought about alterations in the mRNA levels of greater portion of the regulated genes than the pathogenesis. The most important sub class emerging in both array data was Pathogenesis Related (PR) proteins, however, with opposite regulation trend. In case of mutualism, all were repressed while induced in context of pathogenesis.

Cell wall

Both in terms of number and percentage, substantial portion of cell wall proteins were affected in the *P. syringae* treated Arabidopsis plants. Few sub divisions of the cell wall category like cell wall modification proteins, cell wall proteins. AGPs and cell wall degradation pectatelyases and polygalacturonases stood out. Bulk of these genes were repressed rather than induced in this plant microbe interaction. No such clustering was possible in the other array primarily due to differential expression of few genes falling in divergent sub bins.

Hormone Metabolism

Another MAPMAN category where the pathogen affected more Arabidopsis genes by altering its expression than the PGPB (7.6% vs 3.8% of the differentially expressed genes) was hormone metabolism. Further narrowing the research to sub bin level exposed that most of these transcripts are related to auxin synthesis-degradation, ethylene synthesis-degradation, jasmonate synthesis-degradation, gibberellin synthesis-degradation and salicylic acid synthesis-degradation sub classes. The genes pertaining to Auxin were mostly down regulated, however only five of nineteen (at 3g12830, at 5g50760, at 1g44350, at 3g02875 and at 2g45210) were induced. Unlike Auxin, genes in the ethylene sub bin were mostly induced. Two of the genes were among those giving highest expression in terms of log fold change (at 2g30830 with 6.3 and at1g01480 with 4.28 LFC). Both are part of ethylene biosynthesis process. Similarly all transcripts in the jasmonate and salicylic acid synthesis degradation class were highly induced.

Secondary metabolism

The *B. phytofirmans* caused little changes in the genetic components of Arabidopsis found in the Secondary metabolism bin as compared to *P. syringae*. Sub bins like sulfur-containing glucosinolates synthesis, flavonoids anthocyanins and isoprenoids carotenoids were highly represented in plant pathogen interaction as against phenylpropanoid lignin biosynthesis sub category in context of the mutualistic association.

Sub cellular localization of genes

TAIR provides with the functional annotation/categorization function of the query gene(s). The output represents three terms viz. molecular functions,

biological processes, and subcellular compartments (GO Consortium, 2001. The cellular component terms identifies the subcellular compartments of a cell (e.g. plastid).

Taking advantage of cellular component information, the genes with altered expression in each of the array experiment were queried for their sub cellular localization.

The analysis showed that in the PGPB-Arabidopsis interaction, the genes were mostly concentrated in the cellular components like chloroplast, extracellular and plastids. The share of differentially regulated genes in these compartments upon challenge by *B. phytifirmans* was greater than observed for *P. syringae* infected plants. In the later interaction, genes with altered expression were chiefly localized in nucleus, plasma membrane, cytosol, cell wall and endoplasmic reticulum (ER). The difference in the localization pattern of the regulated genes indicates a clear cut divergence as far as Arabidopsis response to a mutualistic and a pathogenic bacterium is concerned (Fig. 4).

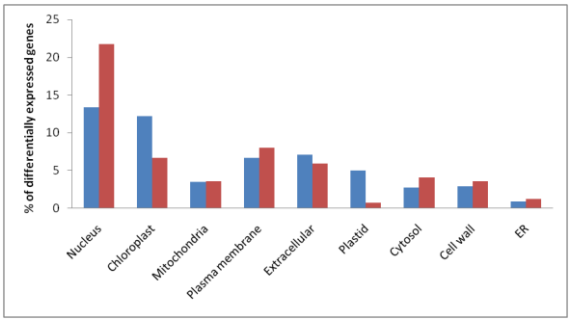


Fig. 4. Comparative sketch of sub cellular localization of differentially expressed genes. Red bars represent Arabidopsis (*P. syringae)* and blue Arabidopsis (*B. phytofirmans)* interaction.

Discussion

In the recent study we compared the Arabidopsis global transcriptome response to inoculation from a Plant Growth Promoting Bacteria *Burkholderia phytofirmans* Ps JN and a plant pathogen *Pseudomonas syringae* pv. tomato DC 3000. The available scientific literature provides us with the Arabidopsis global transcriptional changes both uponr pathogen (De Vos *et al.,* 2005; Lee *et al.,* 2009; Marathe *et al.,* 2004; Thilmony *et al.,* 2006) and PGPR (Cartieaux *et al.,* 2003; Wang Yanqing *et al.,* 2005a; Zhang *et al.,* 2007) challenge. However fragmented data is available focusing on their comparative analysis. Our analysis, in the first instance, helped to sort plant responses that were specific to either a PGPB or pathogen. The comparison between the significantly expressed transcripts of the two array data clearly demonstrated that very few (25) genes were commonly regulated, describing at the same time that very different sets of genes were regulated by the two different stimuli. The dichotomy in the expression pattern is further strengthened by the fact that even most of these twenty five genes exhibited different direction of regulation, meaning if up regulated in plant pathogen interaction, then down regulated in the plant association with the mutualistic bacteria and vice versa.

The categorization and clustering of the differentially expressed genes in both experiments further pointed towards the fact that very few pathways were equally represented in both types of plant microbe interaction. Otherwise unique trend prevailed here too. As pointed out in the results section that in the plant- PGPR array, the classes significantly highly represented include, RNA regulation of transcription, Signaling and stress while the highly representative bins in a plant pathogen context were Cell wall, Hormone metabolism and Secondary metabolism. Even at the sub bin level, the sub classes under each data differed significantly from each other. For example, in the main bin RNA regulation of transcription, different transcription factor families surfaced in each array data.

In addition to bin and sub bin level, significant differences were also observed between the two experiments at individual enzyme level. The case in point is the Pathogenesis Related (PR) proteins under the sub bin biotic stress and bin signaling.

In the mutualistic scenario three (at 5g58120, at 5g46450 and at 1g72900) out of four PR proteins were found to be TIR-NBS-LRR class putative disease resistance genes, all with repressed expression trend. These Nucleotide Binding Sites (NBS) and Leucine Rich Repeats (LRR) domains are characteristic features of Resistance (R) genes (Martin *et al.,* 2003) which play a crucial role in the second and more robust tier of plant innate immune response alias Effect or Triggered Immunity (ETI) (Jones and Dangl 2006). Contrary to that, the putative R genes were highly induced in the plant Pseudomonas interaction. The other class of PR proteins which were markedly affected by the pathogen infection was Plant Defensing Like proteins (PDF). PDF are small, basic peptides getting their name from structurally related defensing in other organisms, including humans (Thomma *et al.,* 2002)**.** The induction of both of these types of PR genes coincides with the nature of inoculation. Similar findings were recorded for other classes like secondary metabolism, hormone metabolism, cell wall etc.

Besides trend of gene expression and biological processes these differentially regulated genes were involved in, remarkable differences were also noticed as far as sub cellular localization of these transcripts is concerned. For the PGPR colonized plants, highest portion of expressed genes were localized in the nucleus. This pattern augments functional categorization scheme in the same case where the pathway, RNA regulation of transcription, was highly represented than in the pathogenic context.

In addition to the aspects discussed above, *P. syringae* inflicted dramatic reprograming in transcription both in terms of number of transcripts with altered expression levels and intensity of that change as compared to changes in Arabidopsis (*B. phytofirmans)* association.

In nutshell we can state that Arabidopsis responded very differently in terms of changes in the mRNA transcripts to mutualistic and pathogenic bacteria.

The results are helpful in determining the unique genetic components underlying in Arabidopsis interaction with a pathogen and a PGPR. Future comparisons involving many transcriptome studies might lead to better understanding of this complex relationship. Particular to mention are the Plant Growth promoting Bacteria, whose role as bio fertilizers and biocontrol agents to combat food security problem, prioritize them for future investigations.

Novelty Statement

Individual transcriptome profiling data of Arabidopsis upon challenge by a pathogen or mutualistic microbe is available; however, their comparative bioinformatics analysis has been seldom carried out. This work is an attempt in this direction.

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