Importance of omics approaches in plant-microbe interactions in plant disease control

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Abstract: The concept of omics-based technological approaches has promoted translational research by integrating knowledge from diverse areas to understand their dynamics by exploring the molecular mechanisms underlying various processes paving the way for further improvements in the crops quality by providing sound knowledge on controlling plant diseases. This area is not profoundly investigated within a decade and hence has become exceedingly important in modern times to be narrated as it has got potential for being utilized in crop improvement programs. In this review, the contributions of different omics technologies including genomics, transcriptomics, proteomics, and metabolomics in understanding and materializing the ways involved in the plant pathogen interaction (PPI) are discussed. Furthermore, opportunities, challenges, and perspectives of omics linked to signaling mechanisms that are significantly linked to plant-microbe interactions, have also been highlighted.

Keywords: Crop improvement; Omics; Pathogenesis; Plant-microbe interactions (PPI), Resistance

1. Introduction

The combat between pathogens and plants has been unending facing each other's pressure constantly to triumph over the other while enduring the constantly changing environment as well (Swarupa et al., 2016; Kumar et al., 2021a; Ramlal et al., Unpublished (a,b)). Microbes grow and flourish below ground, above ground as well as inside plants, and at the same time, plants host different microbes naturally showing both kinds of impacts viz positive and negative (Imam et al., 2016; Sharma et al., 2020). Several of these microorganisms cause various diseases when either their immunity is activated late or not triggered at all in plants including agronomically important crops leading to enormous economic losses that severely compromise crop productivity and yield (Macho and Zipfel, 2014; Ellouze et al., 2020; Gorshkov and Tsers, 2022). The microbes and plants face each other in a number of ways, sometimes having mutualistic relationships, such as biocontrol agents (Kumar et al., 2021b), arbuscular mycorrhizal associations (Mishra et al., 2018; Ellouze et al., 2018) and also in various other detrimental roles since their origin, while some others remain neutral. The field of plant-microbe interactions has always been a fascinating and emerging area of research and still, the complexities of their interactions largely remain unidentified and unexplored.

With the technological advancement and inclusion of several sophisticated high-throughput techniques, the concept of 'omics' is being utilized in deciphering and unraveling the intricacies that are involved in plant-pathogen interactions (PPI) (Bhadauria, 2016; Gomez-Casati et al., 2016; Singh and Kothari, 2017). This term encompasses all the processes that exist in biological systems and covers all the fundamental processes including transcriptomics, proteomics, and metabolomics along with other major omics that have proven to be helpful in unravelling the mysteries of complex processes underlying PPI. The omics-based approaches have led to the development and identification of genome-scale resources and promoted translational research by integrating knowledge to understand the PPI dynamics including the ecology of plant pathogens, molecular mechanisms and underlying principles of pathogenesis (Crandall et al., 2020). The field not only provided a means to investigate the related genomics, metagenomics, volatilomics, and spectranomics, but also worked out ways for improvement and development of resistance in crops and thereby proved to have an immense potential that can be utilized in crop breeding and improvement programs (Crandall et al., 2020). Simultaneously, this information on the characteristics of pathogenesis will provide useful insights on the emergence of diseases, ecology, and epidemiology of diseases, the occurrence of genetic changes, and underlying defensive mechanisms evolved in both plants and microbes because of co-evolution and their effective management practices (Macho and Zipfel, 2014; Ellouze et al., 2020; Crandall et al., 2020).

The current review provides an overview of the existing state of knowledge about the various branches of omics involved in identifying and elucidating the complexities of plant-pathogen interactions (PPI) and updates on the recent information that has been added to the various aspects of PPI currently form part of scientific discussion. Furthermore, the importance of omics-based approaches as applied to PPI in the light of recent researches are discussed that are supposed to unfold vistas for new research designs for effective management of plant diseases suited for commercial utilization. The various branches of omics are discussed as follows:

i. Genomics

The era of genomics started with the availability of genome sequences of the first two bacterial species in 1995 namely *Mycoplasma genitalium* (Fraser et al., 1995), and *Haemophilus influenzae* (Fleischmann et al., 1995), and simultaneously the first complete genome sequence for plant pathogenic bacteria, *Xylella fastidiosa* was made available in 2000 (Simpson et al., 2000). With the availability of such sequences, it was made possible for the researchers to dig more deeply into understanding the PP interactions and became a routinely and widely used laboratory methodology that aid in the understanding of their interactions (Xu and Wang, 2019). On a similar note, the availability of next or second (next-generation sequencing, NGS) and third-generation sequencing technologies is referred to as high-throughput DNA sequencing (HTS) approaches made (Xu and Wang, 2019; Aragona et al., 2022). So far, there are 126 plant pathogenic bacteria (Xu and Wang, 2019), and 191 fungal species whereas 61.3% of them cause diseases in food crops (Aylward et al., 2017) whose genome sequences are available. There are two primary components of genomics that play important role in identifying the ecology and health during plant-microbe interactions namely structural genomics which focuses on assigning and mapping the genes and markers onto the chromosomes and thereby constructs a physical map of the whole genome. While the other component, functional genomics integrates nucleotide (genomic) sequences with the transcriptomic information (transcripts produced by an organism) and proteomic data (encoded proteins) to describe the functions and interactions of a gene (Crandall et al., 2020). Furthermore, the other related fields include comparative and population genomics which involves the identification of conserved domains of structural motifs across the kingdoms and relates the functional aspects and phylogenomics describes the interrelations between species of a population and among different populations (Crandall et al., 2020). For instance, Wolfe and McDermott (1994) studied the population genetics of a pathosystem which included *Erysiphe graminis*

f. sp. *hordei* that infect the wild population of barley (*Horduem spontaneum* K. Koch.) (Wolfe and McDermott, 1994).

With the availability of genomic sequences, expressed sequence tags (ESTs), and microarray-based expression profiling, the responses of the plant-pathogens interactions have been characterized and elucidated in a comprehensive manner (Wan et al., 2002). Baldwin et al. (1999) identified 117 genes that showed alteration of mRNA expression in maize 6 h after different treatments with the fungal pathogen *Cochliobolus carbonum* using the DNA microarray (Baldwin et al., 1999). Metagenomics is yet another powerful tool that is used for the identification of microbial communities from a sample containing various microbes in order to know their taxonomy and functional roles. Moreover, this method can be used to distinguish between symptomatic and non-symptomatic microbes therefore, can be helpful in the diagnosis of plant diseases (Aragona et al., 2022). For instance, using the RNA-seq of tomato as the reference, the root microbiota was analyzed (Chialva et al., 2019).

i. Transcriptomics

Following the inception of functional genomics, transcriptomics is yet another 'omics' approach that boosted and revolutionized the understanding of the processes involved in PPI. For instance, various beneficial interactions like *Trichoderma*–*Arabidopsis*–*Pseudomonas syringae* & *Piriformospora indica*–barley–powdery and have found that the fungi as such have significantly no effects (in absence of pathogens) on the host until pathogens attack the hosts (Molitor et al., 2011; Brotman et al., 2012) and detrimental interactions such as *Verticilium dahliae* which infects roots of plants (Tan et al., 2009; Xu et al., 2011) or elicitation signaling upon recognition of pathogen-associated molecular patterns (PAMPs) with the involvement of defense-related hormones (jasmonic acid, salicylic acid, etc.) (Livaja et al., 2008; Schenk et al., 2012) during a bacterial attack in *Arabidopsis* have been analyzed using transcriptomics and observed that flagellin and lipopolysaccharide are common bacterial elicitors indicating both are involved in signaling transduction. In the case of herbivory, when *Arabidopsis* was fed with aphids and caterpillars, an array of genes was found to be both up-regulated and down-regulated (Schenk et al., 2012; Appel et al., 2014). Similar observations were found when a non-pathogenic root-colonizing bacterium, *Pseudomonas* induced systemic responses in *Arabidopsis* was obtained using transcriptomic data (Verhagen et al., 2007)

One of the subsets of this omics method is metatranscriptomics. It is an emerging field that explicitly focuses on characterizing the gene expression patterns displayed by microbial communities through sequencing of genes that are getting expressed. The widely used NGS platforms in metatranscriptomics analysis include the Genome Sequencer FLX system (Roche) and the Illumina Genome Analyzer IIx (Schenk et al., 2012). With the involvement of high throughput sequencing technology, it is made possible to understudy and identify isoforms, novel transcripts, alternative splice variants, and, as consequence, genomic variants using the whole transcriptome sequencing (Aragona et al., 2022) while bioinformatics provided an added advantage of analyzing the data simultaneously boosted to perform computational studies for understanding the PPI in more detail (Aragona et al., 2022).

i. Proteomics

Techniques like mass spectrometry, electrospray ionization, and matrix-assisted laser desorption/ionization (MALDI) along with the gel- (2D & 3D) & non-gel-based (LC, MudPIT, etc.) methods have increased the amount of data and helped in understanding the interactions at a proteomic level (Mehta et al., 2008; Quirino et al., 2010). There are various receptors and kinases which are involved and trigger signaling cascade upon confrontation with pathogens. Kinases such as MAP, calcium-dependent protein kinases (CDPKs), and receptor kinases (flagellin receptor FLS2) as soon as they perceive signals initiate downstream processes along with phosphorylation events (Mehta et al., 2008; Quirino et al., 2010).

i. Epigenomics

Epigenetics is an emerging area of research yet has revealed immense potential by widening the base of the genetics and refers to the changes which are stimuli-triggered followed by gene expression arising independently of changes in the underlying DNA sequences through the modifications in DNA methylation, histones, DNA silencing through non-coding RNAs (ncRNAs) and chromatin-remodelling (Gomez-Diaz et al., 2012). Recently, it has been shown that plants have both kinds of abilities to modify their constitution and makeup through inheritance via genetic or epigenetic ways, thereby adapting to the changing environmental conditions (Arnholdt-Schmitt, 2004; Madlung and Comai, 2004; Takeda and Paszkowski, 2006; Boyko and Kovalchuk, 2011). Being the host-pathogens interactions are dynamic in nature, there has been certain gaps still in this area, in what ways or how the epigenetics regulate or function in case of PPIs. Gomez-Diaz et al. (2012) reviewed the epigenetic changes that are to be involved in the PPIs.

i. Metabolomics

Plant metabolism (primary and specialized) is itself a complex process involving numerous mechanisms to promote plant growth and development. Specialized metabolism is generally involved during the recovery process from abiotic and/or biotic stresses. Therefore, this omics-based approach has also tremendously assisted in knowing the PPIs involving the host & microbe mechanisms. In the traditional method, morphological pieces of evidence were used to identify and differentiate between susceptible/resistant and diseased/non-diseased (primary screening), while molecular analysis includes identification of callose deposition at the infection site, and analyzing defense-related molecules like reactive oxygen species (ROS), etc. (Castro-Moretti et al., 2020).

Metabolites perform different functions during the plant–pathogen interactions such as surveillance against pathogen attack, signal transduction, enzyme regulation, cell-to-cell signaling, and anti-microbial activity (Vinayavekhin et al., 2010; Castro-Moretti et al., 2020). understand the dynamics of chemical compositions and their roles during PPIs, metabolomics that deal with the metabolites of key importance in a reaction occurring inside the plants/crops under typical physiological condition has played a pivotal role in deciphering the PPI states of the plants (Castro-Moretti et al., 2020).

Table 1. Important metabolites involved in the plant-microbe interactions envisioned in the metabolomics contexts.

Role	Molecule	Function	Secreted by	References
Attack	Coronatine	Effector	*Pseudomonas syringae*	Nomura et al., 2005; Geng et al., 2012
	phenylacetic acid	Toxin	*Rhizoctonia solani*	Drizou et al., 2017
	Spermine	Interruption of ROS	*Heterodera schachtii*	Li et al., 2019
	Sphingolipids	Required for appresorium	*Magnaporthe oryzae*	Hu et al., 2018

	extracellular polysaccharides	virulence factor	*Ralstonia solanacearum*	Milling et al, 2011
	Putrescine	virulence factor		Lowe-Power et al., 2017
	toxA	Toxin	*Pyreniphora tritici-repentis*	Manning et al, 2009
	Daidzein and genistein	Growth	Soybean (attracts *Pseudomsonas sojae*)	Morris et al., 1998
	Cochliophilin A	Growth	Soybean (attracts Aphanomyces cochlioides)	Tahara et al., 2001
Defence	Ethylene	cell signaling against rice blast disease	Rice	Helliwell et al., 2016, Yang et al., 2017; Tezuka et al., 2019
	methyl jasmonate			
	salicylic acid			
	quinic acid	defense against bacterial wilt	Tomato	Puupponen-Pimja et al., 2001; Koutelidakis et al., 2016; Zeiss et al., 2019; Wang et al., 2019
	eriodictyol, kaempferol			
	Hexoses			
	feruloyl-serotonin			
	R-linalool	defense against insects	Maize	Tolosa et al., 2019; Huff et al., 2019

(Z)-3-hexenyl propionate	defense against *Pseudomonas syringae*	Tomato	López-Gresa et al., 2018
(Z)-3-hexenyl butyrate			
Camalexin	defense against *Phytophthora brassicae*	*Arabidopsis*	Schlaeppi and Mauch, 2010; Buxdorf et al., 2013
indole glucosinolates	defense against *Alternaria brassicola*		
4-methoxyxyclobrassinin	defense against *Plasmodiophora brassicae*	Canola	Pedras et al., 2008
Sarcotoxin	Defense against canker	Transgenic citrus	do Prado Apparecido et al., 2017

i. Effectoromics from host perspective:

Effectoromics is a specialized omics category which is based on the hosts as they secrete effector molecules against the invading pathogens and microbes. It is a high-throughput functional genomics technique that uses effectors to bait to detect and identify the R genes from the germplasm of plants and has proven a potent contribution to modern resistance breeding (Du and Vleeshouwers, 2014: Nejat et al., 2017). Du and Vleeshouwers, (2014) have summarized the advantages of the technique for identifying and detecting the R genes in plants. One of the serious diseases in wheat affecting severely and resulting in huge crop loss is the *Fusarium* head blight (FHB) caused by *F. graminearum* and *F. culmorum*. This omics was applied to uncover the nucleotide-binding site leucine-rich repeat (NBS-LRR) class of *R* genes of potato and *Arabidopsis* (Gorash et al., 2021).

Table 2. Various aspects of histone post-translational modifications (PTMs) are described that provide practical cues to our understanding of histone PTMs during plant-microbe interactions.

Histone modifications	**Host**	**Pathogen**	**Function during plant-host pathogenesis**	**Method of identification**	**References**
H3K9 (dimethylated; H3K27me2) H4K12ac	*Phaseolus vulgaris L*	*Uromyces appendiculatus*	Differential expression of genes upon infection thereby	ChIP and RNA-Seq	Ayyappan et al., 2015

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			indicating regulatory functions.		
H2BK11, H3K14, H3K18, and H3K27 acetylations	Wheat	*Pseudomonas piscium* and *Fusarium graminearum*	Deacetylation of modifications of acetylation in fungal growth, virulence, and mycotoxin biosynthesis and in bacterium as well	In vitro acetylation assay	Chen et al., 2018
H3K27 (trimethylated; H3K27me3)	*Oryza sativa* cv. YT16	*Magnaporthe oryzae* wild type strain Guy11 (French Guiana)	Down and up-regulation of many genes upon infection with the pathogen in the host thereby indicating regulatory functions.	Multi-omics approach and molecular genetics (chromatin immunoprecipitation sequencing(ChIP-Seq) and RNA sequencing (RNA-Seq)	Zhang et al., 2021
H3K9ac, H3K9me2, and H3K27me3	*Oryza sativa*	*Meloidogyne graminicola*	Differential expression of genes upon infection and targeting specifically H3K9.	ChIP and RNA-Seq	Atighi et al., 2020

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Several post translational modifications of histones (Table 2) that include methylation, acetylation and others have been reviewed by Pfluger and Wagner (2007), which are effected by the action of exogenous (environmental) factors that include also pathogens (Pfluger and Wagner, 2007) and especially bacterial pathogens (Hamon and Cossart, 2008). Similarly, Ramirez-Prado et al. (2018) and Perrone and Mertinelli, (2020) have reviewed epigenetic changes such as chromatin modifiers and modifications with their physiological responses involved in the PPIs (Ramirez-Prado et al., 2018; Perrone and Mertinelli, 2020). Lai et al. (2022) have reviewed the chromatin modification of the filamentous fungal pathogens in plants and insects (Lai et al., 2022), key in plant pathogenesis. An omics-based approach in this direction will invariably open up more diverse vistas of knowledge on the mechanism of plant pathogenesis and allow scientific intervention to manipulate disease progression towards complete control. Also, biosafety measures and ethical issues related to the omics in PPIs are vividly explained (Sharma et al., 2021) that add value to these being adopted in field trials.

i. Conclusions and future directions

Further intensive studies are required in understanding the plant-microbe interactions using omics-dependent approaches obtained from the branches of genomics, transcriptomics, and metabolomics along with other methods to identify specific interactions and unravelling complexities involved deep within them, also elucidating knowledge on metabolites that are involved in key biological processes, such as mutualist recruitment, pathogen suppression, and immune signaling. With the advent of omics along with the inclusion of NGS and HTS technologies supplemented with computation and bioinformatics analyses, the rich plant microbes plethora has become easier to be deciphered and still needs to be explored in order to align future studies on a deeper understanding of plant immunity to facilitate the development of innovative approaches for crop protections, improvements, and breeding programs. Not only these techniques have boosted the research in understanding the interactions among the plants with their unwelcomed guests but also opened new scope and provided novel tools for assisting in plant breeding programs. The next decade will surely witness a dramatic surge of new discoveries found using these omics-based technologies in plant-microbe interactions. Role of epigenetics needs to be explored extensively that can lead to not only opening up new mechanisms of disease progression but also their complete control strategies, thus having better potential for plant disease management.

While addressing the issues that challenges this area more focuss needs to be given to the studies directed on the subject of metabolites of hosts (plants) and pathogens (bacteria, fungi, oomycetes, viruses etc.) that need better methods for their identification and data obtained on them be integrated with the omics data gathered from other aspects. All these are important and require hands on skills in handling and currently, there are scarcity of trained personnel in this area and adequate software, the areas that can be worked upon for future technical developments for establishing better omics datasets in future..

Competing interests :

The authors declare no competing interests exist.

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