



Review article

Plant response to biotic stress: Is there a common epigenetic response during plant-pathogenic and symbiotic interactions?



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ABSTRACT

Plants constantly interact with pathogenic and symbiotic microorganisms. Recent studies have revealed several regulatory mechanisms controlling these interactions. Among them, the plant defense system is activated not only in response to pathogenic, but also in response to symbiotic microbes. Interestingly, shortly after symbiotic microbial recognition, the plant defense system is suppressed to promote plant infection by symbionts. Research studies have demonstrated the influence of the plant epigenome in modulating both pathogenic and symbiotic plant-microbe interactions, thereby influencing plant survival, adaptation and evolution of the plant response to microbial infections. It is however unclear if plant pathogenic and symbiotic responses share similar epigenomic profiles or if epigenomic changes differentially regulate plant-microbe symbiosis and pathogenesis. In this mini-review, we provide an update of the current knowledge of epigenomic control on plant immune responses and symbiosis, with a special attention being paid to knowledge gap and potential strategies to fill-in the missing links.

1. Introduction

Plants are sessile organisms that constantly interact with their environment, including microbes. To properly recognize, then interact with microbes, plants have developed specific responses to pathogenic and symbiotic microbes to prevent or promote infection, respectively. Recent studies have revealed several regulatory mechanisms controlling the interactions between plants and microbes. Among these mechanisms, the plant epigenome has emerged as a key modulator of both pathogenic and symbiotic plant-microbe interactions [1–5]. It is evident that DNA methylation is important to prevent leaky expression of genes involved in plant defense against pathogens and the establishment of symbiotic relationships. For instance, changes in the plant genomic DNA (gDNA) methylation profile greatly influence the efficiency of nitrogen fixation by rhizobia in soybean and medicago plants [6–9]. Similarly, pathogen attack leads to changes in the gDNA methylome and the expression of defense genes in *Arabidopsis* [10,11]. Overall, work done in *Arabidopsis* also suggests that gDNA demethylation promotes plant resistance to microbial pathogens [12–14] and symbiotic relationships [6,7].

This mini-review highlights our current understanding of the impact of epigenomic modifications on plant response to both symbiotic and pathogenic microbes. After introducing the fundamental concepts associated with plant-microbe interactions, we present and discuss our

current understanding of the role of the epigenome (e.g. gDNA methylation and small RNAs) in controlling symbiotic and pathogenic plant-microbe interactions. As a perspective to this review, we open a discussion on the cellular complexity of plant tissue used to generate transcriptomic and epigenomic data sets to better understand plant-microbe interactions. Specifically, advantages and limitations that come with the use of multicellular or single cell-type samples will be assessed. We also highlight knowledge gaps in our understanding of the epigenomic responses during pathogenesis and symbiosis.

2. Plant responses during pathogenic and symbiotic microbe interactions

At the root-soil interface, plants constantly interact with symbiotic and pathogenic microbes. As a result, plants have evolved to specifically recognize then interact with microbes [15]. This evolution led plants to perceive invading microorganisms through the recognition of conserved molecular signals termed MAMPs [Microbe Associated Molecular Patterns; e.g., flagellin (flg22), Elongation factor Tu (EF-Tu; elf18/26) and chitin] by plasma membrane receptors [16–18]. Similarly, during the early stage of plant-microbe symbioses, Nod and Myc factors, which are signaling molecules produced by bacterial and fungal symbionts respectively, are also recognized by specific plant receptors to promote symbiosis [19–21].

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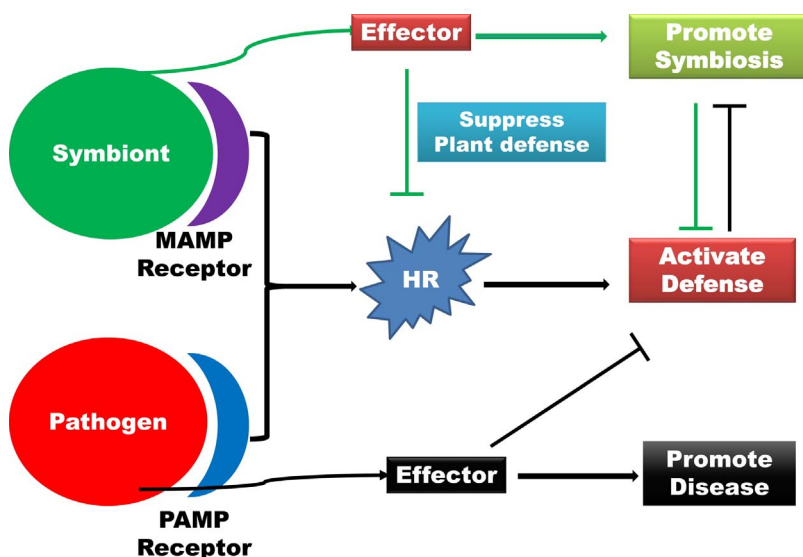


Fig. 1. Plant response to microbes.

The initial response of plants to microbial symbionts and pathogens is through the recognition of molecular microbial patterns by plant receptors, thereby triggering hypersensitive response. Both types of microbe secrete effectors capable of suppressing plant immune responses. In the presence of symbiotic microbes, the plant defense is suppressed to promote the establishment of symbiosis. However, activation of plant defense significantly delays establishment of symbiotic relationships.

Upon MAMPs recognition, a signal transduction leads to oxidative burst and transcriptomic reprogramming that either promote symbiosis or activates immune responses against pathogens [22–25] (Fig. 1). The promotion of plant-microbe symbiosis suggests that the plant immune response must be repressed. Indeed the inhibition of reactive oxygen species (ROS) production and salicylic acid (SA) accumulation concomitantly to the repression of the expression of the defense gene *PR1* was demonstrated in *M. truncatula* to promote symbiosis [26–28]. Recent studies also revealed that arbuscular mycorrhizal fungi symbiosis (AMS) and rhizobia root nodule symbiosis (RNS) are promoted by the use of symbiont effectors that suppress plant defense [29–31]. Interestingly, AMS also induces systemic acquired resistance (SAR)-like immunity that protects the host plant from pests and diseases [32].

In a more complex scenario, herbivory research demonstrated that gut symbionts of insect pests downregulate the jasmonic acid-induced defense system used by plants against herbivores [33,34]. Specifically, using tomato as a model plant, Chung et al. demonstrated that the larvae of the Colorado potato beetle (CPB; *Leptinotarsa decemlineata*) secrete gut bacterial symbionts onto leaf surfaces. On the plant leaf, these symbionts secrete effectors that can suppress anti-herbivore defenses, thereby promoting larvae feeding and growth [34]. It is intriguing to note that the majority of these secreted symbionts were from the genus *Enterobacter* and *Acinetobacter* [34] which are known as plant growth promoting endophytes [35–38]. Thus, since these insect-secreted symbionts may not be recognized as pathogens by the plants, but as beneficial endophytes, they are used by insects as a decoy to promote their feeding habit.

3. Epigenome and its role in plant defense and symbiosis

The epigenome is defined as the genome wide composition of heritable or non-heritable chemical modifications of DNA (C5-methylcytosine) and histone proteins (e.g., acetylation and methylation). As a consequence, the epigenome influences transcription and the overall function of an organism's genome without altering the DNA sequence [39,40]. Such epigenomic modifications as well as activities of small interfering RNA (siRNA) and transposable genetic elements (TEs), influence plant response to environmental cues including plant-microbe interactions as reviewed below.

3.1. Epigenomic responses during plant defense

3.1.1. DNA methylation and histone modifications

DNA methylation, which is critical to the maintenance of the

silencing of TEs, is also a regulatory mechanism of gene activity, which usually occurs through the RNA-directed DNA methylation (RdDM) pathway. This pathway is dependent on the activity of small interfering RNAs (siRNAs) and enzymes such as polymerase IV, ARGONAUTE 4 and DOMAINS REARRANGED METHYLTRANSFERASE (DRM) [41,42]. The pattern of DNA methylation can either be maintained by the catalytic activities of METHYLTRANSFERASE1 (MET1) and CHROMO-METHYLASE3 (CMT3) methyltransferases [43,44] or erased by DNA glycosylases such as REPRESSOR OF SILENCING1 (ROS1), and DEMETER-LIKE2 and 3 (DML2 and DML3) [45].

DNA methylation plays a central role in plant-microbe interactions. For instance, research reports demonstrated that plants defective in DNA methylation are more resistant to pathogens while enhanced DNA methylation makes plants more susceptible [10,14,46,47]. In fact molecular work done in Arabidopsis revealed that the gDNA methylation profile influences callose deposition and the expression of the salicylic acid-dependent *PATHOGEN RELATED 1* (*AtPR1*) gene in response to the oomycete pathogen, *Hyaloperonospora arabidopsidis* (*Hpa*) [14].

The initial exposures of plants to biotic and abiotic stresses are kept in memory to promptly activate a more robust defense in response to future stresses. An example of such preparedness reported in Arabidopsis and named systemic acquired resistance (SAR) or defense priming usually promotes hypersensitivity and rapid expression of defense genes [48,49]. The Arabidopsis protein NONEXPRESSION OF PR GENES1 (NPR1/NIM1) is a key SAR regulatory protein that is involved in priming of defense inducible genes [50,51]. Interestingly, NPR1/NIM1 was reported to epigenetically regulate the expression of these genes through chemical modifications of histone H3 [52]. Similarly, Chromatin Assembly Factor-1 (CAF-1) tightly regulates defense priming by changing the nucleosome occupancy around the transcription start sites (TSSs) of defense response genes such as *PR1*, *PR5*, *WRKY6* and *WRKY53*. In addition, CAF-1 also controls the trimethylation of H3K4 to promote the transcriptional activation of defense genes [49]. Other histone post-translational modifications are also regulating the expression of plant defense genes in response to microbes. For instance, the Arabidopsis histone deacetylase HDA19 was reported to promote histone deacetylation of the *PR1* and *PR2* promoters to better regulate their expression in response to pathogens [53]. More recently, the Arabidopsis Flowering locus D (FLD) was also reported to influence histone methylation of the *WRKY29* and *WRKY6* promoters, thereby activating SA-dependent SAR defense [54–56]. Also, Arabidopsis mutant plants defective in histone acetyltransferase are compromised in bacterial resistance, suggesting the importance of histone acetylation in controlling the plant defense system [57].

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