

Chromatin Modifications and Plant Immunity in *Phaseolus vulgaris* L.

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Keywords: Histone modifications; Plant immunity; Common bean; Priming

Genetic studies along with biochemical and cell biology analyses in plant model systems have influenced human health research and have enabled researchers to understand how proteins are recruited to chromatin and how they regulate their target genes and to elucidate their functions. Accordingly, it has become evident that almost all human genes that were assumed or known to participate in disease have orthologs in the model plant *Arabidopsis thaliana* and in many other plants (e.g. the common bean, *Phaseolus vulgaris*). Also, it is now recognized that many defence mechanisms in *Arabidopsis* are under epigenetic control, similarly to the mechanisms regulated by members of the animal Polycomb Group (PcG)/Trithorax Group (TrxG) complexes involved in the regulation of disease and cancer, though it is not clear how plant pathogens manipulate, for example, host post-translational modifications (PTMs) and how they use these PTMs to solve their own biological requirements. Despite the fact that a number of stress responses include epigenetic components, we are just beginning to elucidate the mechanisms and molecular interactions. Thus, it is imperative to broaden our knowledge in such areas of research.

In addition to structural barriers and secondary metabolites, plants have evolved inducible defense mechanisms to protect against pathogens and insects [1]. Such mechanisms involved in induced resistance are either activated directly or 'primed' for increased expression upon pathogen attack. These inducible defenses are controlled by the plant's innate immune system. For example, pathogen-associated molecular patterns (PAMPs), microbe-associated molecular patterns (MAMPs), damage-associated molecular patterns (DAMPs), pathogen effectors, or wound stimuli, all initiate a defense response that involves the priming of cells, both in tissue exposed to the stress, and also in the systemic tissue [1]. Therefore, primed plants exhibit faster and/or stronger activation of defense responses when they are exposed to a second kind of either biotic or abiotic stress, often associated to the development of local and systemic immunity and stress tolerance [1]. Furthermore, it is believed that the primed defense state can be maintained long after the initial stimulus, something considered as a form of plant immunological memory. Consequently, priming of defense allows plants to enhance their innate immune system and offers a long-term adaptation to disease-conducive conditions.

Defense priming in plants is in general triggered by signals that indicate up-coming attack by pathogens or herbivores. A classic example of this defense mechanism is "systemic acquired resistance" (SAR), which is triggered by localized pathogen attack and give rise to a systemic priming of salicylic acid (SA)-inducible defense mechanisms [2,3]. Another example of stress-indicating priming signals are volatile organic compounds (VOCs), which are emitted by herbivore-infested plants. Several VOCs can prime jasmonic acid (JA)-dependent defenses in systemic plant parts and neighbouring plants [4]. However, not all priming responses are generated by negative signals. For example, priming can be triggered by plant-beneficial organisms, such as non-pathogenic rhizobacteria and mycorrhizal fungi, which results in an

"induced systemic resistance" response [5]. In addition to biological agents, there are various chemicals that can mimic biologically induced priming phenomena (e.g. 3-Aminobutanoic acid, Benzothiadiazole, 2,6-Dichloroisonicotinic acid). Application of these chemicals delivers a more consistent and less variable priming response, thereby making the phenomenon of priming more accessible for molecular and genetic studies.

Chromatin remodelling has recently emerged as an important regulator of plant defense. Thus, regarding the molecular mechanisms of priming, it has been hypothesized that chromatin modifications prime the defense genes for faster and more robust activation [6]. Accordingly, the concept of epigenetic control of defense priming has been recently suggested by several groups. For example, Berr et al. have demonstrated that induction of JA-dependent defense by JA or fungal infection is accompanied with SET DOMAIN GROUP 8 (SDG8)-mediated methylation of histone H3 lysine 36 (H3K36) at promoters of JA-inducible defense genes. Such structural changes could allow for a long-lasting priming of JA-dependent defense genes against future attacks by necrotrophic fungi [7]. Additionally, Jaskiewicz et al. demonstrated in *Arabidopsis* that priming of SA-dependent defense is associated with NONEXPRESSER OF PR GENES 1 (NPR1)-dependent PTMs of histone H3 and H4 tails at gene promoters of defense-regulatory transcription factor genes [8]. Furthermore, priming the promoter of the WRKY transcription factor 29 gene (WRKY29) with benzothiadiazole is associated with the tri-methylation of histone H3 lysine 4 (H3K4me3) and H3K4me2, as well as with the acetylation of H3K9, H4K5, H4K8, and H4K12 [8]. However, these modifications did not activate expression of the WRKY29 gene until the plants were challenged with an additional stress stimulus. Therefore, chromatin marks associated with gene activity are put together during priming before true activation of defense genes [8]. These chromatin modifications could loosen the interaction of histones and DNA and, in this way, generate an open chromatin structure and/or docking sites for transcription co-activators, chromatin remodelling factors, or other effector proteins in chromatin.

On the other hand, histone acetylation and DNA methylation are also considered major epigenetic modifications in eukaryotes. And, for example, histone deacetylation has been strongly correlated with gene silencing and heterochromatin formation. Then again, in *Arabidopsis*, the histone deacetylase 6 (HDA6) protein work together with DNA methylation on its direct target locus in the gene silencing mechanism

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Received March 20, 2013; Accepted June 14, 2013; Published June 20, 2013

Citation: Alvarez-Venegas R (2013) Chromatin Modifications and Plant Immunity in *Phaseolus vulgaris* L.. J Plant Biochem Physiol 1: 112. doi:10.4172/jpbp.1000112

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[9]. Furthermore, it has been shown that in *Arabidopsis thaliana*, immune priming to *Pseudomonas syringae* pv tomato DC3000 (PstDC3000) is transmitted between plant generations through the DNA hypomethylation of defense-related genes [10]. Moreover, several researchers have demonstrated similar transgenerational resistance phenomenon in response to priming-inducing stimuli. For example, Slaughter et al. revealed that progeny of *Arabidopsis* treated with β -aminobutyric acid or an avirulent isolate of PstDC3000 (PstavrRpt2) are primed for SA-dependent resistance against *Hyaloperonospora arabidopsidis* and PstDC3000 [11]. Whereas Rasmann et al. showed that when *Arabidopsis* and tomato (*Solanum lycopersicum*) are subjected to herbivory or mechanical damage they produce progeny that are primed to express JA-dependent resistance against herbivores [12]. Thus, trans-generational priming of defense could be considered a powerful and widely distributed mechanism of phenotypic plasticity in plants to environmental stress and points toward an epigenetic basis of the phenomenon [10].

Nowadays, genome sequencing has uncovered many genes encoding SET-domain proteins (with a histone-lysine N-methyltransferase activity), as well as histone deacetylases, in plants; in particular, *Arabidopsis* genes are the best annotated and characterized, and SET-domain proteins have been shown to play critical functions in diverse processes including flowering time control, leaf morphogenesis, floral organogenesis, parental imprinting and priming. However, genome sequences of an increasing number of plant species, with an agro-economical importance, in addition to the model plants have also been completed. And, for example, at least 47, 33, 31, 43, 49, 59 and 41 SET-domain containing genes have been identified in *Arabidopsis*, grape, maize, rice, *Brassica rapa*, *Populus* and in the legume *Phaseolus vulgaris*, respectively (www.phytozome.net). However, contrary to other plants, most legumes can establish an unmatched endosymbiosis with nitrogen-fixing soil bacteria, collectively named *Rhizobium spp.* *Rhizobium* bacteria, in the root nodules of legumes, let their hosts access to combined nitrogen. The regulatory networks and molecular mechanisms that underlie this unique property cannot be investigated through the examination of non-legume species. Additionally, priming of defense responses is not solely confined to the SAR response. Priming of defense responses has also been demonstrated in rhizobacterium-mediated induced systemic resistance (ISR). ISR develops as a result of colonization of plant roots by specific plant growth-promoting rhizobacteria and is mediated by a jasmonate (JA)-and ethylene (ET)-sensitive pathway [13].

In view of that, it is of great significance to study the epigenetic mechanisms involved in the priming phenomenon by using synthetic compounds as well as during the interaction *Phaseolus vulgaris*-pathogen/symbiont. This kind of research is significant because it is expected to provide the knowledge needed to develop in the future new drugs or treatments to manipulate and selectively activate/inhibit enzymes to counter pathogens, to treat important diseases and to increase crop productivity. New approaches of this kind and the development of new technologies will certainly increase our knowledge of currently known post-translational modifications and facilitate the understanding of their roles in host-pathogen interactions. Furthermore, these and other approaches should provide important insight on how the plant

epigenome changes in response to developmental or environmental stimuli, how chromatin modifications are established and maintained, to which degree they are used throughout the genome, how chromatin modifications influence each another, and how epigenetically distinct chromatin compartments are established and maintained.

Acknowledgment

CONACYT CB-2011/167693.

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