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Defense Priming

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Defense priming is an adaptive strategy that improves the defensive capacity of plants. This phenomenon is marked by an enhanced activation of induced defense mechanisms. Stimuli from pathogens, beneficial microbes, or arthropods, as well as chemicals and abiotic cues, can trigger the establishment of priming by acting as warning signals. Upon stimulus perception, changes may occur in the plant at the physiological, transcriptional, metabolic, and epigenetic levels. This phase is called the priming phase. Upon subsequent challenge, the plant effectively mounts a faster and/or stronger defense response that defines the post challenge primed state and results in increased resistance and/or stress tolerance. Priming can be durable and maintained throughout the plant's life cycle and can even be transmitted to subsequent generations, therefore representing a type of plant immunological memory.

Key words: epigenetic, Microbe-associated molecular patterns (MAMPs), Pathogen-associated molecular patterns (PAMPs), Herbivore-associated molecular patterns (HAMPs), Plant-growth-promoting rhizobacteria (PGPRs), plant-growth-promoting fungi (PGPFs).

Introduction

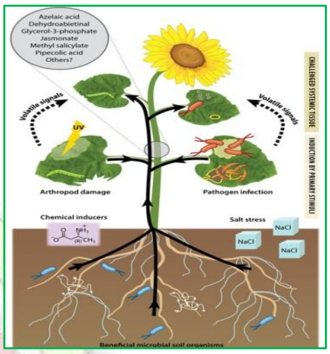
Through evolution, land plants developed structural barriers e.g., a cell wall and a waxy layer, constitutive secondary metabolites e.g., phytoanticipins, and inducible defense mechanisms (e.g., defense gene expression and phytoalexin accumulation) to ward off potentially dangerous microbes and insects. These measures are part of the innate immune system of plants that lack adaptive immunity.

However, it has been known for a long time that components of the plant immune response can also learn from past incidents. For example, upon recognizing the molecular patterns of microbes [microbe-associated molecular patterns (MAMPs)], pathogens [pathogen-associated molecular patterns (PAMPs)], or herbivores [herbivore-associated molecular patterns (HAMPs)], or after perceiving damage-associated molecular patterns (DAMPs), pathogen effectors, or certain xenobiotics (e.g., some pesticides), plants are often promoted to a primed state of enhanced defense.

Defense priming establishes in the tissue exposed to the PAMP, MAMP, HAMP, DAMP, effector, or chemical compound and in the systemic, unharmed, or untreated parts of the plant (Bekers and Conrath, 2007). When primed, plants respond to very low levels of a stimulus in a faster and stronger manner than unprimed plants (Conrath *et al*., 2009). Therefore, primed plants show more rapid and robust activation of defense responses when challenged by pathogens, insects, or abiotic stress, and this is frequently associated with local and systemic immunity and stress tolerance .When the plants are exposed to PAMPs, DAMPs, effectors, certain physical or chemical stimuli, and/or root-colonizing nonpathogenic microorganisms, they can result in expression of a suite of defense responses in both a local and systemic manner.

These responses are typically associated with systemic acquired resistance, induced systemic resistance, and mycorrhiza-induced resistance. These different types of resistance help the plant to contain the attacker and are characterized, for instance, by the direct induction of antimicrobial proteins. In this seminar, we will discuss the priming phenomenon from the initial stimuli to the changes that take place in the plant to create a more robust and efficient defense. We will also discuss both long-term and transgenerational aspects of priming and lastly various artificial chemicals which can induce defense responses and their application in agriculture.

Priming-Inducing Stimuli



Plants possess a remarkable capacity to perceive numerous environmental signals that allow them to respond to their surroundings. Stimuli from pathogens, beneficial microbes, or arthropods, as well as chemicals and abiotic cues, can trigger the establishment of priming by acting as warning signals.

We will discuss in detail about following priming inducing stimuli:

1. **Pathogens derived stimuli**
2. **Beneficial microbes derived stimuli**
3. **Arthropods derived stimuli**
4. **Chemical stimuli**
5. **Abiotic stimuli**

1) Pathogen-Derived Stimuli

Pathogens themselves, or pathogen-derived molecules, can act as priming stimuli in plants. Broadly, molecules produced by pathogens are referred to as PAMPs and effectors, whereas molecules released by the host plant following an attack are referred to as DAMPs (Boller and Felix, 2009). Pathogen-derived molecules can be of different biochemical natures (peptides, polysaccharides, or lipids) and are perceived by plants through appropriate protein receptors (pattern recognition receptors or resistance proteins) (Boller and Felix, 2009).

Unlike effectors, PAMPs, by definition, are not strain or species specific and do not contribute to pathogen virulence; they are thus present in both pathogenic and nonpathogenic microorganisms. Structural molecules such as lipopolysaccharides and flagellin (or its derived 22-amino-acid peptide, flg22) from bacteria, chitin from fungi, and β-glucans from fungi and oomycetes (Boller and Felix, 2009) are clear examples of PAMPs. Lipopolysaccharides and flg22 are probably the best-known priming PAMPs (Flury *et al.*, 2013.

2) Beneficial-Microbe-Derived Stimuli

Beneficial microbes include plant-growth-promoting rhizobacteria and fungi that exert positive effects in the interplay between microbes and hosts.

❖ **Plant-growth-promoting rhizobacteria and fungi**

Plant-growth-promoting rhizobacteria (PGPRs) and plant-growth-promoting fungi (PGPFs), both of which induce systemic resistance, can also trigger defense priming. The subtle costs associated with these interactions are negligible under pathogenic pressure, and many studies have provided evidence that the induced resistance they trigger is based on priming (Kloepper *et al.*, 2004).

The goal of the initial chemical interplay between microbe and plant is the establishment of symbiosis. However, the involved signals can also serve as stimuli for defense priming. For instance, the first chemical stimuli exchanged to start the symbiosis are hormones and flavonoids from the host and nodulation (Nod) factors from rhizobacteria (Oldroyd *et al.*, 2009). Beneficial microbes also need to suppress local immune responses in the host; two well-known effectors from mycorrhizal fungi are secreted protein 7 (SP7) and mycorrhiza-induced small secreted protein 7 (MiSSP7). In addition, the interaction between beneficial microbes and host plants is mediated by compounds with eliciting activity.

3) Arthropod-Derived Stimuli

Herbivore-associated stimuli can be of biological or physical origin. Biological stimuli include oral secretions, insect-associated microbes, insect-associated molecular patterns (IAMPs), and oviposition signals (Hilker and Fatouros, 2015); physical signals consist of spatiotemporal repeated patterns and trichome sensing of insects walking on leaf surfaces. Moreover, herbivore-induced plant volatiles have been described as elicitors of priming because they act as stimuli to neighboring plants. All of these stimuli are produced during challenge with an arthropod, which obviously triggers direct defenses in the plant, but when these physical or biological stimuli are used experimentally, they can induce a faster and/or stronger defensive behavior in the attacked plants.

4) Chemical Stimuli

Numerous chemical compounds, often of natural origin, have been shown to act as priming stimuli. Among these chemicals are β-aminobutyric acid (BABA), probenazole, benzothiadiazole (BTH), and salicylic acid (SA), all of which can induce resistance in plants by protecting against a broad range of pathogens. SA is a hormone that triggers several direct responses in plants, but at low doses it has been reported to enhance flg22-induced MITOGEN-ACTIVATED PROTEIN KINASE 3 (MPK3) and MPK6 activation. BTH and BABA have been thoroughly studied as priming agents against pathogens and insects. Similarly to SA, both of these chemicals may directly induce defenses when applied at high doses (Van Hulten *et al.*, 2006).

5) Abiotic Stimuli

A study carried out on *Arabidopsis* demonstrated that repetitive exposure of a plant to mild abiotic cues, such as heat, cold, or salt, can enhance resistance against virulent *Pseudomonas syringae* pv. *tomato* (*Pst*) DC3000 by acting at the epigenetic level (Singh *et al.*, 2014). Importantly, when plants were subjected to long-term exposure or high salt concentrations, priming did not occur.

The Priming Phase: Changes Following Stimulation

The priming phase refers to the biological process of acquiring priming, which takes place from the initial stimulation through the exposure to a challenging stress. includes all changes that occur in the plant after the perception of a stimulus and prepare the plant for enhanced responsiveness when a challenge occurs. These changes can take place at the physiological, molecular, and epigenetic levels; can occur within seconds or hours after stimulation; can be transient or maintained throughout the lifetime of a plant; and can even be inherited by subsequent generations.

1) Physiological and Transcriptional Change

Transient changes in the level of intracellular calcium occur within a few seconds or minutes and are among the best-known early responses to stimulation. Cytosolic calcium rapidly increases, for instance, in cells neighboring a wound site or after leaf rubbing, and the calcium increase is crucial for local priming by wounding Calcium fluxes could also play a role during AMFroot colonization: For example, *Oryza sativa* calcium-dependent protein kinase 18 (OsCPK18) is strongly upregulated at the gene level in cortical cells, suggesting that an increase in cytoplasmic calcium is triggered by AMFs (Campos-Soriano *et al.*, 2011).

2) Metabolic Changes

The accumulation of inactive forms of defense-related hormones seems to be implied in the sensitization of defenses. For instance, the constitutively primed *Arabidopsis* mutant *nitrate transporter 2.1* (*nrt2.1*) has low basal levels of free SA that rapidly increase after challenge with *Pst* On the basis of studies that have analyzed different priming stimuli, a common subset of shared compounds can be identified that are then referred to as the priming fingerprint. These compounds undergo a slight induction after stimulation, but their accumulation following challenge is faster and/or stronger in challenged plants than it is in un stimulated controls (Gamir *et al.*, 2014).

3) Epigenetic Changes

Genetic imprinting, paramutations, transposon activity and gene silencing are epigenetic phenomena known to take place in all living organisms. The mechanisms behind these phenomena involve changes in chromatin structure, which can ultimately alter genomic processes such as gene transcription, replication, and recombination.

Conclusion

Defense Priming is an effective strategy to combat biotic and abiotic stresses, and it therefore represents a potential approach to enhance plant protection in agricultural systems. As there is an urgent need for new strategies that do not rely on pesticides or single resistance genes, the exploitation of the capacity of the plant immune system in combination with other strategies may hold the potential to achieve better protection of crops.

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