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Priming During Systemic Acquired Resistance in Plants

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Abstract: Priming is an intrinsic part of all induced resistance mechanisms in plants. Priming can be induced by a wide variety of biotic and abiotic stimuli. Stimuli induce physiological, molecular, and epigenetic changes that prepare the plant for enhanced responsiveness. Priming also occurs in systemic leaves of plants exhibiting Systemic Acquired Resistance (SAR). In the SAR state, plants are primed (sensitized) to more quickly and more effectively activate defense responses the second time they encounter pathogen attack. The primed state can last for the lifetime of a plant and can even be transmitted to its descendants, and forms "plant memory". The attractiveness of priming for agricultural protection is also associated with the fact that this phenomenon, unlike the direct activation of defenses, does not incur major developmental costs.

Keywords: *Agriculture, defense, memory, primed state, stimuli.*

1. INTRODUCTION

Priming is the process by which the plant defenses would be activated by the further presence of the pathogen. Under conditions of disease pressure, primed plants exhibit a higher fitness than non-primed plants or defense-expressing plants. Systemic Acquired Resistance (SAR) is characterized by broad-spectrum disease resistance and is mediated via a salicylic acid (SA) dependent process (Mauch-Mani and Metraux, 1998; Dempsey and Klessig, 2007).

2. SYSTEMIC ACQUIRED RESISTANCE (SAR)

SAR is the phenomenon by which plant's own defense mechanisms are induced by prior treatment with either a biological or chemical agent (Percival, 2001). It is characteristically associated with accumulation of SA, enhanced expression of pathogenesis-related (*PR*) genes and accumulation of their expression products, activation of phenylpropanoid pathway, leading to the synthesis of higher phenolic compounds toxic to microbial pathogens (Durrant and Dong, 2004). The term "pathogenesis-related proteins" is a collective term for all microbe-induced proteins and their homologues to the extent that enzymes such as phenylalanine ammonia-lyase (PAL), peroxidase (POX), and polyphenoloxidase (PPO), which are generally present constitutively and increased only during most infections, are often also referred to as PR proteins (Van Loon et al., 2006).

3. WHAT IS PRIMING?

Priming is an adaptive mechanism which enhances the defense property of plants. This phenomenon is characterized by an induction of 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.

4. STIMULI FOR PRIMING

Priming stimuli cover a wide range of physical, biological, or chemical environmental inputs to which a plant responds by acquiring a memory. These inputs induce low-cost changes in the plant that include the accumulation of numerous metabolites. Many of these natural molecules, when applied exogenously, can themselves act as priming stimuli, generating a plant memory that boosts induced defenses and improves the plant's performance upon challenge. This is the case, for example, for some hormones. 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 (MAPK3) and MAPK6 activation. BTH and BABA have been thoroughly studied as priming agents against pathogens and insects (Mani et al., 2007). Similarly to SA, both of these chemicals may directly induce defenses when applied at high doses. Natural secondary metabolites that had been found to mediate systemic acquired resistance, including JA, azelaic acid, dehydroabietinal, glycerol-3-phosphate, methyl salicylate, and pipecolic acid. These compounds, however, are likely to trigger priming, as has been confirmed, for example, for azelaic acid and pipecolic acid. Because the molecular mechanisms behind the induced resistance by chemicals are not fully understood, it is not always easy to classify them as priming stimuli (Main et al., 2006).

5. PRIMING EVENTS DURING DEFENSE

While treating plants or suspension cells with high concentrations of SA or its functional analogs directly induces defenses, low concentrations elicit little to no response. Following subsequent infection, however, defenses are activated more rapidly and/or strongly (Main et al., 2006). This phenomenon, termed priming, also occurs in systemic leaves of plants exhibiting SAR. Although not fully elucidated, the molecular mechanisms of priming likely involve the accumulation of transcripts and/or inactive forms of MAPKs, elevated levels of PRRs, and chromatin remodeling. This latter mechanism may also promote the inheritance of defense priming. The sequential steps of defense priming. Stimuli stemming from pathogenic or beneficial fungi, bacteria, rhizobacteria, arthropods, and abiotic stresses are perceived by the plant, leading to a slight induction of various compounds and activities in the so-called priming phase. These compounds are referred to as the priming fingerprint, and a subset of these compounds may be common to several stimuli. Upon challenge with an attacker, these primed plants display an enhanced perception of the attackers and therefore are able to mount a more robust defense against it in the post challenge primed state.

The first implication for the involvement of priming in SAR arose from studies using chemical elicitors. Low amounts of benzothidiazoles (BTH) and SA did not directly activate defense responses but rather accelerated the expression of *PAL* and *PR* genes (Mur et al., 1996; Kohler et al., 2002). The enhanced capacity to express infection induced basal defenses is called priming (Conrath et al., 2006).The fitness costs of which are substantially lower than those of constitutively activated defenses (Van Hulten et al., 2006). *Arabidopsis* NON-EXPRESSOR OF PR1 (NPR1) is a transcription co-activator that plays a central role in regulating the transcriptional response to plant pathogens (Shi et al., 2013). A role for NPR1 in priming of SA-mediated defense response was demonstrated by Kohler 2002. Priming leads to more robust induction of defense responses

and resistance, which may include improved perception and/or amplification of the defense response-inducing signal from the pathogen. It is associated with increased accumulation, and/or posttranslational modification of inactive cellular signaling proteins that play an important role in signal amplification. Subsequent exposure to stress could activate, or modulate these "dormant" signaling proteins, thereby initiating the signal amplification leading to faster and/or stronger activation of defense responses and SAR.

The enhanced plant's defense capacity by priming is correlated with a potentiated expression of defense genes and *de novo* synthesis of antimicrobial compounds such as PR proteins, which are expressed in uninfected tissue in response to first infection (Ramos Solano et al., 2008).

Although the phenomenon has been known for decades, most progress in our understanding of priming has been made over the past few years. The molecular mechanisms underlying priming and its importance in the overall plant resistance still remain to be investigated (Tonelli et al., 2011). The events associated with priming during induced resistance in plants are shown in Figure 1 (Goellner and Conrath, 2008).

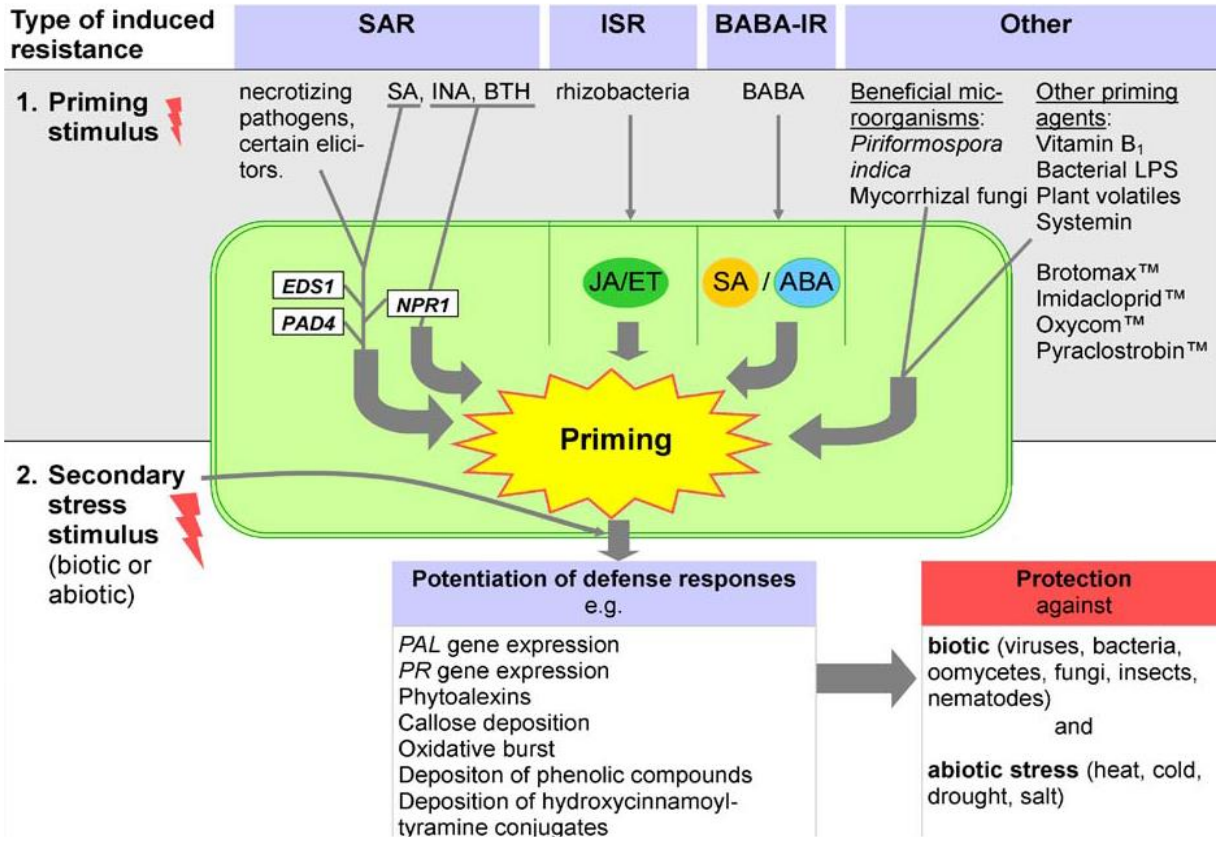

Fig: 1. Priming events associated with induced resistance phenomena in plants [Source: Goellner and Conrath, 2008)

6. PRIMING DURING SAR

The enhanced plant's defense capacity by priming is correlated with a potentiated expression of defense genes and *de novo* synthesis of antimicrobial compounds such as PR proteins, which are expressed in uninfected tissue in response to first infection. Pretreatment with chemical SAR inducer, BTH primed *Arabidopsis* for more robust induction of the *PAL* gene after infection with virulent *P.syringae* pv. *tomato* DC3000. In *Arabidopsis* the vitamin B1-induced priming required hydrogen peroxide and the *NPR1* gene (Ahn et al., 2007). The effects of compost tea could be comparable to the effect of beneficial microorganisms in the induction of plant resistance (ISR) by priming (Segarra et al., 2009). *Pseudomonas* spp.-induced systemic resistance to *Botrytis cinerea* is associated with induction and priming of defense responses in grapevine (Verhagen et al., 2010). Seed treatment with aqueous

Viscum album leaf extract induces resistance to pearl millet downy mildew pathogen with increased PAL and POX activities (Chandrashekhara et al., 2010). Green tea extract induces resistance in lime plants against *Xanthomonas citri* subsp. *citri* by priming of expression of PR proteins (Sharifi-Sirchi et al., 2011). Treatment with BABA, a non-protein amino acid chemical inducer, itself primes the induction of *PR* genes, although levels are lower than that observed after pathogen attack (Zimmerli et al., 2008). Treatment with BABA or inoculation with avirulent bacteria induces priming against *P. syringae* pv. *tomato* DC3000 correlated with increased levels of SA-dependent gene transcripts of *PR1*, *PR2* and *PR5* upon infection, indicating general changes in the regulatory mechanisms of defense gene expression (Slaughter et al., 2012).

7. ROLE OF PLANT DEFENSE GENES IN DEFENSE RESPONSE

PR proteins are currently classified into 17 families although some families do not have representative members from tomato yet. Pathogenesis-related (PR) and similar proteins have been found to be inducible by infection with various types of pathogens in many plant families and have been classified into 17 families [Table 1].

Table 1: Plant defense genes in defense response

Family	Type member	Properties	Target
PR-1	tobacco PR-1a, tomato PR-1b1, PR-1b2, P4, P6, P14, P14a, P14b, P14c, C_2, C_4	antifungal	Fungal pathogen
PR-2	tobacco PR-2, tomato Cel1 EGase, P3, P5, C3, C5, P31, P36, Q'a, Q'b	class I, II, and III endo-β -1,3-glucanases	Glucans
PR-3	tobacco P, Q tomato C6, C7, P26, P30, P31, P32, P34	class I, II, IV, V, VI, and VII endochitinases	Fungal chitin
PR-4	tobacco R tomato P2	antifungal, *win*-like proteins, class I, II endochitinase activity, similar to prohevein C-terminal domain	Fungal chitin
PR-5	tobacco S tomato AP24, NP24, P23	antifungal, thaumatin-like proteins, osmotins, zeamatins, permeatins, similar to α-amylase/trypsin inhibitors	Fungal hyphal growth and spore germination
PR-6	tomato inhibitor I	protease inhibitors	Nematodes and herbivorous insects; Microbial proteinases
PR-7	tomato P_{69}, P_{70}, Rcr3	Endoproteases	Pathogenic proteins and peptides; microbial cell wall
PR-8	cucumber chitinase	Class III chitinases, chitinase/lysozyme	Fungal chitin; bacteria
PR-9	lignin-forming peroxidase tomato Cevi-1, TPX1, TPX2	peroxidases, peroxidase-like proteins	Pathogenic reactive oxygen intermediates
PR-10	parsley PR-1 tomato STH-2	ribonucleases, Bet v1-related proteins	RNA viruses
PR-11	tobacco class V chitinase	Class I endochitinase activity	Fungal chitin
PR-12	radish Ps-AFP3 tomato tgas118	plant defensins	Microbial cell membranes
PR-13	*Arabidopsis* THI2.1 Tomato Thi2.1	Thionins	Cytotoxic
PR-14	barley LTP4 tomato LpLtp1, LpLtp2, LpLtp3	nonspecific lipid transfer proteins (ns-LTPs)	Bacterial and fungal pathogens
PR-15	barley OxOa (germin)	oxalate oxidase	-
PR-16	barley OxOLP	oxalate-oxidase-like proteins	-
PR-17	tobacco PRp27	Unknown	-

8. CONCLUSION

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.

Priming during SAR is an effective strategy to combat biotic and abiotic stresses, and it therefore represents a potential approach to enhance plant protection in agricultural systems.

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