Review

The 'prime-ome': towards a holistic approach to priming

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Plants can be primed to respond faster and more strongly to stress and multiple pathways, specific for the encountered challenge, are involved in priming. This adaptability of priming makes it difficult to pinpoint an exact mechanism: the same phenotypic observation might be the consequence of unrelated underlying events. Recently, details of the molecular aspects of establishing a primed state and its transfer to offspring have come to light. Advances in techniques for detection and quantification of elements spanning the fields of transcriptomics, proteomics, and metabolomics, together with adequate bioinformatics tools, will soon allow us to take a holistic approach to plant defence. This review highlights the state of the art of new strategies to study defence priming in plants and provides perspectives towards 'prime-omics'.

The integration of priming

Plants are constantly exposed to stressful situations due to changing environmental conditions or through their contact with numerous pests and pathogenic microorganisms that are rapidly evolving to evade host defences. To be more efficient in countering such situations, plants make use of their 'priming memory'. Priming (see Glossary) has been defined as an induced state whereby a plant reacts more rapidly and or more efficiently to a stress [1]. Priming events can occur as a result of interindividual or interspecies communication, such as induced resistance mediated by rhizobacteria, mycorrhizal fungi, or virulent or avirulent pathogens or by natural or axenic compounds [2,3]. Plants 'remember' such events and, depending on the type of primary stimulus (initial trigger for priming) and the pathosystem involved (target of priming), primed plants can deploy a diverse set of defence mechanisms. Recently, it has become apparent that the specific defence mechanisms also depend strongly on the priming state and priming has been divided into a 'priming phase', a 'post-challenge primed state', and a 'transgenerational primed state' [4,5] (Figure 1).

The elucidation of priming phenomena usually focuses on a genetic, proteomic, metabolomic, or physiological approach. Consequently, it deals with only part of the entire priming event. In mammalian cells, recent reports show that mRNA regulation explains only about 40% of the changes in protein abundance [6]; thus, focusing on one of the omics might lead to misinterpretation of physiological responses. In potato (*Solanum tuberosum*) plants primed by β-aminobutyric acid (BABA), the low overlap between transcript regulation and apoplast protein abundance after infection confirms the importance of combining several approaches [7]. Metabolites, as the final product of most cellular metabolic pathways, act as regulatory components of biological information and thus allow a more complete picture of the physiological state of a plant [5]. Here we review recent advances in priming against biotic stresses from an omics viewpoint and concentrate on the priming

Glossary

β-Aminobutyric acid (BABA): non-proteinogenic amino acid that primes plants for an augmented defence capacity towards biotic and abiotic stress.
Abscisic acid (ABA): plant hormone involved in development, disease resistance, and abiotic stress tolerance.
Direct defence: defensive mechanism that directly affects the attacker.
Ethylene (Et): gaseous plant hormone involved in development and disease resistance.
Herbivore-induced plant volatiles (HIPVs): plant volatiles released on insect feeding that can move through the vascular system as well as outside the plant.
Indirect defence: defensive mechanism involving the action of a second organism for protection against an attacker.
Induced systemic resistance (ISR): wide-spectrum state of systemic resistance in plants mediated by nonpathogenic rhizobacteria and depending on the phytohormones JA and Et.
Methyl-jasmonate (MeJA): gaseous plant hormone involved in development and disease resistance.
Omics: suffix added to represent a large body of biological data.
Primed state: the physiological state of a plant that has been subjected to priming. Usually starts on exposure of such a plant to a challenging stress.
Prime-omics: the totality of transcriptional, proteomic, and metabolic data available to describe the priming of plants.
Priming: induction of a physiological state that allows a plant to deploy a more rapid and stronger defence response compared with a non-primed plant.
Priming stimulus: the initial event that triggers priming.
Salicylic acid (SA): plant hormone involved in disease resistance and an inducer of SAR.
Systemic acquired resistance (SAR): wide-spectrum state of systemic resistance in plants induced on the recognition of specific microbe-derived molecules.
Transgenerational priming: transfer of a primed state from a parental plant to its progeny.
Virulent pathogen: a microorganism that has the ability to cause disease in a specific host.

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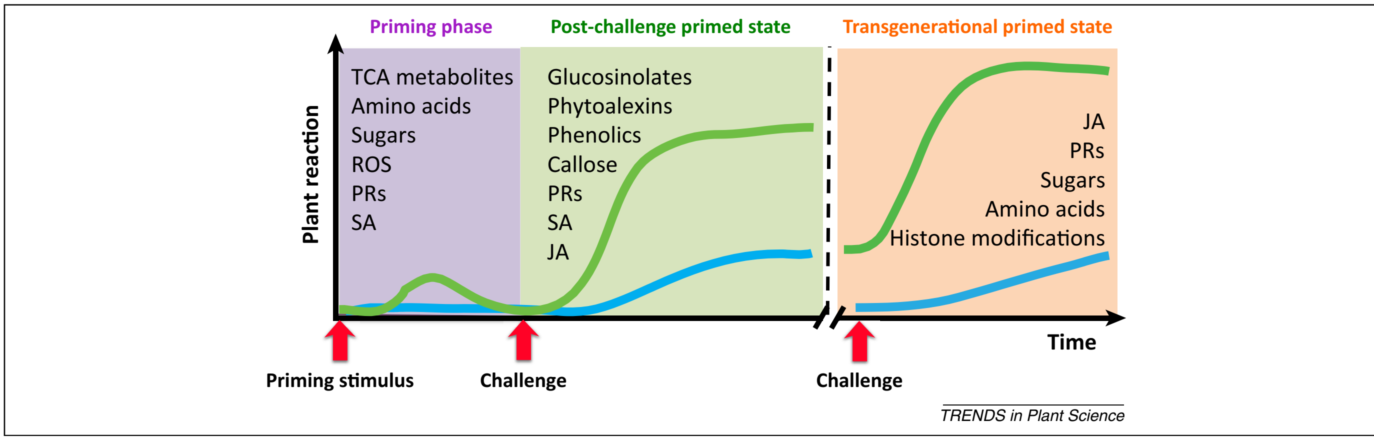

Figure 1. The various states in priming. The priming state is triggered by a priming stimulus and lasts until the plant is exposed to a challenging stress. During the priming stage, the levels of various primary and secondary metabolites, enzymes, hormones, and other molecules are slightly altered, putting the plant in a standby state. On challenge with a stress, the plant enters the post-challenge primed state during which the appropriate reactions to combat the given stressor are induced rapidly. The transgenerational primed state is found in plants generated from seeds stemming from primed parental plants that have a priming memory and are thus able to react more rapidly and more adequately when challenged by a stressor. The green line represents the reaction level and speed of plants that have been primed and the blue line shows the reaction level of plants that have not been primed.

component of resistance-inducing mechanisms such as systemic acquired resistance (SAR) and induced systemic resistance (ISR) [8,9]. Although priming is an integral part of both ISR and SAR, only priming has no or minimal negative impact on the host plants' energy status. Primed plants deploy their defence repertoire only during pathogen attack and not in a constitutive manner. Induction of direct defences is often associated with high physiological costs that can minimise the benefits of the enhanced protection. By contrast, primed plants show almost equal protection levels but suffer from considerably lower fitness costs [10,11]. This makes priming-based approaches valuable for crop protection strategies (Box 1).

Omics in research on priming for defences against pathogens and pests: prime-omics

In recent years the availability of improved analytical techniques revealed that plant priming can be separated into distinct stages [4]. The priming phase, starting immediately after perception of the priming stimulus and ending with the exposure to a challenge, was hitherto generally described as uneventful and strong up- or downregulation of gene activity was observed only in the post-challenge primed phase. Recently, the effect of priming was recognised to be active in the progeny of a primed plant; that is, at the transgenerational level [12–15]. Table 1 gives an overview of recently available information about priming against biotic stressors including bacteria, oomycetes, fungi, nematodes, and arthropods and the following sections give details of the underlying mechanisms.

Box 1. Exploiting priming for the generation of more robust crop plants

In nature, a plant's capacity for priming is a crucial survival parameter, especially when it is confronted by changing environmental conditions. The availability of rapidly growing transcriptomic, proteomic, and metabolomic datasets – the prime-ome – describing the state of primed plants will allow us to define the elements that are responsible for the capacity of certain plants to be more efficiently primed than others and, thus, to exploit this knowledge by introducing these traits into crop plants. Such plants are expected to have an increased capacity to cope with stress and therefore ultimately lead to a lower input of protective/curative chemicals into the environment.

Prime-omics in defences against bacteria

Events in the priming phase

This phase usually involves changes in primary metabolites such as sugars, amino acids, and tricarboxylic acid derivatives [5]. Although priming with BABA and with avirulent bacteria leads to the same resistance phenotype, their impact on the plant's metabolome partially differs [5]. Interestingly, conjugated forms of plant hormones accumulating during the priming state support the idea that they can be rapidly hydrolysed to their active forms to respond faster against a pathogenic invasion [5,16]. Using a qRT-PCR approach to analyse selected marker genes, *Trichoderma asperellum* was described to prime *Arabidopsis thaliana* defence against virulent *Pseudomonas syringae* (Pst) without causing major changes in gene expression during the priming phase. Only a few genes – most of them related to ethylene (Et)/jasmonic acid (JA) signalling – were significantly affected in leaves of plants primed by *T. asperellum*. However, compared with non-primed plants, *T. asperellum*-inoculated plants that suffered subsequent infection by Pst showed major differences in defence gene expression patterns [17]. At the metabolomic level, various amino acid precursors of plant defence metabolites [18] have been shown to accumulate to a higher level following priming with *T. asperellum*, but also with chemicals such as pipecolic acid [17,19].

Most efforts in characterising the changes occurring in primed plants on bacterial infection have concentrated on targeted approaches based on expression profiling of key plant defence genes involved in salicylic acid (SA), JA, and Et defence signalling, accumulation of mitogen-activated protein kinases (MAPKs), and production of reactive oxygen species (ROS). Proteomic and metabolomic mechanisms remain poorly understood.