Title: The Impact of Microbes in Plant Immunity: Sustainable Approach for Crop Protection

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Abstract

One of the biggest demanding situations for food security in the 21st century is to enhance crop yield stability through the improvement of diseases-resistant crops. Managing plant health is a major challenge for modern food production and compounded by the lack of common ground among the many disease control disciplines involved. All plants simultaneously engage with billions of microbes which can be collectively referred to as the plant microbiome. Most microbes inside the plant microbiome are harmless or even beneficial to the plant as they promote plant growth or provide protection in opposition to diseases. However, some of these microbes also cause disease with devastating effects on crop yields. To prevent pathogen infection, plants have evolved an advanced innate immune system that recognizes conserved cell surface molecules that most pathogen possesses. Activation of the plant immune system stops the invading pathogen, however this comes with fitness cost that significantly reduces plant growth and leads to yield penalty. Apart from their innate immune system controlling pre-programmed defense reactions, plants can also increase the responsiveness of their immune system in response to selected environmental signals. This phenomenon is known as "defense priming". Although defense priming rarely provides full protection, its broad-spectrum effectiveness, low-fitness cost, long-lasting durability and inherited to future generations make it attractive for sustainable crop protection.

Key words: Microbiome, Plant Immunity, Priming, Transgenerational Immune Priming (TGIP)

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Introduction

Plant pathogens can destroy up to 30% of worlds agricultural output (Savory et al., 2019), and hence, there is therefore an urgent need to develop disease-proof cropping systems. Plants are colonized by way of a massive variety of micro organisms which could reach cell densities much more than the number of plant cells (Mendes et al., 2013). The rhizosphere is highly complex surroundings that consist of the narrow area of nutrient-rich that surrounds plant roots and is influenced. It is densely populated by various microorganisms which include fungi, bacteria, protists, nematodes and invertebrates. Plant roots secrete an assortment of primary metabolites (e.g., organic acids, carbohydrates, and amino acids) and secondary metabolites (e.g., alkaloids, terpenoids, and phenolics) which are believed to shape, signal, interfere with, or in some way affect the rhizosphere microflora (Venturi and Keel, 2016). This release or exudation in the rhizosphere of a large assortment of chemicals comes at a significant cost of carbon and nitrogen for the plant, with the ultimate benefit of attracting and promoting beneficial microorganisms while combating pathogenic or otherwise harmful ones (Venturi and Keel, 2016). This release or exudation in the rhizosphere of a large assortment of chemicals comes at a significant cost of carbon and nitrogen for the plant, with the ultimate benefit of attracting and promoting beneficial microorganisms while combating pathogenic or otherwise harmful ones (Venturi and Keel, 2016). The rhizosphere is one of the key exchange interfaces between plants and their environment, biological activity and interplay with the surrounding environment (Hartmann et al., 2008; Jones and Hinsinger, 2008; Brink 2016). Rhizosphere immunity could be the key target for an integrative management of plant immunity.

Plants generally overcome the threats caused by pathogenic microbes by their innate ability to perceive signals from potential pathogens. Thereafter, the plants reprogram their defense systems appropriately to overcome these threats (Jain et al., 2012). Rhizosphere microbiome performs a considerable function in reprogramming the defense responses of plants (Spence et al., 2014). One of the maximum mentioned limitations of plant defense is the absence of acquired immunity that allows immunological memory, which may be activated to remove re-infecting pathogens (Sharrock and Sun, 2020). As a result improving disease control management via by focusing on plant immunity gives restrained possibilities as innate resistance genes ought to be slowly constructed into the genome through breeding, while pathogens can easily overcome the resistance due to their noticeably faster rate of evolution.

Alternative procedures to supplement the missing plant immune functions through genetic engineering (Dong and Ronald, 2019) or by using extensive amounts of pesticides are problematic due to lack of legal framework, public acceptance and direct adverse consequence on soil health (Raman, 2019; Hawkins et al., 2019). Thus, the situation arises where production must increase without relying heavily on the use of pesticides. Therefore, the sustainable preservation of agricultural productivity calls for new strategies for crop protection. In order to improve the plant disease management, one solution is to shift away from the reductionist view, where the plant health is studied by focusing on individual components in isolation, to a more holistic framework where the plant immunity is considered to emerge as a result of interactions with plant-associated microorganisms and environmental conditions (Teixeira et al., 2019).

Priming is an adaptive approach that improves the defensive capability of plants. This phenomenon is marked by way of a progressed activation of induced defense mechanisms. Stimuli from pathogens, beneficial microbes, or arthropods, spider mites as well as chemicals and abiotic cues, can trigger the establishment of priming by acting as warning signals (Mauch-Mani et al., 2017; Singh et al., 2017). The process of priming occurs when prior exposure to a biotic or an abiotic stimulus sensitises a plant to express a more efficient defence response to future biotic stress (Mauch-Mani et al., 2017) Primed plants display either faster and/or stronger activation of the various defence responses that are induced following pathogen or insect attack or exposure to abiotic stress (Mauch-Mani et al., 2017; Singh et al., 2017). 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. (Luna et al., 2017; Singh et al., 2017). Although defense priming rarely provides full protection, its broad-spectrum effectiveness, low-fitness cost, long-lasting durability and inherited to future generations make it attractive for sustainable crop protection.

The below ground plant immunity

Immune signaling in roots

Microbes associated with plant's root are relatively diverse. The complex microbial communities related with plant species is referred as the second genome of the plant which is considered to be of splendid significance for the plant health and development**.** Hidden belowground, the rhizosphere can be seen as the powerhouse of the plant immune system, in which where plants, microorganisms and soil together form a tightly connected network that plays an essential role in preventing pathogen attacks (Wei et al., 2020). The plant genome encodes several traits which together form an intricate innate immune system that enables plants to detect and combat pathogens (Dangl and Jones, 2001; Chisholm et al., 2006). Plant-encoded immune functions are based on the recognition of conserved microbe-associated molecular patterns (MAMPs) which detect pathogens by binding to specific receptors (Bittel et al., 2007; Newman et al., 2013). Upon MAMP recognition, pathogen recognition receptors (PRRs) recruit regulatory receptor kinases to form PRR complexes which ultimately activate a multilayered immune signalling cascade via receptor-like cytoplasmic kinases (Macho & Zipfel, 2014). The activated immune signalling events, known as MAMP-triggered immunity (MTI), work to remove potential pathogenic infections (Macho & Zipfel, 2014).

Our understanding of plant immune signaling mainly comes from studies on interactions between microbes and aboveground plant parts. Nevertheless, plant roots may additionally mount strong immune responses upon PRR-mediated recognition of MAMP, such as callose deposition, camalexin biosynthesis, and defence-associated gene activation (Stringlis, Proietti, et al., 2018). Intriguingly, beneficial microbes possess immunogenic MAMPs that are very similar to those of pathogens (Stringlis, et al., 2018). During their initial contact with roots, beneficial microbes are identified via plant PRRs and activate immune signalling. Root immune activation via beneficial microbes was determined in many root–microbe associations. For example, *Bradyrhizobium japonicum* strongly induces defence-related gene expression at the early stage of infection in soybean root hair cells (Libault et al., 2010). Also, the arbuscular mycorrhizal fungus *Glomus versiforme* induces a substantial set of defence- and stress-related genes during the initial contact with Medicago truncatula (Liu et al., 2003). Similarly, the cellular components of two PGPRs, *Pseudomonas simiae* WCS417 (hereafter, WCS417) and *Pseudomonas capeferrum* WCS358 (hereafter, WCS358), trigger immune responses in Arabidopsis roots and tobacco cells, including ROS production, MAMP-responsive gene expression, and callose deposition (Stringlis et al., 2018). Moreover, *Piriformospora indica* has significantly reduced colonization of the roots of a MAMP-hyper-responsive Arabidopsis mutant pub22/23/24, indicating that this PGPF can be recognized by plant PRRs (Jacobs et al., 2011). Together, these studies show that beneficial microbes actually induce responses, too. However, this induction appears to be restricted to the early stages of these beneficial associations, suggesting an active interference by useful microbes in the root immunity.

In additions, pathogens, in turn, have evolved to produce and secrete effector proteins that interfere with either the recognition of MAMPs or the subsequent immune responses caused by MAMPs, , leading to a co evolutionary arms race with their host plant (Carstens et al., 2007; Anderson et al., 2010). While plants can respond to infections by systemically enhancing their immune defense, they do not have immunological memory that would help their immune system to specifically recognize of previously encountered pathogens.

The interactions between plant, microbe, and soil

Rhizosphere microorganisms form a dense biofilm around plant roots (Danhorn and Fuqua, 2007) and can contribute to disease suppression in multiple ways (Berendsen et al., 2012). Because of niche speciation, microbial species within the rhizosphere can coexist by occupying together within the rhizosphere through occupying subsets of root area and consuming distinct sets of plant- and soil-derived resources. Consequently, highly diverse microbial communities probably leave only a few niches unoccupied and available for potential invading pathogens (Meade and O’Farrelly, 2019; Wei et al., 2015). Moreover, as a side effect of the ongoing chemical interactions linked associated with microbial competition, some species generate inhibitory compounds that may restrict pathogen growth and virulence (Mazurier et al., 2009; Hu et al., 206). As a result, root-associated microbes have the potential to provide plants with extended immunity when they are associated with species that display antagonism toward the pathogen that restricts its invasion (Raaijmakers and Mazzola, 2016).

Soils are a few of the densest and diverse microbial habitats observed on our planet (Fierer & Jackson, 2006). Growing in the soil, the roots of plant associate closely interact with this plethora of microorganisms. The complicated interactions between the roots and their associated microbiomes are crucial plant fitness determinants (Mauchline & Malone, 2017; Raaijmakers & Mazzola, 2016). Soil structure can constrain the ability of a pathogen to move toward its host plant and gain access to available nutrients, while soil pH can constrain pathogen growth, and soil particles adsorb and immobilize pathogens or their toxins (Gu et al., 2017; Ngeno et al., 2019).

Plants recruit microorganisms, such as by secreting root exudates made up of a mixture of nutrients and bioactive compounds (Sasse et al., 2017). These selected microorganisms will, in turn, interact with physiology of the plant and can influence plant immune responses to pathogens (Lebeis et al., 2015).

A major limitation of plant immunity is the lack of adaptive immunity. Unlike animals or even bacteria, plants do not have immunological memory that would enable them to recognize and trigger a robust secondary response against a pathogen previously found. Nevertheless, when microbiome components are included, rhizosphere immunity can also be regarded as an adaptive mechanism in which immunological memory is provided by pathogen-suppressive microbes than can restrict re-infecting pathogens within and between plant generations (Wei et al., 2020).

The ability of plants to respond to aggressive environments by sensitizing the immune system in response to stress signals has evolved to make their immune system even more fascinating. This is known as priming, a phenomenon that is defined by psychologists as the implicit memory effect in which exposure to a stimulus influences the response to a subsequent stimulus (Gulan and Valerjev, 2010). In evaluation/comparison with the animal immune system, primes of defence often describes as plant vaccination.

Priming: an alternative to direct activation of defense

In everyday language, to prime means to prepare or make ready. In-plant defense, priming is a physiological system by using which a plant prepares to extra quick or aggressively responds to future biotic or abiotic stress. The circumstances of readiness executed by means of priming have been termed the “primed state” (Conrath et al., 2006). Defense Priming has been reported for a range of plant taxa, including wild species and cultivated varieties, and from herbaceous to long-lived woody plants (Hilker et al., 2015). Defense priming is postulate to an adaptive, low-cost defensive measure because defense responses are not, or only slightly and transiently, activated by means of a given priming stimulus. Instead, defense responses are deployed in a faster, stronger, and/ or more sustained manner flowing the perception of a later challenging signal (triggering stimulus); that is, in times of stress (Conrath *et al.*, 2015) (Fig. 1). Because priming initiates a state of readiness that does not confer resistance per se but rather permits for accelerated induced resistance as soon as an attack occurs. One presumed gain of priming is that it does not impose the costs related to complete implementation of induced defense response. In comparison with the animal immune system, priming of plant defence is often described as plant vaccination. Priming a powerful enhanced basal resistance, that’s controlled by a multitude of genes; therefore, priming of basal resistance is effective towards a broad range of biological threats (Ahmad et al., 2010; Conrath et al., 2015).

Priming stimuli

Priming stimuli covers a wide range of biological, physical, or chemical environmental inputs to which a plant responds by obtaining a memory. Plant defense priming can be induced by chemical compounds (BABA, salicylic acid, jasmonic acid, hexanoic acid, pipecolic acid, or volatile organic compounds), plant pathogens, insect herbivores (Conrath *et al.*, 2015; Llorens *et al.*, 2016). These inputs result in low-cost changes in the plant that include the accumulation of several metabolites.

The defense immune priming in plant life is initiated once the microbial extracellular systems and molecules such as exopolysaccharide, proteins, flagellins, etc., come in contact with the cellular receptors at the surfaces of the plants (Enebe and Babalola, 2018). Local infection of plants by pathogens will also result in structural and functional damage to the part affected. This disruption in the disruption in the structural and functional network will provoke signal transduction from the local site of the attack to distal parts of the plats for correct immune sensitization. This system is mediated through the amino acid glutamate and triggers long-distance calcium-based plant protection signaling (Toyota et al, 2018). In other words, this initiates the activation of a cascade of defense genes to produce reactive oxygen molecules, superoxide dismutase, peroxidise, and a host of other biomolecules (Luiz et al., 2015). These chemical compounds work both within and outside plants to achieve desired inhibitory effects on the pathogen. Priming of defense genes in plants as a result of inducers (microbes) or elicitors is termed induced systematic resistance. (Stangarlin et al., 2011). Plants defences can also be primed by beneficial microorganisms such as rhizobacteria and rhizofungi (Pieterese et al., 2014). Priming of plants with jasmonates or jasmonic acid is highly efficient and even deters relatively large insects such as pine weevils from de-barking coniferous plants (Berglund et al., 2016).

Enhanced defence responses to infection by *Pseudomonas syringa*e pv *tomato* bacteria were determined in diverse plants following foliar applications of thiamine confirmed that it has diverse, species, and genotype-specific priming effects. Moreover, when applied to seeds, thiamine also enhances resistance of numerous crops (including pea, barley, oat, wheat, and millet) against aphid pests (Hamada *et al.*, 2018; Hamada *et al.*, 2013) and fungal infections (Pushpalata et al., 2011).

Unlike mammals, plants life has a nonadaptive immune system that relies on biochemical changes. Nevertheless, priming of induced resistance influences responses after an initial stimulus, and it, therefore, represents a form of immunological memory that allows plants to recall stressful situations. Epigenetic modifications are one of the mechanisms that enable plants to acquire memory and can cause long-term alterations to gene responsiveness (Singh et al., 2014; Balmer et al., 2015; Mauch-Mani et al., 2017). Recent development has been made in comprehending the molecular basis of priming. For example, chemically induced priming in Arabidopsis is associated with the accumulation of inactive mitogen-activated protein kinases (Beckers et al., 2009). Priming has also been linked to di- or tri-methylation at lysine 4 of histone H3 (H3K4me2 and H3K4me3, respectively) and to lysine acetylation of histone H3 at lysine 9 (H3K9) or at lysine 5, 8, or 12 of histone H4 (H4K5, H4K8, and H4K12, respectively) in the promoter regions of defense-related genes (Jaskiewicz et al., 2011, Singh et al., 2014)

Transgenerational Immune Priming (TGIP)

Exposure to biotic stress can also generate long-term immunological 'memory', which enables the individual to develop faster and stronger defence responses to future exposures. Over recent years, evidence has accumulated that exposure of an individual to stress can also influence future stress responses in its offspring. Such effects are stated to as 'transgenerational', and are assumed to have evolved to maximize survival of an individual's gene pool in future generations which might be probable to stumble upon similar stresses. Although defence priming hardly ever provides full protection, its broad-spectrum effectiveness, long- lasting durability and inherited to future generations make it attractive for disease management. Recent findings revealed that defense priming can be inherited; a phenomenon refers to as transgenerational immune priming (TGIP) or transgenerational memories of plant defense. Progeny of the parental plants primed by treatment with BABA or infection with avirulent *P. syringae* bacteria, showed enhanced expression of SA-dependent defence genes and stronger resistance to infection by both virulent *P. syringae* and the downy mildew pathogen *Hyaloperonospora arabidopsidis* (Slaughter et al., 2012). Luna et al. (2012) also established priming of the progeny generation when parental Arabidopsis plants had been subjected to several inoculations with virulent bacteria *P. syringae*. In this study, not only was the primed state passed to the immediate offspring generation, but increased disease resistance could also be detected in the grandchildren of the original infected plants, and was therefore inherited over one stress-free generation.

Recently (Singh et al., 2017) made the important discovery that progeny from diseased plants are more resistant than genetically identical offspring from healthy plants. This increased resistance persisted over at least two stress-free generations, suggesting epigenetic inheritance. Resistant progeny did not show multiplied defence activity in the absence of pathogens, however rather exhibited increased responsiveness of defence genes to infection. This is a classical example of transgenerational immune priming since progeny plants are 'primed' to respond more rapidly to infection. Transgenerational immune responses have essential implications for natural plant populations and present a possibility for exploitation in sustainable agriculture. The capability to enhance resistance to pests and diseases through epigenetic manipulation presents a new mechanism by which reliance on chemicals can be reduced while not having to change the genetic makeup of our elite crop varieties.

Priming: Green Vaccination

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 (Walters et al., 2013). As there is an urgent need for new techniques that do not rely on pesticides or single resistance genes, the exploitation of the potential of the plant immune system in combination with other strategies may maintain the ability to achieve higher safety of crops. The elegance of priming for agricultural safety is also associated with the fact that this phenomenon, unlike the direct activation of defences, does not incur major developmental costs (van Hulten et al., 2006). There has already been a considerable translation of knowledge from the laboratory to the field (Walters et al., 2013).

Plant defense priming provides broad spectrum resistance against pests and pathogens, and is also durable. Once induced, priming can be maintained all through the life of a plant and so primed crops should require fewer pesticide applications in order to reach similar levels of protection. By reducing pesticide inputs, integration of transgenerational priming into existing crop protection schemes could provide multiple benefits to both growers and to the environment (Singh and Roberts, 2015). In agriculture, transgenerational priming of plant defences has the capability to make a contribution to sustainable intensification. An efficient induction of TGIP would allow poor farmers to collect their own seed stocks of more resistant crop varieties, thereby making their food production less vulnerable to outbreaks of pests and disease.

Priming would assist to develop new crop types that are better suited to modern agriculture. I argue that crop improvement efforts must include using elicitors to prime or activate induced resistance in the field and, above all, to select for triggered heritable epigenetic states in progeny that is primed for defense.

Conclusion

The plant immune system prevents most pathogens from entering the root or reaching levels that are harmful to the plant. Irrespective of whether or not the association is harmful, neutral, or beneficial to the plant, microbes can avoid and intrude with the plant immune system. A good method for crop disease management is the use of microbes capable of antagonistic behaviour against pathogens to induce systemic resistance in plant. Also, the application of elicitors on plants is yet another method of pathogen control. However, to achieve full defense of plants against pathogens, an integrated approach to disease management and control involving the use of microbes, their metabolites, synthetic chemicals, and plant extracts formulation which will applied simultaneously to the plant, will allow farmers win the war against plant pathogens, increase crop yields, and achieve a sustainable agricultural production. Plant defense priming seems an attractive strategy to achieve this (Fig. 2). Induced resistance by means of defence priming is durable. Once induced, priming can be maintained during the life of a plant and inherited epigenetically to subsequent generations. In addition to this, the activation of priming and the selection of cultivars with transgenerational defence priming holds many benefits to breeding programs for the development of beneficial new traits in crops. The capacity to enhance resistance to pests and diseases through this mechanism provides a new mechanism via reliance on chemicals can be reduced without having to change the genetic make-up of our elite crop varieties. This could similarly provide a valuable tool for reducing the residues of chemical pesticides in the fruits and also additionally generate valuable knowledge for aid programmes in India, where poor infrastructure and limited economic ability demand a small-scale and self-sustaining mode of agriculture. Under these circumstances, crop seed stocks are commonly maintained by means of farmers themselves. An efficient induction of TGIP would allow poor farmers to collect their own seed stocks of more resistant crop varieties, thereby making their food production less vulnerable to outbreaks of pests and disease.

In addition induced resistance may not provide the "normal" degree of protection that we generally observe after the application of pesticides; however, priming can be used in combination with pesticides, microbes, biological control, resistance breeding, or any other integrated disease management strategy. However, before it could be able to commercially applied, several aspects, starting with the priming mechanisms have to be elucidated. Assessments of priming treatments' persistence (duration of priming effects) and the range of biotic and abiotic stresses they may protect against are also warranted. Elucidation of mechanisms behind these diverse effects may provide highly interesting insights and opportunities in sustainable agriculture. I think it will not be exaggerating to conclude that plant defence priming/green vaccination is a smart plant health care for human welfare and could be a sustainable approach for crop protection with and broad effectiveness. We stand at the beginning of an exciting new road of research, wherein the mechanisms, ecological significance and potential applications of transgenerational plant defence just starting to be revealed.

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Figures:

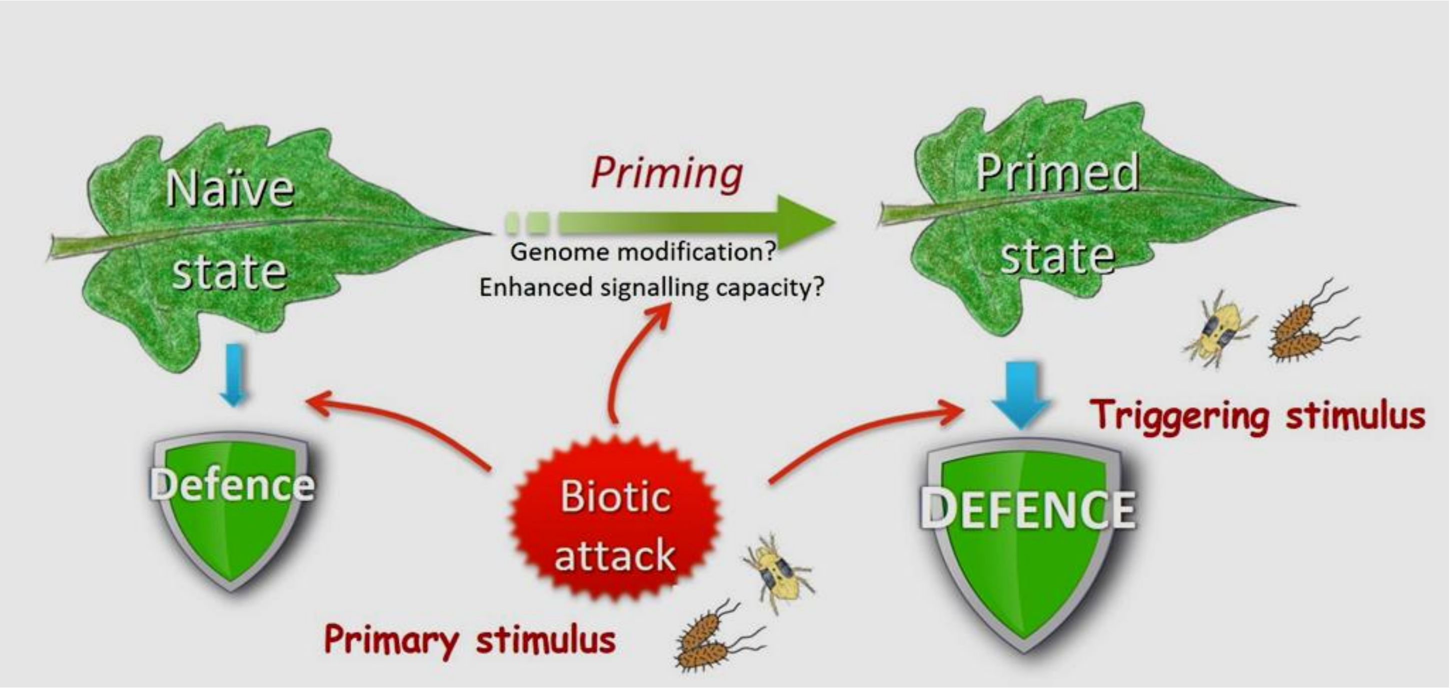

Figure 1. Diagram illustrating the principle of priming for defence. Leaves previously exposed to a priming signal are somehow able to responds more effectively to biotic attack, and consequently generate higher levels of resistance.

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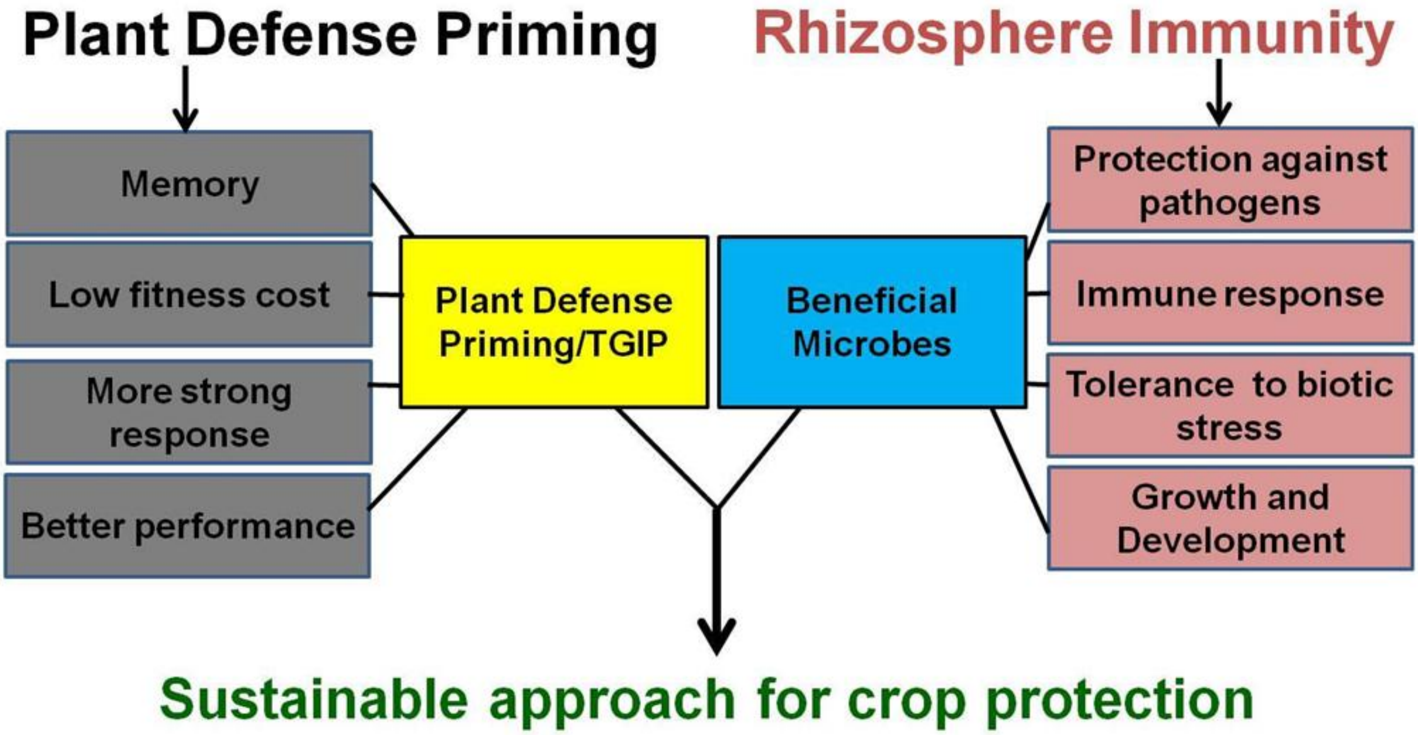

Figure 2. Schematic overview of the integration of priming and rhizosphere immunity as described in the main text for sustainable approach for crop protection.