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Research review paper

Bio-based resistance inducers for sustainable plant protection against pathogens

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ABSTRACT

An increasing demand for environmentally acceptable alternative for traditional pesticides provides an impetus to conceive new bio-based strategies in crop protection. Employing induced resistance is one such strategy, consisting of boosting the natural plant immunity. Upon infections, plants defend themselves by activating their immune mechanisms. These are initiated after the recognition of an invading pathogen via the microbe-associated molecular patterns (MAMPs) or other microbe-derived molecules. Triggered responses inhibit pathogen spread from the infected site. Systemic signal transport even enables to prepare, i.e. prime, distal uninfected tissues for more rapid and enhanced response upon the consequent pathogen attack. Similar defense mechanisms can be triggered by purified MAMPs, pathogen-derived molecules, signal molecules involved in plant resistance to pathogens, such as salicylic and jasmonic acid, or a wide range of other chemical compounds. Induced resistance can be also conferred by plant-associated microorganisms, including beneficial bacteria or fungi. Treatment with resistance inducers or beneficial microorganisms provides long-lasting resistance for plants to a wide range of pathogens. This study surveys current knowledge on resistance and its mechanisms provided by microbe-, algae- and plant-derived elicitors in different crops. The main scope deals with bacterial substances and fungus-derived molecules chitin and chitosan and algae elicitors, including naturally sulphated polysaccharides such as ulvans, fucans or carageenans. Recent advances in the utilization of this strategy in practical crop protection are also discussed.

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Introduction

In agriculture, plant varieties were domesticated and over time bred for yield and fruit quality. As a consequence, plant disease resistance is often decreased compared to wild varieties. Most crops are susceptible to numerous diseases caused by different microorganisms (pathogens). Diseases decrease crop yield and quality, and toxins released by some microorganisms may be present in the harvest. Formerly, plant diseases were responsible for severe economic and nutritional crises and are still currently responsible for a considerable loss in the worldwide crop production. To date, ensuring a satisfactory yield and the quality of the harvest requires an extensive use of numerous phytochemical pesticides. However, pesticides harm crops, the environment, even the health of farmers and consumers. Using pesticides also leads to the selection of resistant pathogen strains. For these reasons alternative and sustainable disease management is required. Alternatives include organic and integrated farming practices, biological control, the use of resistant hybrids or transgenic crops. However, some national legislative bodies do not allow genetic crop improvement by transgenesis and assisted crossing may also be prohibited for some crops, such as wine, protected by appellation seals. The strategy of induced resistance represents one alternative compatible with organic-farming. It consists of stimulating the plant immune system with elicitors, natural molecules that mimic a pathogen attack or a danger state, or by living organisms. Induced resistance may represent an interesting strategy for crops when fungicide-provided control is undesired.

Plant immunity

Plants possess an efficient and multifaceted immune system that is able to cope with most microbial invaders, such as bacteria, fungi, oomycetes or viruses, ubiquitously present in the environment. Besides the physical and chemical constitutive barriers, such as cuticle, cell walls, and antimicrobial phytoanticipins, plants possess a defense line that can be induced by the detection of microbial presence via immune receptors. The main and evolutionary older layer of this inducible immunity is based on the external recognition of "non-self" signals, notably microbe/pathogen-associated molecular patterns (MAMPs/PAMPs). These are conserved molecular structures essential for the overall fitness of microbes (Boller and Felix, 2009), such as flagellin from bacterial flagella or chitin or different glucans present in fungal/oomycete cell walls. Already many diverse MAMPs have been described; they can be (glyco) proteins, carbohydrates or lipids (Newman et al., 2013). The early external recognition is also achieved with the host-derived "danger" signals or damage-associated molecular patterns (DAMPs), such as pectin-derived oligogalacturonides, produced as a consequence of enzymatic microbial activities and toxins (Boller and Felix, 2009; Dodds and Rathjen, 2010). MAMPs and DAMPs are recognized by plasma-membrane localized pattern recognition receptors (PRRs) and induce a broad variety of defense responses commonly referred to as MAMP/PAMP/pattern-triggered immunity (MTI/PTI). First, following MAMP/DAMP binding, PRRs trigger a complex cascade of signaling events, including ion fluxes leading to plasma membrane depolarization, production of reactive oxygen species (ROS), nitric oxide (NO) and activation of Mitogen-Activated and Calcium-Dependent Protein Kinases (MAPKs and CDPKs; Boller and Felix, 2009; Boudsocq et al., 2010). These signaling events modulate transcription factor (TF) activities leading to massive transcriptional reprogramming related to defense. Defense gene activation results in the accumulation of different enzymes and stress-specific metabolites. Frequently found among them are, i) the pathogenesis-related (PR) proteins including hydrolytic enzymes (β-1,3-glucanases and chitinases), which degrade microbial cell walls, cationic defensins disrupting pathogen membrane, peroxidases, proteinase inhibitors or lipid-transfer proteins; ii) compounds with antimicrobial activity such as phytoalexins; iii) lignin and callose deposited to the cell wall assuring its strengthening. Other key stones of pattern-triggered immunity (PTI) are, iv) production of ROS with a signaling role and direct antimicrobial effect, or, v) stomatal closure (Boller and Felix, 2009; Dodds and Rathjen, 2010; Melotto et al., 2006). The immune responses are orchestrated by and depend on phytohormones, such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA; Glazebrook, 2005). The interplay and fine tuning between these hormones and others, such as auxins, brassinosteroids (BR) or giberellins, coordinate the activation of these above-mentioned defenses and allow directing immune responses against the specific intruder (Robert-Seilaniantz et al., 2011). Many of the defense responses depend strictly on these phytohormones (Glazebrook, 2005; Robert-Seilaniantz et al., 2011).

During infection, plant defenses are also activated by the recognition of pathogen effectors, molecules that pathogen secretes specifically upon infection to disrupt host immune system and gain more nutriments. The mechanisms of effector-triggered immunity (ETI) are similar to the above-mentioned PTI. Additionally, ETI is associated with hypersensitive response (HR), a strong local defense leading to programmed cell death at the site of infection (Dodds and Rathjen, 2010).

Besides the local defenses, an infection further triggers systemic acquired resistance (SAR; Fig. 1, Pieterse et al., 2009). In SAR, the defense alert is amplified and transferred from the site of infection by a system of mobile signals into distal (systemic) plant parts (Conrath, 2011). The phenomenon of priming is a critical component of SAR. Primed tissues are in an alert state that enables them to more rapidly and efficiently confront both biotic and abiotic stresses. In such potentiated cells, the defense compounds are only expressed upon the pathogen challenge (Conrath, 2011). Because defense is costly, priming thus saves energy by minimalizing allocation costs and limits the impact on the growth and development (Conrath, 2011; Zamioudis and Pieterse, 2012). Some of the molecular mechanisms that underlie priming have

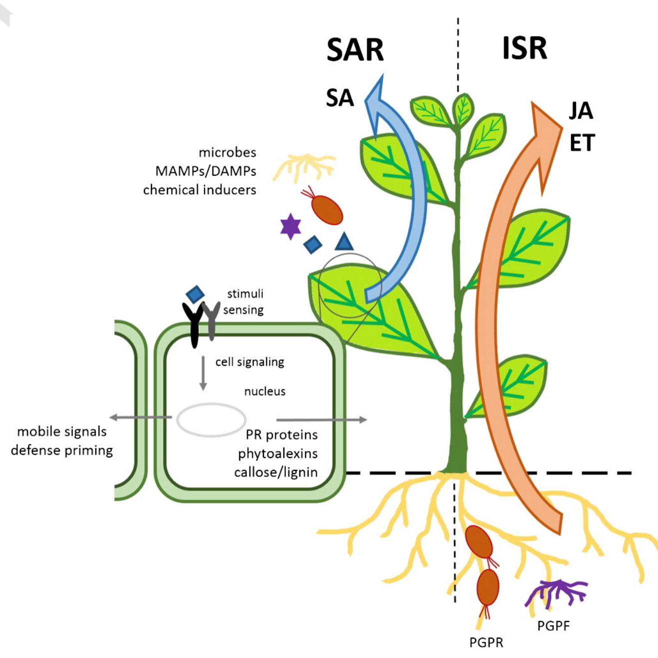

Fig. 1. Scheme of different types of systemic resistance. The systemic acquired resistance (SAR, the left scheme part) is triggered upon pathogen attack, foliar treatments of plants with MAMPs, DAMPs, plant phytohormones or chemical activators. After the recognition by a sensor, the plant cell triggers complex signaling and defense responses, including production of pathogenesis-related (PR) proteins, antimicrobial phytoalexins or cell wall fortification with callose or lignin. Local defenses are followed by the production of mobile signals that are transported via xylem and prime distal plant parts for defense compounds accumulation. Induced systemic resistance (ISR, the right scheme part) can be triggered by root colonization with plant-growth-promoting rhizobacteria (PGPR) or fungi (PFPF). ISR is SA-independent, governed mainly by jasmonic acid (JA) and ethylene (ET). Both SAR and ISR prime for enhanced and accelerated defenses upon subsequent biotic and abiotic stresses. Redrawn and modified from Pieterse et al. (2009).