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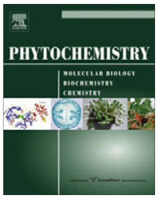

Review

Jasmonate signaling in plant interactions with resistance-inducing beneficial microbes

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ABSTRACT

Beneficial soil-borne microorganisms can induce an enhanced defensive capacity in above-ground plant parts that provides protection against a broad spectrum of microbial pathogens and even insect herbivores. The phytohormones jasmonic acid (JA) and ethylene emerged as important regulators of this induced systemic resistance (ISR). ISR triggered by plant growth-promoting rhizobacteria and fungi is often not associated with enhanced biosynthesis of these hormones, nor with massive changes in defense-related gene expression. Instead, ISR-expressing plants are primed for enhanced defense. Priming is characterized by a faster and stronger expression of cellular defense responses that become activated only upon pathogen or insect attack, resulting in an enhanced level of resistance to the invader encountered. Recent advances in induced defense signaling research revealed regulators of ISR and suggest a model in which (JA)-related transcription factors play a central role in establishing the primed state.

Contents

Abbreviations: BTH, benzothiadiazole; ET, ethylene; ETI, effector triggered immunity; ISR, induced systemic resistance; JA, jasmonic acid; LPS, lipopolysaccharides; MAMPs, microbe-associated molecular patterns; MAPKs, mitogen activated protein kinases; PAMPs, pathogen associated molecular patterns; PGPR, plant growth-promoting rhizobacteria; PGPF, plant growth-promoting fungi; PR, pathogenesis related; PTI, PAMP-triggered immunity; RT-PCR, real-time reverse transcriptase polymerase chain reaction; SA, salicylic acid; SAR, systemic acquired resistance; VOCs, volatile organic compounds.

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1. Introduction

Plant roots are surrounded by a nutrient-rich habitat, called the rhizosphere, which provides a niche to a large and diverse community of microorganisms that thrive on root exudates (Lugtenberg et al., 2001; Walker et al., 2003). Within this community of competing and interacting microbes, a whole range of parasitic and beneficial microorganisms can be found that either cause disease or enhance plant performance, respectively. Mycorrhizal fungi and *Rhizobium* spp. are amongst the best-studied beneficial microorganisms. Mycorrhizal fungi provide the host with an enhanced root surface to absorb water and mineral nutrients such as phosphate (Harrison, 2005; see review by Hause and Schaarschmidt in this issue), whereas *Rhizobium* spp. fix nitrogen from the atmosphere into ammonium which can be used for amino acid biosynthesis (Spaink, 2000; see review by Hause and Schaarschmidt in this issue). Plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF) are another class of soil-borne microbes with beneficial effects on plant performance. PGPR and PGPF are non-pathogenic and occur in large numbers in the rhizosphere. They can stimulate plant growth by enhancing the plant's photosynthetic capacity (Zhang et al., 2008), by increasing tolerance to abiotic stress (Yang et al., 2009), or by suppressing plant diseases (Harman et al., 2004; Kloepper et al., 2004; Pozo and Azcon-Aguilar, 2007; Van Loon et al., 1998) and insect herbivory (Van Oosten et al., 2008; Zehnder et al., 2001). The disease suppressive activity of PGPR and PGPF is exerted either directly by hampering growth and development of soil-borne pathogens through competition for nutrients or secretion of antibiotics in the rhizosphere (Bakker et al., 2007; De Bruijn et al., 2007; Debode et al., 2007; Handelsman and Stabb, 1996; Kamilova et al., 2008), or indirectly by eliciting a plant-mediated systemic resistance response (Kloepper et al., 2004; Van Loon et al., 1998; Van Wees et al., 2008). Systemic resistance triggered by beneficial microorganisms confers a broad-spectrum resistance that is effective against different types attackers. The phytohormone jasmonic acid and its derivatives, collectively called jasmonates (JAs), emerged as important regulators of this systemic immune response. Here, we review our current understanding of the signaling pathways that control the immune responses that are triggered by beneficial microbes, with special emphasis on the regulatory role of JAs in this process.

2. Systemically induced disease resistance

2.1. Systemic acquired resistance

In the 1960s, Ross demonstrated that limited primary infection with a pathogen rendered non-infected plant tissues more resistant to subsequent pathogen attack. This long-lasting and broad-spectrum induced disease resistance is referred to as systemic acquired resistance (SAR; Durrant and Dong, 2004; Ross, 1961). The onset of SAR is associated with increased levels of salicylic acid (SA), and is characterized by the coordinate activation of a specific set of *PATHOGENESIS-RELATED* (*PR*) genes, many of which encode PR proteins with antimicrobial activity (Van Loon et al., 2006). Studies with transgenic and mutant plants that are impaired in the production or perception of SA demonstrated a central role for this phytohormone in SAR (Loake and Grant, 2007; Vlot et al., 2008). The regulatory protein NPR1 (NONEXPRESSOR OF *PR* GENES1) emerged as an important transducer of the SA signal, which upon activation by SA acts as a transcriptional co-activator of *PR* gene expression (Dong, 2004). Besides SA, other hormones are implicated in SAR signaling as well. In tobacco, Verberne et al. (2003) demonstrated that ethylene (ET) perception is required for the onset of SA-dependent SAR that is triggered upon infection by tobacco mosaic virus. In addition, Truman et al. (2007) showed that the JA-signaling mutants *sgt1b* (*suppressor of g2 allele of SKP1 1b*), *opr3* (*12-oxo-phytodienoate reductase 3*) and *jin1* (*jasmonate insensitive 1*) failed to develop SAR upon leaf infiltration with an avirulent strain of the pathogen *Pseudomonas syringae* pv. *tomato*, suggesting that JAs play a role in SAR as well. However, other JA-signaling mutants such as *jar1* (*jasmonate resistant 1*), *eds8* (*enhanced disease susceptibility 8*), and *coi1* (*coronatine insensitive 1*) were shown to develop normal levels of SAR (Attaran et al., 2009; Cui et al., 2005; Pieterse et al., 1998; Ton et al., 2002a). Hence, the exact role of JA signaling in SAR needs to be further explored.

2.2. Induced systemic resistance

Besides pathogens, also non-pathogenic microbes can elevate the level of disease resistance in plants. This was first evidenced by experiments in which colonization of plant roots by PGPR were shown to protect above-ground plant tissues against different types of pathogens (Van Loon et al., 1998). Like pathogen-induced SAR, this PGPR-mediated induced systemic resistance (ISR) has been demonstrated in many plant species and has a broad-spectrum of effectiveness (Kloepper et al., 2004; Van Loon and Bakker, 2006; Van Loon et al., 1998; Van Wees et al., 2008). Among the ISR-inducing PGPR documented to date are many non-pathogenic *Pseudomonas* spp. and *Bacillus* spp. (Kloepper et al., 2004; Van Loon and Bakker, 2006). Although both SAR and ISR are effective against different types of pathogens, their range of effectiveness is partly divergent. For instance, in *Arabidopsis thaliana* it was shown that SAR triggered by an avirulent strain of the bacterial leaf pathogen *P. syringae* pv. *tomato* and ISR elicited by the PGPR *Pseudomonas fluorescens* WCS417r (WCS417r) are similarly effective against diseases caused by virulent *P. syringae*, the fungal root pathogen *Fusarium oxysporum*, and the downy mildew pathogen *Hyaloperonospora arabidopsidis* (Pieterse et al., 1996; Ton et al., 2002b). However, SAR was shown to be effective against turnip crinckle virus, whereas ISR was not (Ton et al., 2002b). Conversely, ISR was shown to protect *Arabidopsis* against the necrotrophic pathogens *Alternaria brassicicola* (Ton et al., 2002b), *Botrytis cinerea* (Van der Ent et al., 2008) and *Plectosphaerella cucumerina* (Segarra et al., 2009), whereas SAR was ineffective against these pathogens. Over the last decade it has become clear that, like PGPR, many PGPF are able to trigger a similar broad-spectrum ISR. Amongst the documented ISR-inducing PGPF are mycorrhizal fungi (Pozo and Azcon-Aguilar, 2007) and non-pathogenic strains of *F. oxysporum* (Duijff et al., 1998; Paparu et al., 2007), *Trichoderma* spp. (Vinale et al., 2008), *Penicillium* sp. GP16-2 (Hossain et al., 2008), *Pythium oligandrum* (Hase et al., 2008), *Piriformospora indica* (Waller et al., 2005) and related *Sebacinales* spp. (Waller et al., 2008).