



A review of the effects of soil organisms on plant hormone signalling pathways



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ABSTRACT

Plants interact with a large number of soil organisms. For a long time, these interactions have been the research area of soil ecologists and trophic relationships and physico-chemical modifications of the soil matrix were generally proposed as mechanisms underlying plant-soil organism interactions. However, some specific symbioses and diseases have been well characterized at the molecular level by plant biologists and microbiologists. These interactions involve a physical contact between soil organism and plant. They are mediated through signal molecules that play upon the different plant hormonal signalling pathways, leading to modifications in plant development and defence. Nowadays, the role of signal molecules emerges as an important feature of interactions between plants and free-living soil organisms. In this review we discuss genetic and physiological evidences of hormone signalling involvement in plant response to physically associated but also free-living soil organisms, for very different taxa ranging from the micrometer to the centimetre scales. The same hormone signalling pathways seems to be activated by very different kinds of soil organisms such as bacteria, nematodes, collembola and even earthworms, with common consequences on plant growth, development and defence. Plant hormonal homeostasis appears to be the corner stone to understand and predict the issue of the multiple interactions that plants entertain with the community of soil organisms.

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1. Introduction

Soil organisms, defined as organisms spending one part of their life cycle in the soil and interacting with plant belowground organs, coevolved with plants, becoming more or less strong selective constraints. The physical association between plants and soil organisms such as arbuscular-mycorrhiza (AM), ecto-mycorrhiza (ECM) and pathogens has led to co-evolution *sensu stricto*, revealed by a molecular dialog between plant and soil organism (Desbrosses and Stougaard, 2011; Robert-Seilaniantz et al., 2011). These organisms generally dependent on plant for their resources and their habitat could even hijack plant morphogenesis to create their own niche (Odling-Smee et al., 1996). The production of elicitor specifics of the host plant is required for the establishment of a compatible association. Free-living organisms without physical contact with plants have developed diffuse co-evolution with plants (Janzen, 1980), since biotic and abiotic environment of the two partners influences

their relationships. These organisms are less dependent on plants for their survival and reproduction. In this case, the release of non-specific diffusible signal molecules initiate the dialog between plant and free-living organisms.

Up to now, knowledge about soil organism impact on plants is generally viewed as a collection of studies involving a plant and one specific soil organism well known by a restricted number of specialists. Few papers consider analogies in plant response to very different soil organisms (Grunewald et al., 2009b; Hause and Schaarschmidt, 2009; Lohar et al., 2004). However, we will show that the development of the use of mutants or -omic methods reveals common features in plant response to a diversity of soil organisms such as bacteria, fungi, but also protozoa, nematodes and earthworm. Here, we propose the hypothesis that the diversity of plant-soil organism interactions is mainly based on signal molecules which impact a restricted number of plant signalling pathways. Our review aims at describing a general emerging framework for soil organism effects on plant signalling pathways, covering a large spectrum of taxa from microorganisms to micro-, meso- and macro-fauna, physically associated or not with plants. Interactions between plants and leaf pathogens have been

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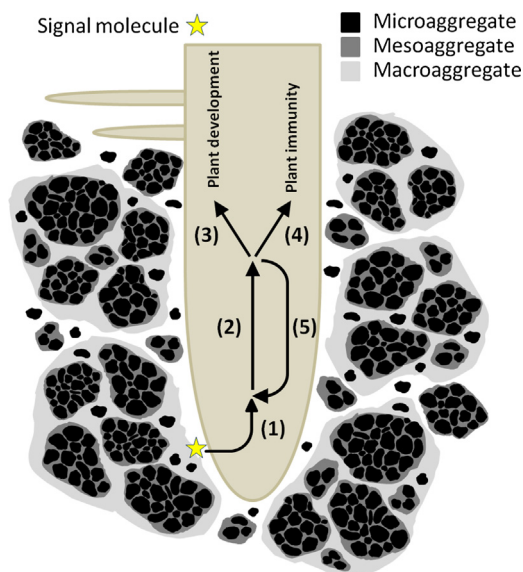


Fig. 1. From perception to adaptation of plants to soil organisms. (1) Signal molecules produced by soil inhabitants are perceived by plant receptors. (2) This leads to changes in plant hormone transport and signalling pathways. (3) Plant development or (4) immunity is modified according to hormonal signalling pathways. (5) Positive and negative feedback loops on the same hormone or crosstalk with other ones reinforce or temper plant adaptation to the soil community. Note that described mechanisms can occur within the whole root system and not exclusively at the root tip level. These different steps are detailed successively in Section 3.

reviewed elsewhere (see Robert-Seilaniantz et al., 2011; Denancé et al., 2013 for recent and comprehensive reviews). They will be excluded from the review even if these pathogens spend some life stages in the soil.

2. Soil from a biotic perspective

Soil is made of aggregates, produced by organisms and called biogenic structures (Fig. 1). Biogenic aggregates are temporary structures which disappear after a given period of time and are replaced by new ones in the presence of soil organisms (Lavelle et al., 1997; Six et al., 2004). In these aggregates, soil particles are gathered through weak bounds thanks to organic matter and clays, but also by organic compounds produced by soil organisms such as mucilage, exopolysaccharides and biofilms. These aggregates are often embedded one in another, according to their size (Fig. 1) (Six et al., 2004). The larger ones, called macroaggregates, are produced by macrofauna, e.g. earthworm's casts (dejections) and burrows, termite's mounds and foraging shelters, ant's nest and mounds. Mesoaggregates are shaped by millipedes (myriapodes) and spring-tails (collembolan) by a digestive process, and microaggregates are produced by bacteria and fungi through organic compound emission and biofilm production (Lavelle and Spain, 2001). These biogenic structures exhibit specific physical, chemical and biochemical properties, which influence plant physiology. Among these biochemical compounds, signal molecules are involved in the communication between soil organisms and plants (Zhuang et al., 2013). Inside the plant, hormone signalling pathways are likely the major hubs of complex networks that link plant with soil organisms (Atkinson and Urwin, 2012; Kazan, 2013). The perception of biochemical signals emitted by soil organisms and its transduction via plant hormone signalling pathways can be used by plants to get information on its biotic environment especially to specific soil communities (Bais et al., 2006; Kazan, 2013). In the following section we will provide a quick summary on plant hormone signalling networks.

3. Signal molecules and hormone signalling networks involved in plant development and defence

Genetic evidences of the involvement of hormone signalling in the response of plants to soil organisms are generally provided using loss-of-function or gain-of-function mutants affected in one or more gene encoding proteins involved in hormone signalling pathway. Using this strategy, several steps from signal perception to adaptation have been identified (Fig. 1): after (1) the perception of biochemical compounds, (2) these signals are transduced in cells and modulate gene expression; during the signalling step *sensu stricto* different response mechanisms are activated leading to (3) the modification of plant development or (4) defence mechanisms, with consequences on plant growth; (5) feedback loops on the same or other signalling pathways ensure a coordinated response. These different steps are detailed successively in the following sub-sections.

3.1. Signals

Signal molecules are molecules with strong effects on organism physiology despite their presence at very low concentration in the environment (Zhuang et al., 2013). They are generally associated with qualitative changes (e.g. development and/or defence), which could result in quantitative changes (e.g. growth). They differ from nutrients which are constitutive of biomass, generally present at relatively high concentration and responsible for quantitative changes, not always due to qualitative ones. The main signal molecules in plants are hormones, such as auxins (IAA), cytokinins (CK), gibberellins (GA), abscisic acid (ABA), ethylene (ET), jasmonic acid (JA) and salicylic acid (SA) synthesized in plant cells. Several soil microorganisms exhibit their own biosynthetic pathway for the major plant hormones, which can be produced in culture media (Frankenberger and Arshad, 1995; Persello-Cartiaux et al., 2003; Robert-Seilaniantz et al., 2011). Soil organisms can also produce phytotoxin like coronatine, a mimic of jasmonic acid (JA)-isoleucine, but also signal molecules recognized as elicitors of plant defence such as chitin, flagellin and lipopolysaccharide (Bakker et al., 2007; Pieterse et al., 2009). Some of these signals are gaseous molecules, generally volatile organic compounds (VOCs) (Desbrosses et al., 2012; Ping and Boland, 2004). Some soil organisms can degrade plant hormones or their precursors; for example, bacteria are able to reduce ET concentration through an 1-Amino cyclopropane-1-carboxylic acid deaminase (AcdS) activity, which degrades the plant ET precursor 1-amino cyclopropane-1-carboxylic acid (ACC) in α -ketobutyrate and ammonia (Desbrosses et al., 2012; Glick, 2005). In a lesser extent, signal molecules could also be components of the plant released during interaction with pathogens (Hernández-Mata et al., 2010).

3.2. Hormonal signalling networks

After signal perception by the plant, the transfer of this signal is relayed by hormonal signalling pathways under the influence of major plant hormones (Fig. 2). Here we will provide background elements to the neophyte, in the aim to get straight to the point in the following sections.

3.2.1. Auxin

Indole acetic acid (IAA) signalling relies on the influx of IAA into the cells through IAA influx carrier (AUX1) proteins. IAA stabilizes the interaction between the F-Box transport inhibitor response 1/auxin signalling F-box (TIR1/AFB) receptor located into the Skp Cullin F-Box (SCF) SCF^{TIR1/AFB} E3 ubiquitin ligase complex and the negative regulator of IAA responsive genes auxin/indole-3-acetic

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