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Chemical communication: An evidence for co-evolution between plants and soil organisms

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ABSTRACT

What we call "humus" is a huge collection of organic molecules, among which physiologically active compounds with important ecological roles can be found. These molecules are produced by soil organisms and plants. Soil organisms physically associated with plants such as some bacteria are well known for their effects on plants through signal molecules inducing changes in plant hormone signaling pathways and growth. It has been recently shown that soil animals such as earthworms, which live in the bulk soil without physical contact with plant roots, are also able to modify plant development, immunity and growth through signal molecules. Modification of plant growth and fitness through the emission of signal molecules is in fact a general mechanism in the aboveground-belowground interactions. Plants also produce root exudates among which many molecules are interpreted as signals by soil organisms. Because of this reciprocal signal emission and subsequent adaptations with important consequences on plants and soil organisms' fitness, I propose that coevolution exist between plants and soil organisms.

1. Introduction

The humus system is a huge reservoir of mineral and organic molecules shaped by soil organisms. Humic substances are very diverse and the specific role of many of them is still poorly documented. However, it is acknowledged that humic acids may display hormone-like activity on plant physiology, i.e. they can have huge effect on plant physiology even at low concentration. The best documented case studied since 1914 (Bottomley, 1914) is the auxin-like effects of low molecular size humic fraction which can enter in root cells, with modifications of many physiological mechanisms (reviewed in Nardi et al., 2002). Signal molecules can be either produced by soil organisms, defined as organisms spending one part of their life cycle in the soil, or released following their death. In both these cases, these signals can be either directly absorbed by plant roots, or temporarily stored through adsorption on humus and released later, under the influence of biological activities or physico-chemical mechanisms.

The effects of soil organisms on plants through signal molecules are well studied in plants-microorganisms interactions, especially in the symbiosis between legumes and Rhizobium, plants and mycorrhizae, or plants and Plant Growth Promoting Rhizobacteria (PGPR) interactions.

More recently, it has been shown that soil organisms as "big" as earthworms can also interact with plants through signal molecules. Signal molecules emission by free-living soil organisms is in fact a general mechanism of ecological interaction in the belowground-aboveground relationships, which could help to understand the regulation of food webs (DeAngelis, 2016). However, the evolutionary consequences of this chemical communication are poorly investigated (Barot et al., 2007).

Because soil organisms affect plant development and immunity, but also growth, competition, survival and fitness, plant evolution is closely linked to soil organism activities. Here, I consider "coevolution" as a change in a trait in individuals in one population in response to a trait of the individuals in another population, followed by an evolutionary response by the second population to the change in the first (Janzen, 1980). Showing that adaptive changes in one taxa is associated with adaptive changes in another taxa, especially through signal molecule emission and perception, will help to demonstrate the existence of a coevolution between plants and soil organisms. I will first present recent advances on the involvement of signal molecules in the effect of earthworms on plants as a case study, show that the emission of signals is a very common way through which soil organisms influence plants and then present the reverse way: signal emission by plants with effects on soil organisms.

2. A case study: earthworm effect on plant growth rely on signal molecules

Earthworms are well known for their positive effect on plant growth (Brown et al., 1999; Groenigen et al., 2014; Scheu, 2003). They play a

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major role in soil function and are responsible for many ecosystem services (Blouin et al., 2013). For example, the tropical earthworm *Reginaldia omodeoi* Sims, formerly known as *Millsonia anomala*, can ingest up to 30 times its own biomass of soil per day. Overall, earthworms may ingest 850 to 1350 t dry soil per ha per year and soil of the upper 30 cm is almost entirely comprised of earthworm casts aged 0,5 to 3 years on average depending on depth (Lavelle, 1978; Lavelle and Spain, 2001). Earthworms are thus studied since several centuries for their involvement in humus formation (Darwin, 1881). A hormone-like activity of humic substances has been observed with humic substances extracted from earthworm faeces (Canellas et al., 2002). More precisely, indole acetic acid (IAA), which belongs to the auxin family, has already been identified in the low molecular size humic fraction from earthworm casts (Muscolo et al., 1998). These compounds can affect respiration, photosynthesis, morphology, lateral root development or oxidase activity (Nardi et al., 2002) and the expression of genes coding for nitrate transporters and H^{+}-ATPases (Quaggiotti et al., 2004).

As a consequence, changes in plant morphogenesis and resistance to pathogens have been observed in the presence of earthworms (Blouin et al., 2005; Jana et al., 2010) or in the presence of the compost they produce (Arancon et al., 2003; Zaller, 2007). These plant responses were not due to a trophic mechanism, as suggested by experiments with earthworms and different levels of fertility or nutrient supply (Blouin et al., 2006; Laossi et al., 2009a, 2009b). They were responsible for modifications of plant growth (Brown et al., 1999; Groenigen et al., 2014; Scheu, 2003), competition (Laossi et al., 2009a,b), survival and fitness (Laossi et al., 2011, 2010).

When we looked at plant overall response to earthworm faeces in an *in vitro* device where only signal molecules could have an effect on plant growth (Puga-Freitas et al., 2012), we observed that earthworms were inducing positive or negative effects on different plant species. Then, using an *Arabidopsis thaliana* mutant with an impaired auxin transport, we demonstrated the potential of earthworms to stimulate root growth and to revert the dwarf mutant phenotype (Fig. 1). Finally, we performed a comparative transcriptomic analysis of *Arabidopsis thaliana* in the presence and absence of earthworms; we found that genes modulated in the presence of earthworms are known to respond to biotic and abiotic stresses or to the application of exogenous hormones. A comparison of our results with other studies found in databases revealed strong analogies with systemic resistance, induced by signal molecules emitted by Plant Growth Promoting Rhizobacteria and/or elicitors emitted by non-virulent pathogens.

3. Plant hormone signaling pathways: a generic target in the effect of soil organisms on plants

Up to now, knowledge about soil organism impact on plants is generally dispersed in a collection of studies involving a plant and one specific soil taxa well known by a restricted number of specialists. However, new tools developed in plant sciences, such as the use of *Arabidopsis thaliana* mutants or transcriptomic analyses, and conceptual framework developed in soil ecology help in revealing the common features in the effect of many soil organisms on plant development and immunity.

Due to the combined action of soil fauna and microorganisms, humic substances are often embedded in hierarchical structures called micro-, meso- and macro-aggregates (Fig. 2), in an embedded framework of self-organized systems (Lavelle et al., 2006). Soluble molecules can diffuse into the soil matrix. They can pass through root cell membrane by an active or passive transport. Alternatively, they can act as elicitors, being sensed by membrane receptors which induce the release of second messengers. These signal molecules or their messengers can spread in plant organs via the xylem and phloem and induce physiological reactions at a systemic level. As a consequence, plant development and immunity can be modified, with retroaction loops which could repress or amplify the signal (Fig. 2) (Puga-Freitas and Blouin, 2015).

The diversity of taxa involved in modifications of hormone signaling pathways in plants is very important (Table 1). Among this diversity, soil organisms spending at least one part of their life cycle in physical contact with plant roots are the best documented. Some bacterial taxa such as Rhizobium, Agrobacterium and other pathogens have been showed to modify plant development through auxins, cytokinins and ethylene and plant immunity through ethylene, jasmonic acid, salicylic acid, gibberellic acid or abscisic acid. Signaling pathways involved in the effect of AM, ECM, endophytic and pathogenic fungi are the same than for bacteria when plant development is concerned and ethylene, jasmonic acid and abscisic acid pathways when immunity is concerned. Even eukaryotes such as protozoa and nematodes are known to modify plant development through auxins and cytokinins. Their effect on plant immunity has not yet been characterized.

Among free-living soil organisms, Plant Growth Promoting Rhizobacteria (PGPR) are the most famous for their production of a huge number of molecules affecting plant growth through signaling pathways involved in development and immunity (Fig. 3). PGPR belong to different taxonomic groups, but have been studied in depth in the Proteobacteria.They possess many genes involved in plant-beneficial functions, such as nitrogenase (nitrogen fixation), pyrroloquinoline

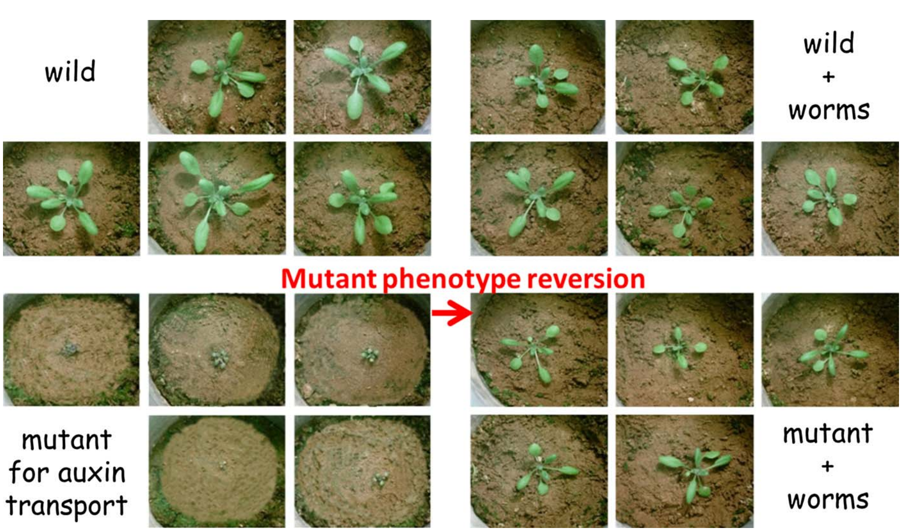

Fig. 1. Effects of the earthworm *Apporectodea caliginosa* on the growth of Arabidopsis thaliana cv. Columbia and aux1-7;axr4-2 mutant (aux is a gene encoding an auxin transporter and axr is a gene involved in the localization of the AUX protein at the top of the cell, which is responsible for a polarized transport from shoot apex to root tips.
Modified from Puga-Freitas et al., 2012, Public Library of Science One.