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Review

Comparative proteomic studies of root–microbe interactions

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ABSTRACT

The growth and performance of roots are significantly influenced by microbes colonizing the rhizosphere, including bacteria, fungi and nematodes. These root–microbe interactions can be beneficial, neutral or detrimental to the plant host. To improve plant growth, the use of specific soil microbes could be an affordable and sustainable strategy. A growing number of proteomic studies are focusing on determining the effects that microbes have on roots, in order to identify genes and proteins that are specifically induced by microbes. Studies have particularly focused on two mutualistic symbioses of roots, those of legumes with nitrogen-fixing rhizobia and those of a large range of plants with mycorrhizal fungi. In addition, the pathogenic relationships between roots and endoparasitic nematodes, fungi and oomycetes have been studied to unravel the molecular communication between roots and pathogenic microbes. These studies have led to new insights into the detection of microbial signal molecules by plants, the balancing of defense responses, nutrient exchange and the alteration of plant development by microbes. This review highlights some of the recent advances gained by proteomic studies focusing on symbiotic and pathogenic root–microbe interactions.

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1. Introduction

Many plants enter into symbioses with soil-borne microorganisms, which can support nutrient uptake, increase resistance against pathogens and enhance plant growth. In the last ten years, proteomics has been applied to the identification of proteins that are important in the plant responses to microorganisms. A particular challenge is the physical intimacy of plant and microbial partners, which are often housed inside plant tissues as endophytes. Previous reviews have addressed some of the technical difficulties of proteomics approaches taken to study plants and plant–microbe symbioses [1–6]. The application of proteomics in plant–pathogen interactions has had its major focus on pathogens targeting the shoot with a lesser emphasis on root pathogens [7,8]. This review will focus on proteomic analyses that have studied root symbionts and pathogens to provide an overview of the insights gained in our understanding of how roots deal with the complex array of micro-organisms they are exposed to in the soil.

2. Symbiotic root–microbe interactions

2.1. *The symbiotic legume–rhizobia interaction*

One of the best studied symbiotic root–microbe interactions is that between legumes and nitrogen-fixing soil bacteria called rhizobia (Fig. 1). Rhizobia invade the roots of specific legume partners through root hairs or via crack entry, largely avoiding plant defense responses. Rhizobia produce species-specific lipochitin oligosaccharides (Nod factors) which are perceived by plant LysM-like receptors and activate a signal transduction pathway required for the invasion process and the subsequent development of a new root organ, the nodule [9,10]. Rhizobia remain outside the plant cytoplasm and are engulfed in a symbiosome membrane, which functions to regulate nutrient exchange between the partners. Nodules arise from re-differentiating root pericycle and cortical cells and are later invaded by rhizobia [11]. After further growth and differentiation of the nodule, the rhizobia start converting nitrogen from the air into ammonia, which is exported to the plant as amino acids. In exchange, rhizobia import carbon from the plant. This nutrient exchange requires coordination of transport processes by both partners [12]. The *Rhizobium*-legume (hereafter abbreviated RL) symbiosis also requires feedback mechanisms, so that symbiosis can be limited at times of sufficient nitrogen supply of the plant [13].

Symbioses between nitrogen-fixing bacteria and legumes are very specific and do not occur in the model plant *Arabidopsis thaliana*. Therefore, two model legumes have been in the forefront of proteomic and genomic research into symbiotic root–microbe interactions, *Medicago truncatula* and *Lotus japonicus* [14,15]. Both legumes have small diploid genomes of 470 to 550 Mb in size, have short regeneration times, are self-fertile and are relatively easy to transform and regenerate. Soybean is a third important legume with a more complex genome, but of major importance as a crop itself and as a model for beans [16]. Genomic and EST sequences of these three model legumes are available which have been essential for the identification of proteins by mass spectrometry

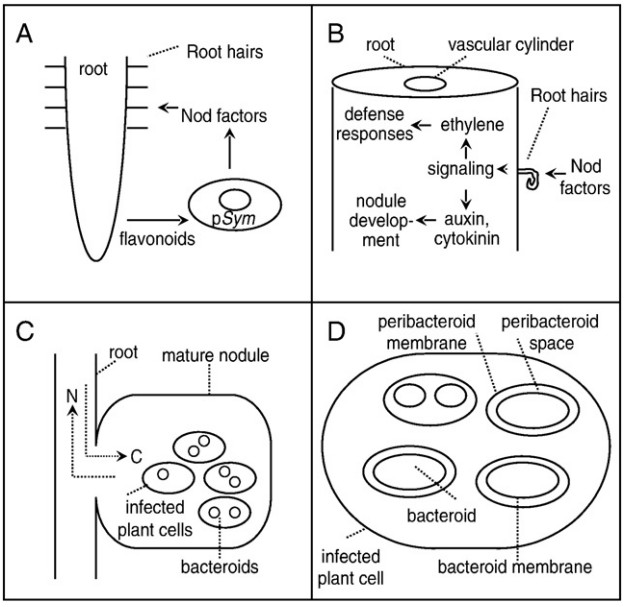

Fig. 1 – Schematic diagram of different stages in the *Rhizobium*-legume symbiosis. A: During the earliest stages of the interaction, the root exudes flavonoids from the zone behind the root tip. Certain flavonoids activate the expression of nodulation genes, typically encoded on the *Sym* plasmid(s) (p*Sym*) of rhizobia. This leads to the synthesis of Nod factors, which are perceived by receptors in the host root hairs. B: Nod factor perception triggers a signal transduction cascade in the root which is required for nodule development and the regulation of defense responses. Nodule development is partially controlled by changes in the hormone balance (mainly auxin and cytokinin); defense responses are partially mediated by ethylene signaling. C: After stimulating nodule development, rhizobia infect root cells and differentiate into bacteroids. Bacteroids fix atmospheric nitrogen which is exported to the plant (e.g. as amino acids or ureides), while plant carbon is redirected into the functioning nodule. D: A plant cell inside the central infection zone of a nodule is typically infected by thousands of bacteroids. The bacteroids are surrounded by the peribacteroid (or symbiosome) membrane (derived from the plant plasma membrane), as well as the bacteroid membrane (derived from the bacterial membrane). Each peribacteroid membrane can engulf one or several bacteroids. N.B. figure is not to scale.

[17]. In addition, the genomes of several nitrogen-fixing bacteria have been sequenced, including *Sinorhizobium meliloti*, the symbiont of *M. truncatula* [18], *Mesorhizobium loti*, the symbiont of *L. japonicus* [19] and *Bradyrhizobium japonicum*, the symbiont of soybean [20]. The complete sequenced genomes of these rhizobia enabled the dissection of the proteomes of the bacterial partners harbored inside nodule tissues and a comparison of rhizobia protein accumulation in free-living compared to symbiotic conditions [21,22]. Partial proteome reference maps of root tissues have been established which provide a baseline of root-expressed proteins in legumes [23–28].

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