



Review article

Early signaling, synthesis, transport and metabolism of ureides

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ABSTRACT

The symbiosis between α nitrogen (N_2)-fixing *Proteobacteria* (family Rhizobiaceae) and legumes belonging to the Fabaceae (a single phylogenetic group comprising three subfamilies: Caesalpinioideae, Mimosoideae and Papilionoideae) results in the formation of a novel root structure called a nodule, where atmospheric N_2 is fixed into NH_3^+ . In the determinate type of nodules harbored by *Rhizobium*-nodulated Fabaceae species, newly synthesized NH_3^+ is finally converted into allantoin ($C_4H_6N_4O_3$) and allantoic acid ($C_4H_8N_4O_4$) (ureides) through complex pathways involving at least 20 different enzymes that act synchronously in two types of nodule cells with contrasting ultrastructure, including the tree nodule cell organelles. Newly synthesized ureides are loaded into the network of nodule-root xylem vessels and transported to aerial organs by the transpirational water current. Once inside the leaves, ureides undergo an enzymatically driven reverse process to yield NH_4^+ that is used for growth. This supports the role of ureides as key nitrogen (N)-compounds for the growth and yield of legumes nodulated by *Rhizobium* that grow in soils with a low N content. Thus, a concrete understanding of the mechanisms underlying ureide biogenesis and catabolism in legumes may help agrobiologists to achieve greater agricultural discoveries. In this review we focus on the transmembranal and transorganellar symplastic and apoplastic movement of N-precursors within the nodules, as well as on the occurrence, localization and properties of enzymes and genes involved in the biogenesis and catabolism of ureides. The synthesis and transport of ureides are not unique events in *Rhizobium*-nodulated N_2 -fixing legumes. Thus, a brief description of the synthesis and catabolism of ureides in non-legumes was included for comparison. The establishment of the symbiosis, nodule organogenesis and the plant's control of nodule number, synthesis and translocation of ureides via feed-back inhibition mechanisms are also reviewed.

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Contents

1. Introduction.....	97
2. Early events of the symbiosis and nodule organogenesis.....	98
3. Symbiotic N_2 fixation in <i>Rhizobium</i> -nodulated ureidic legume species.....	98
3.1. Synthesis of ureides in root nodules.....	98
3.2. Xylem loading of ureides (source-to-sink organs).....	100
4. Ureide catabolism.....	104
5. Ureides in non-legume species.....	104
6. Conclusions and future perspectives.....	104
Acknowledgments.....	105
References.....	105

1. Introduction

Nitrogen (N) is indispensable for the growth of all plant species and, although N_2 is the most abundant gas in the earth's atmosphere, it cannot be fixed directly by higher plants (Hoffman et al.,

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2014). As a result of millions of years of evolution, plants belonging to a single phylogenetic group, the Fabaceae, comprising three subfamilies (Caesalpinioideae, Mimosoideae and Papilionoideae), and referred to as the N_2 -fixing clade, developed the ability to establish a symbiosis with α N_2 -fixing *Proteobacteria* of the Rhizobiaceae family to fix N_2 (Sprent, 2007; Werner et al., 2014). The evolution of this complex symbiotic trait between legumes and N_2 -fixing rhizobia, which provokes root nodule morphogenesis, involves the legume's recruitment of a mechanism that perceives mycorrhizal lipo-chitooligosaccharides (Geurts et al., 2012; Ivanov et al., 2012; Soyano and Hayashi, 2014), and mutations in the regulation of nitrate-regulated (NIN) gene expression (Suzuki et al., 2013; Soyano and Hayashi, 2014). Throughout this symbiosis, the rhizobia fix N_2 into NH_3^+ to satisfy the N hunger of legumes growing in N-poor soils (Mulder et al., 2002; Baral et al., 2012; Baral et al., 2014) in exchange for dicarboxylic acids (Udvardi and Day, 1997), as a carbon (C) source for the bacteria. A recent report (Larrainzar et al., 2014) provides evidence of the direct interactions between the effectiveness of nodulating rhizobia and the rate of C catabolism in the nodule, which is mostly associated with enhanced sucrose synthase activity within the nodules.

Rhizobium-nodulated legume species belonging to the Fabaceae generally form a determinate type of nodules where allantoin ($C_4H_6N_4O_3$) and allantoic acid ($C_4H_8N_4O_4$), both ureides, are the final products of symbiotic N_2 fixation (SNF). Ureides comprise up to 90% of the total N transported in the xylem of N_2 -fixing tropical legumes (Todd et al., 2006; Raso et al., 2007), and can be stored in high amounts in different plant organs (Tan et al., 2008). Proof of the importance of ureides in N transport and storage in legumes has been quantified as 2–3 mg C mg⁻¹ symbiotic N fixed (Valentine et al., 2010). Thus, a concrete understanding of ureide biogenesis and the ultimate fate of ureides, information about the enzymes involved in that process and a conceptual analysis of different organelles in legumes may help agrobiologists to achieve greater agricultural discoveries. Therefore, in this review we have focused on the late events of the symbiosis leading to the synthesis of ureides in ureidic N_2 -fixing legume species harboring a determinate type of root nodule. Special attention is paid to the synthesis of NH_3^+ by bacteroids, its conversion into N-precursors and finally into ureides inside the nodules. The biogenesis of ureides in the nodules and their transport to the aerial parts of plants requires the harmonious participation of a large number of organelles, enzymes and membrane N-transporters coordinated by the expression of several gene families. Biological membranes provide a natural barrier for the free transport of N-compounds and other substances from different cell compartments in a to-and-fro movement, causing plants to develop a specialized mechanism that tightly regulates the activity of N-molecule transporters to ensure optimal N nutrition (Rentsch et al., 2007). Furthermore, to fully comprehend the complex mechanisms underlying the biogenesis of ureides, attention must be paid to the early events of nodule formation resulting from the correct exchange of signaling molecules between the plant and free-living soil rhizobia as well as the functional genomics in nodule functioning and N_2 assimilation.

2. Early events of the symbiosis and nodule organogenesis

The first major event in the biogenesis of nodules is the recognition of flavonoids that exist in the seed coat or are excreted by roots by selected soil rhizobial strains (Oldroyd and Downie, 2008) via high-affinity receptors (Heidstra and Bisseling, 1996), followed by the attachment of free-living rhizobia to plant root hairs. These events are tightly coordinated by: (i) the simultaneous transcription of the nodulation (*Nod*) genes (*nodabcg*) required for the production of Nod factors (NFs) (Wang et al., 2012), and

glgX genes located in the nod operon (Oliveira et al., 2010), the regulatory genes (*nody/K* and *nolr*), and the N_2 -fixing (*nifH*) genes in the rhizobia (Maj et al., 2010; Menna and Hungria, 2011; Sugawara and Sadowsky, 2014); (ii) the expression of host-specificity genes (*nodfe*, *nodh*, *nodg*, *nodpq*, *nodz* and others) that determine the host range of microsymbionts and influence the rate and frequency of nodule formation, and (iii) the perception of NFs by a highly specific class of Lys motif domains (NFR1 and NFR5) receptor kinases in the host plant in conjunction with lectin nucleotide phosphohydrolase (LNP), a protein that binds NFs (Antolin-Llovera et al., 2012; Han et al., 2014; Granqvist et al., 2015). The NFs, in turn, elicit: (i) Ca^{2+} -mediated signaling in the bacterial symbiont (Moscatiello et al., 2010); (ii) induction of the rhizobial *Nod* genes, which regulate the polar transport of auxin and reactive oxygen species (ROS) outburst inside root hairs that activate Ca^{2+} channels, Ca^{2+} influx, Ca^{2+} spiking, and membrane depolarization that trigger polar root hair curling at ca. 360° (Emons and Mulder, 2000). A description of the infection chamber and a two-step model for rhizobial infection initiation in legume root hairs was recently published (Fournier et al., 2015); and, (iii) initiation of the nodule meristem formation (Gourion et al., 2015; Laplace et al., 2015). Thus far, 48 identified microRNAs are differentially regulated during the infection of root hairs in response to *Bradyrhizobium japonicum* infection (Yan et al., 2015). A lectin/nucleotide phosphohydrolase (ecto-apyrase Db-LNP) with widely varying capacities of binding NFs and involved in root hair deformation and nodulation, was found to be differentially distributed along the surface of the root axis in a pattern correlated with the root nodulating zone (Kalsi and Etzler, 2000; Nygren et al., 2012). The onset of a symbiosis is thus triggered by the concomitant effects of plant-synthesized flavonoids and rhizobial NFs (Hassan and Mathesius, 2012). A novel β -expansin gene is relevant to the biogenesis of determinate types of root nodules (Li et al., 2015).

Recent experiments have identified NFs secreted into the rhizosphere that seem not only to be involved in the development of nodules but also in the control of plant immunity during the establishment of the symbiosis (Okazaki et al., 2013). An increasing number of studies have pointed out the close link between the onset of nodulation and shut down of all plant defense mechanisms, including the accumulation of ROS (Izaguirre-Mayoral and Garrido, 2010; Gourion et al., 2015). Oxidative metabolism in nodules and redox control during rhizobial colonization of root hairs, bacteroid differentiation and nodule functioning were recently reviewed (Ribeiro et al., 2015). In general, the development of nodules and their functional effectiveness is totally restricted under the legume's genetic control (Simms and Taylor, 2002). The final size of the nodule mass is controlled by the plant via an exchange of systemic signals between the roots and shoot to regulate the number of nodules (Djordjevic et al., 2015). An update of the signaling exchanges between rhizobia and the plant are outlined in Fig. 1A and B.

3. Symbiotic N_2 fixation in *Rhizobium*-nodulated ureidic legume species

3.1. Synthesis of ureides in root nodules

Previously published reports support the general assumption that ureides are the final products of the N_2 fixed in legumes belonging to the Phaseoleae, Desmodieae and Indigofereae tribes (Dunn, 2014), which harbor a determinate (phaseoloid) type of nodule. The synthesis of ureides takes place inside root nodules with a determinate type of morphology characterized by possessing a complex anatomy composed of a central core of rhizobially infected and non-infected cells (Downie, 2014).

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