Plant Science 239 (2015) 36–43

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review article

Phosphorus homeostasis in legume nodules as an adaptive strategy to phosphorus deficiency

Saad Sulieman[a,*], Lam-Son Phan Tran[b,**]

[a] Department of Agronomy, Faculty of Agriculture, University of Khartoum, 13314 Shambat, Khartoum North, Sudan
[b] Signaling Pathway Research Unit, RIKEN Center for Sustainable Resource Science (CSRS), 1-7-22, Suehiro-cho, Tsurumi, Yokohama 230-0045, Japan

ARTICLE INFO

Article history:
Received 5 March 2015
Received in revised form 16 June 2015
Accepted 16 June 2015
Available online 25 June 2015

Keywords:
Acid phosphatase
Molecular adaptation
Nitrogenase activity
P deficiency
P homeostasis
Symbiosis capacity

ABSTRACT

Legumes have a significant role in effective management of fertilizers and improving soil health in sustainable agriculture. Because of the high phosphorus (P) requirements of N_2-fixing nodule, P deficiency represents an important constraint for legume crop production, especially in tropical marginal countries. P deficiency is an important constraint for legume crop production, especially in poor soils present in many tropical degraded areas. Unlike nitrogen, mineral P sources are nonrenewable, and high-grade rock phosphates are expected to be depleted in the near future. Accordingly, developing legume cultivars with effective N_2 fixation under P-limited conditions could have a profound significance for improving agricultural sustainability. Legumes have evolved strategies at both morphological and physiological levels to adapt to P deficiency. Molecular mechanisms underlying the adaptive strategies to P deficiency have been elucidated in legumes. These include maintenance of the P-homeostasis in nodules as a main adaptive strategy for rhizobia–legume symbiosis under P deficiency. The stabilization of P levels in the symbiotic tissues can be achieved through several mechanisms, including elevated P allocation to nodules, formation of a strong P sink in nodules, direct P acquisition via nodule surface and P remobilization from organic-P containing substances. The detailed biochemical, physiological and molecular understanding will be essential to the advancement of genetic and molecular approaches for enhancement of legume adaptation to P deficiency. In this review, we evaluate recent progress made to gain further and deeper insights into the physiological, biochemical and molecular reprogramming that legumes use to maintain P-homeostasis in nodules during P scarcity.

Contents

* Corresponding author. Tel.: +249 185 310101; fax: +249 185 315439.
** Corresponding author. Tel.: +81 45 503 9593; fax: +81 45 503 9591.
E-mail addresses: saadsulieman@hotmail.com (S. Sulieman), son.tran@riken.jp (L.-S.P. Tran).

http://dx.doi.org/10.1016/j.plantsci.2015.06.018
0168-9452/

1. Introduction

Legumes are an essential part of sustainable farming systems because they develop a mutualistic symbiotic relationship with one group of soil bacteria that has the capacity to fix atmospheric nitrogen (N_2) [1]. Legumes have successfully been used in crop rotations from Roman times and earlier. Symbiotic N_2 fixation takes place in nodules that are root outgrowths induced by N_2-fixing rhizobial bacteria of a number of genera, including *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Sinorhizobium*. N_2 fixation is a renewable and environmentally sustainable source of nitrogen (N), and can complement or be an alternative source for chemical fertilizers [2]. However, the symbiotic association between the leguminous plant and its microsymbiont partner is dramatically affected by various biotic and abiotic constraints [3]. Stressful events, such as drought, salinity, low pH, extreme temperatures, heavy metals and low nutrient availability, are major constraints for legume production in most of the areas where these plants are cultivated [4–6]. Sub-optimal soil phosphorus availability is the environmental constraint that has received considerable attention [4].

Phosphorus (P) is an essential macronutrient for plant growth and development. It is a major component of essential structural molecules and is important constituent for energy transformation and regulation of various enzymatic activities [7]. Examples of molecules containing P include nucleic acids, proteins, lipids, sugars, and adenylate in which P is central to a majority of the molecular constituents required for the functioning of plant cells [8]. This element plays a role in many metabolic processes related to the aboveground organs, including but not limited to, energy generation, nucleic acid synthesis, photosynthesis, respiration, glycolysis, membrane synthesis and integrity, activation/inactivation of enzymes, redox reactions, signaling and carbohydrate metabolism [9]. As such, the low availability of P in soil imposes serious limitations for plant growth and development. Of particular importance, P limitation directly reduces photosynthesis through its negative effects on leaf area development and photosynthetic ability per unit leaf area [10,11]. The assimilation and subsequent partitioning of carbon between shoots and belowground organs might be greatly affected by suboptimal P supply conditions. Given the fact that aboveground metabolism and development are closely connected with the symbiotic tissues, such negative effects are predicted to have serious implications on the growth and functioning of the nodule because of the specific requirement of P for symbiotic N_2 fixation as an energy-requiring process.

Several lines of evidence support the fact that N_2 fixation of legumes demands more P for optimal functioning than non-nodulating plants. The high P requirement may be linked to the pivotal role of this element in nodule energetic transformations. There is considerable evidence that nodulated legumes require more P than non-symbiotic plants grown solely on a mineral-N source [12]. The significant correlation between N_2 fixation with nodule P content provides an added evidence for this strong relationship [11,13]. Under P deficiency, the growth of the N_2-fixing legumes severely retards since the N_2 fixation that occurs in bacteroids, as well as the ammonium assimilation into amino acids and ureides that occur in the plant cell fraction of nodules are not sufficient to support the requirements for plant growth. These metabolic pathways require a large amount of P in energy transfer that takes place during nodule functioning [14,15]. Moreover, the P requirement for nodule development, particularly for syntheses of mitochondrial and symbiosome membranes, further increases the P demand by N_2-fixing legumes [16]. These observations together suggest that legumes will particularly greatly suffer by any lack of soil P availability. Most cultivated soils have insufficient amounts of P to support the efficient N_2 fixation in legumes. Indeed, sub-optimal soil P availability is nearly universal and represents an important constraint for plant growth over the majority of the earth's land surface [8]. Furthermore, the high-quality rock phosphates, which remain the primary source of P fertilizers, are projected to be depleted within 30–50 years [17]. Current estimates indicate that mined rock phosphate provides about 90% of the P fertilizers used in agriculture [18]. Thus, legume growth and production are thought to be particularly affected by P availability which is expected in near future.

As P is critically important for legume–rhizobia symbiosis, different nodulated plants have evolved a diverse array of responsive and adaptive strategies that could help conserve the supply of P, thereby maintaining high rates of symbiotic activity under limiting P conditions. These adaptive strategies are composed of complex internal reactions that are multi-coordinated at physiological, biochemical and molecular levels. These strategies include, but are not limited to: (i) maintenance of P concentration in nodules that is much higher than in other organs; (ii) increasing P acquisition (root morphology, root exudation and P uptake mechanisms); (iii) upgrading N_2 fixation per unit of nodule mass which compensates for reduction in the number of nodules; and (iv) higher oxygen (O_2) consumption per unit of reduced N_2 that is associated with a higher nodule permeability (for an extensive review, please see [3,9]. Among these observed strategies, maintenance of P homeostasis in nodules is exceptionally critical for legume growth and symbiosis, especially under P-deficient conditions (Fig. 1). Therefore, it remains a great challenge to understand the physiological basis that could help leguminous plants maintain elevated P concentrations in nodules. Understanding the detailed mechanisms of nodule P stability would enable the development of new approaches for improving legume performance under nutritional P deficiency [14,15]. Indeed, the development of crop plants with more efficient symbiotic capabilities is a necessity for sustainable farming practices. In this review, we evaluate advances, currently being made toward achieving insights into the biochemical, physiological and molecular reprogramming of nodule P homeostasis that may contribute to the understanding of the acclimation of the nodulated leguminous plants to P deficiency.

2. Maintenance of P homeostasis in nodules: adaptation and regulatory implication

Elevated P concentrations need to be conserved in the nodules to maintain growth and high rates of N_2 fixation, particularly during P-starvation conditions [19]. The stabilization of P levels in symbiotic tissues is critical for allowing nodules to ameliorate the negative effects of P deficiency under low P availability, while minimizing the P concentration if plants are supplied with excessive levels of this element. Indeed, higher P applications have been documented to significantly inhibit nodule function in soybean (*Glycine max*) [19] and *Medicago truncatula* [11,20,21]. Thus, nodulated roots appear to have evolved a distinct strategy that adjusts nodule P concentration by regulating the rate of P-influx inside the symbiotic tissues, thereby maintaining high rates of nitrogenase activity [20]. In this part, we review the current state of knowledge of the major mechanisms that leguminous plants might use to maintain P homeostasis, particularly under P-depleted conditions.

2.1. Preferential P allocation to nodules

More P is generally required for legume–rhizobia symbiosis, leading nodulated plants to experience significant changes in plant P allocation. Up to 20% of total plant P was estimated to be allocated toward nodule fraction, supporting and facilitating continued symbiotic function [22–24]. Under P-limited conditions, even much