



## Review article

## Adaptive strategies for nitrogen metabolism in phosphate deficient legume nodules

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## ABSTRACT

Legumes play a significant role in natural and agricultural ecosystems. They can fix atmospheric N<sub>2</sub> and contribute the fixed N to soils and plant N budgets. In legumes, the availability of P does not only affect nodule development, but also N acquisition and metabolism. For legumes as an important source of plant proteins, their capacity to metabolise N during P deficiency is critical for their benefits to agriculture and the natural environment. In particular for farming, rock P is a non-renewable source of which the world has about 60–80 years of sustainable extraction of this P left. The global production of legume crops would be devastated during a scarcity of P fertiliser. Legume nodules have a high requirement for mineral P, which makes them vulnerable to soil P deficiencies. In order to maintain N metabolism, the nodules have evolved several strategies to resist the immediate effects of P limitation and to respond to prolonged P deficiency. In legumes nodules, N metabolism is determined by several processes involving the acquisition, assimilation, export, and recycling of N in various forms. Although these processes are integrated, the current literature lacks a clear synthesis of how legumes respond to P stress regarding its impact on N metabolism. In this review, we synthesise the current state of knowledge on how legumes maintain N metabolism during P deficiency. Moreover, we discuss the potential importance of two additional alterations to N metabolism during P deficiency. Our goals are to place these newly proposed mechanisms in perspective with other known adaptations of N metabolism to P deficiency and to discuss their practical benefits during P deficiency in legumes.

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## Contents

|   |    |
|---|----|
| 1. Introduction.....  | 47 |
| 2. Nitrogen acquisition and assimilation in legumes.....        | 47 |
| 2.1. Soil and atmospheric N sources during P deficiency.....    | 47 |
| 2.2. Synthesis of amino acids during P deficiency.....          | 47 |
| 2.3. Organic acid and N metabolism during P deficiency.....     | 48 |
| 3. Nitrogen export from nodules.....                            | 49 |
| 3.1. Ureides and amino acids export during P deficiency.....    | 49 |
| 3.2. Carbon costs of ureide export during P deficiency.....     | 49 |
| 4. Respiration and amino acid recycling.....                    | 49 |
| 4.1. Respiratory costs of N metabolism during P deficiency..... | 49 |
| 4.2. Amino acid recycling during P deficiency.....              | 51 |
| 5. Future perspectives.....                                     | 51 |
| Acknowledgements.....   | 51 |
| References.....   | 51 |

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## 1. Introduction

Symbiotic biological N<sub>2</sub> fixation occurs within the nodules of legume roots, and is mediated by rhizobia, which form a symbiotic association inside host nodules [1]. The availability of soil P can be one of the most constraining environmental factors that limit the physiology of legumes that are engaged in the symbiotic biological N<sub>2</sub> fixation with rhizobia [2]. Globally, P is abundant in many soils, but the problem with its biological availability to plants is in part due to the complexes that it forms with other soil minerals and compounds. To complicate this situation even further is the fact that this limited P is even more unavailable in acidic soils. A striking feature of acidic soils is the increased toxicity of aluminium, which forms a complex with P and thereby rendering it as biologically unavailable [3]. Since 30% of the earth's total ice-free land mass consists of acidic soils [4] and 40% of its arable agricultural land is considered to be acidic, the deficiency of P in soils is therefore an important consideration for plant production. Furthermore, P deficiency will pose greater problems for agriculture, due to its reliance on P fertiliser, since the economic mining of rock phosphate is estimated to exhaust in 50 years [5]. Consequently the impact of limiting the supply of P to natural and agricultural ecosystems is going to become a global problem. Legumes, as key components in both ecosystems, will therefore be extremely vulnerable to P supply. In particular, P deficiency severely impacts the energy status and metabolic reactions of legume root nodules.

For nodules in particular, the role of P is vital in the metabolic energy processes that drive symbiotic N<sub>2</sub> fixation into NH<sub>3</sub> [6–8], and its subsequent conversion into organic N as amino acid and ureides. P deficiency is, therefore, a critical constraint for legume plants in agricultural and natural ecosystems. However, the development of P deficiency within nodules occurs at a later stage, long after roots have already succumbed to P deprivation [6,7]. Nodules act as strong sinks for P even under adequate P supply [9]. This sink status is exacerbated during P limitation, where nodules may exhibit higher P concentrations when compared to roots and shoots [9]. Moreover, it was also demonstrated that under P-deficiency there is a preferential partitioning of P to nodules, presumably for maintaining biological N<sub>2</sub> fixation rates, and sometimes even at the expense of plant growth [10]. Long-term P starvation leads to a decline in nodular Pi levels [11], which can negatively impact the energy status of nodules in terms of intracellular ADP and ATP availability [12]. These effects certainly have an impact on the nodule's capacity to assimilate N.

Declines in nodule N assimilation during P deficiency, may be related to direct and indirect mechanisms that induce this effect. P deficiency may directly limit N assimilation by reducing the available ATP required for cellular functions, such as enzyme activity and membrane transport. P deficiency also indirectly alters the utilisation of inorganic N sources and affects the availability of organic C skeletons required for amino acid synthesis and bacteroid respiration in the nodules. Therefore, in order to maintain N metabolism, nodules have evolved several strategies to resist the immediate effects of P limitation and to respond to P deficiency, once it eventually ensues. The metabolism of N in legumes is largely underpinned by N acquisition, assimilation, export, and recycling. To date, there has been no clear synthesis of how P stress adaptations in legume species impact the integration of N acquisition and metabolism.

In this review, we synthesise the current state of knowledge on legume nodule adaptations to maintain N metabolism during P deficiency. Moreover, we discuss the potential importance of two additional alterations to N metabolism during P deficiency. These adaptations are related to the modification of N export products and the recycling of amino acids, both of which can improve the N use efficiencies of legumes in agricultural and natural ecosystems. Our goal is to place these mechanisms in perspective with other known

adaptations of nodule N metabolism to P deficiency, and to discuss their functional benefits during P deficiency in legumes. These proposed mechanisms have been elucidated from research mostly conducted on the legume, *Virgilia divaricata*. This species is endemic to the Western Cape of South Africa, and is known to grow in the highly leached, P deficient soils of the Cape Floristic Region, South Africa. Thus, this species is ideal as a model for investigating the adaptations of N metabolism during P deficiency. The approaches of commercial biotechnology and traditional breeding should not only focus on improving N uptake and its routes of assimilation but should also exploit the flexibility of N export and the recycling of organic N. These alterations in N export and organic N recycling, can affect the pools of free and protein-bound amino acids, both of which are vital for crop production and nutritional quality of crop products.

## 2. Nitrogen acquisition and assimilation in legumes

The nodules of legumes such as *Virgilia divaricata* reduce their acquisition N<sub>2</sub> from the atmosphere during P stress, in exchange for a greater preference for soil N uptake by roots [13,14]. This alteration in N source utilisation is observed as reduced biological N<sub>2</sub> fixation while the specific N absorption and assimilation rates by roots are increased during P deficiency [14]. The acquisition and assimilation of various N sources have cost implications for the plant, especially during P deficiency.

### 2.1. Soil and atmospheric N sources during P deficiency

Mineral N and P interact on the growth of nodulated subterranean clover and under different levels of P and N. At the lowest P levels, the plants relied less on biologically fixed N, [15]. This was verified on subterranean clover reliance on symbiotic N fixation [16], which accumulated less N than plants supplied with NH<sub>4</sub>NO<sub>3</sub> (Fig. 1).

In *V. divaricata*, the varying costs of soil mineral and atmospheric N uptake, caused the plants to accumulate more biomass when acquiring N via mineral NH<sub>4</sub>NO<sub>3</sub> rather than via biological N<sub>2</sub> fixation [13]. Indeed, nitrate is recognised as a strong inhibitor of nodulation and biological N<sub>2</sub> fixation in legumes, but this is more likely due to the fact that it is less expensive to assimilate mineral N from the soil than to fix N<sub>2</sub>. In this way, the assimilation of soil N would, therefore, provide more organic C available for growth. In this regard, theoretically, the C costs associated with N<sub>2</sub>-fixation ranges between 3.3–6.6 g C g<sup>-1</sup> N. The precise costs are without a doubt dependent on the legume-rhizobia symbiotic combination, which is still considerably more than mineral N, such as NO<sub>3</sub><sup>-</sup> reduction, which does not regularly exceed a value of 2.5 g C g<sup>-1</sup> N [17]. Although the differences in C costs may be statistically insignificant as they are small, when integrated over the whole growth cycle, the costs do become significant [17]. Previous studies in legumes have found that the acquisition of atmospheric N via symbiotic biological N<sub>2</sub> fixation, requires larger amounts of photosynthates, compared to the assimilation of soil-derived NO<sub>3</sub><sup>-</sup>, thereby affecting the costs of productivity in legumes [18,19]. The alteration in utilising different sources of N during P deficiency refers largely to the inorganic soil and atmospheric sources of N. However and additional source of N as urea is also very relevant, but its potential role during P deficiency is unknown and needs to be investigated.

### 2.2. Synthesis of amino acids during P deficiency

Following the acquisition of inorganic N, the subsequent routes of N assimilation can vary according to the legume host, but may

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