Mineral constraints to nitrogen fixation

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Abstract

Mineral nutrient deficiencies are a major constraint limiting legume nitrogen fixation and yield. In this review general techniques for assessing nutrient involvement in symbiotic nitrogen fixation are described and specific methods are outlined for determining which developmental phase of the symbiosis is most sensitive to nutrient deficiency.

The mineral nutrition of the Rhizobium component of the symbiosis is considered both as the free living organism in the soil and as bacteroids in root nodules. Rhizobial growth and survival in soils is not usually limited by nutrient availability. Multiplication of rhizobia in the legume rhizosphere is limited by low Ca availability. Nodule initiation is affected by severe Co deficiency through effects on rhizobia. Nodule development is limited by severe B deficiency via an effect on plant cell growth. Fe deficiency limits nodule development by affecting rhizobia and strains of rhizobia differ widely in their ability to acquire sufficient Fe for their symbiotic development. Nodule function requires more Mo than does the host plant, and in some symbioses nitrogen fixation may be specifically limited by low availability of Ca, Co, Cu and Fe. The importance of the peribacteriod membrane in determining nutrient availability to bacteroids is considered.

It is concluded that the whole legume-Rhizobium symbiosis should be considered when improving legume growth and yield under nutrient stress conditions. Differences among rhizobial strains in their ability to obtain mineral nutrients from their environment may be agronomically important.

Introduction

Mineral nutrient deficiencies limit nitrogen fixation by the legume-Rhizobium symbiosis in many agricultural soils and as a result seriously depress legume yields below their maximum potential. It is probable that constraints imposed on legume yield and nitrogen fixation by poor mineral nutrition will become more prevalent following the greater use of improved, high-yielding crop varieties and better management practices. The extension of the areas being sown to legumes on to marginal lands will also increase the incidence of mineral nutrient deficiencies. Nutrient limitations to legume production result not only from deficiencies of the more common macronutrients such as phosphorus (P), potassium (K) and sulphur (S), but also of micronutrients such as iron (Fe), molybdenum (Mo), boron (B), etc. The successful treatment of adverse soil conditions requires an understanding of the fundamental nature of the problems for the particular legume concerned, and specific treatments should be devised to correct the adverse condition (Loneragan, 1972). It is therefore essential to understand the nature of limitations imposed by mineral nutrient deficiencies on the legume-Rhizobium symbiosis.

This paper reviews current knowledge of the effects of mineral nutrient deficiencies on the legume-Rhizobium symbiosis. In particular, we concentrate on the mineral nutrition of the Rhizobium component of the symbiosis, both as
the free-living organism in the soil and as the bacterium in the root nodule. Reference will only be made to effects of nutrient deficiencies on the legume symbiosis; other soil chemical factors limiting the symbiosis related to nutrient toxicities, salinity, acidity etc., will not be covered here since these have recently been discussed in detail elsewhere (Munns, 1978, 1979, 1986). Many excellent reviews have covered the mineral nutrition of symbiotic legumes, including: Loneragan (1972); Andrew (1977a), Munns (1977), Edwards (1977), Robson (1978, 1983), Munns and Mosse (1980), but most of these have emphasised the host plant component.

We begin this review with an introduction to the mineral nutrients essential for the legume-Rhizobium symbiosis and a brief discussion of the nature of symbiotic development. It is important to separate effects of nutrient deficiencies on the host plant from effects on the symbiotic system and several experimental approaches have been used to assess the relative nutrient requirements of the different stages during symbiotic development. We will focus on these stages of nodule development with respect to rhizobial nutrition and consider results from laboratory studies on the mineral nutrition of free-living rhizobia as related to the growth and survival of rhizobia in soil and rhizosphere. Nutrient constraints to nodule development and function will be reviewed with an emphasis on the mineral nutrition of symbiotic rhizobia present in the root and nodule.

**Essential mineral nutrients**

The essential mineral nutrients for symbiotic legume nitrogen fixation are those required for the normal establishment and functioning of the symbiosis. To be considered essential, an element must have a direct involvement in the nutrition of the legume host and/or Rhizobium, either as a constituent of an essential cofactor or metabolite, or be required for the activity of an enzyme system. The functions of a particular essential element must not be substituted by other chemical elements. Based on this definition, adapted from Arnon and Stout (1939), the following chemical elements are known to be essential for the legume-Rhizobium symbiosis: C, H, O, N, P, S, K, Ca, Mg, Fe, Mn, Cu, Zn, Mo, B, Cl, Ni and Co. Each essential nutrient has specific physiological and biochemical roles and there are minimal nutrient concentrations required within both legumes and rhizobia to sustain metabolic function at rates which do not limit growth. An organism is considered nutrient deficient when its internal nutrient concentrations fall below these functional requirement levels, and as a consequence metabolic function and growth are impaired.

**The nature of the symbiosis**

An understanding of the nature of limitations imposed by nutrient deficiencies on the legume symbiosis is required before any systematic attempt can be made to correct nutrient limitations. The identification of where in the symbiotic process specific effects of nutrient limitations occur would be an academic exercise if the only remedy for poor legume nutrition was improvement of the soil. An alternative approach is to improve plant tolerance by selection. To select legumes on a rational basis one needs to know whether the symbiosis is more sensitive than the host plant to a particular nutrient deficiency. If it is the symbiosis that is more sensitive then selection should be performed on symbiotically-dependent plants. The possibility also arises that the rhizobia are the weak component and bacterial selection is quicker than plant selection. However, even in situations where the host plant is more sensitive to a nutrient limitation than the symbiosis it is still sensible to select tolerant hosts using symbiotically dependent plants to ensure that improved host lines retain maximum nitrogen fixation ability.

When examining the effects of mineral nutrients on the legume symbiosis, it is important to consider the symbiosis as consisting of a number of different developmental phases, each of which can have specific nutrient requirements. The symbiotic process that begins in the rhizosphere and culminates in the establishment of an effective N2-fixing nodule is a multistage sequence of interdependent steps. Attempts to define environmental effects on the symbiosis by such broad expressions as nodulation or effectiveness are therefore bound to fail and confuse (Vincent, 1980). The symbiosis can be divided into four major phases: host plant growth, rhizobial survival and growth, infection and nodule de-