



How do phosphorus, potassium and sulphur affect plant growth and biological nitrogen fixation in crop and pasture legumes? A meta-analysis



Guillermo A. Divito^{a,b}, Victor O. Sadras^{c,*}

^a Facultad de Ciencias Agrarias UNMdP–INTA, ruta 226 km 73, 7620 Balcarce, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

^c South Australian Research & Development Institute and The University of Adelaide, Waite Research Precinct, 2b Hartley Grove Urrbrae, SA 5064 Australia

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ABSTRACT

Worldwide, legumes are grown on approximately 250 M ha and fix about 90 Tg of N₂ per year. Plants involved in biological nitrogen fixation (BNF) are particularly sensitive to deficiencies of phosphorus (P), potassium (K) and sulphur (S). These nutrients can affect BNF directly; this is modulating growth of rhizobia, nodule formation and functioning, or indirectly by affecting the growth of the host plant. However, several process and mechanisms remain unclear. We compiled a data set (63 studies) on the effects of P, K, and S deficiency on shoot mass, nodule mass and number, nitrogenase activity (estimated by the acetylene reduction activity test, ARA) and the concentration of N, P, K and S in shoots and nodules. Our aims were (1) to compare the relative sensitivity of these traits to nutrient deficiency and (2) to probe for nutrient-specific patterns in trait responses.

Our quantitative analysis confirms that nodule growth and number are more sensitive than shoot mass in response to deficiency of P, K and S. In addition, nodule activity decreases more than both shoot and nodule mass, which indicates a reduction in nodule productivity; this is likely related with direct effects of these nutrients on physiological and metabolic processes of nodules. The conserved shoot N concentration, in comparison to concentration of P, K and S indicates a relatively greater accumulation of N that matches the proposed N-feedback mechanism down-regulating BNF in nutrient-deficient systems. Despite some nutrient-specific differences, i.e. smaller nodules and higher N/K ratio with shortage of P and K, respectively, the patterns of growth, nodule activity and nutrient concentration were similar for all three nutrients P, K and S. This indicates that a unique mechanism could be depressing BNF (N-feedback) in conjunction with direct effects of the nutrients on nodule activity.

Scarcity of data related to N, K and S concentration in nodules is a major constrain for deep analysis of the deficiencies of the nutrients. Critical concentrations of P, K and S in plant and nodule tissues are also a major gap. Models are needed that integrate the direct effect of the nutrients on nodule growth and activity with the N-feedback mechanism.

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1. Introduction

Worldwide, legumes are grown on approximately 250 M ha and fix about 90 Tg of N₂ per year (Kinzig and Socolow, 1994). Biological nitrogen fixation (BNF), offers a series of advantages over nitrogen (N) fertilizer, including higher efficiency in the utilization of N by the plant, the minimization of N leaching, and the reduction of soil and water contamination (Peoples et al., 1995). Moreover, BNF has beneficial effects for subsequent crops in rotations and for

non-legumes in mixed stands, hence its importance for maintaining productivity in many agricultural systems (Graham and Vance, 2000). However, BNF is particularly sensitive to environmental stress like nutrient deficiency.

Phosphorus (P) is, after N, the most limiting nutrient for crops (Vance et al., 2000). Crop yield is limited by P availability in about 40% of the world's arable land, so studies on the response of legumes and rhizobia to P fertilization have received considerable attention (Almeida et al., 2000; Høgh-Jensen et al., 2002; Olivera et al., 2004; Schulze, 2006). To a lesser extent, research has focused on legume-rhizobia responses to potassium (K), which is also deficient in many soils (Römheld and Kirkby, 2010). The effect of sulphur (S) supply on BNF has received less attention, as deficits of this nutrient are less frequent in agricultural soils. Owing to S depletion in some soils,

* Corresponding author at: 2b Hartley Grove Urrbrae, SA 5064, Australia. Tel.: +61 8 8303 9661.

E-mail address: victor.sadras@sa.gov.au (V.O. Sadras).

however, crop S deficiencies have been reported with increasing frequency (Scherer, 2001).

Legumes that acquire N by BNF generally have a higher requirement of P, K and S than those which only rely on soil N (Israel, 1987; Sulieman et al., 2013). These nutrients can affect BNF directly; this is by modulating nodule growth, nodule formation and functioning (Duke et al., 1980; Vadez et al., 1996; Pacyna et al., 2006), or indirectly by affecting the growth of the host plant (Duke et al., 1980; Almeida et al., 2000; Varin et al., 2010). Owing to the high ATP requirements for nitrogenase function, P availability is critical for nodule activity (Ribet and Drevon, 1995; Al-Niemi et al., 1997); and it also plays a role in signal transduction, membrane biosynthesis, and nodule development and function (Al-Niemi et al., 1997). Duke et al. (1980) demonstrated a direct effect of K status on BNF mediated by its influence in nodule growth and function, activity of enzymes involved in ammonia assimilation, amino acid inter-conversions, carbon supply and energy transduction. Varin et al. (2010) showed a close relationship between S supply and nitrogenase and leghaemoglobin content in nodules. Scherer et al. (2008) determined that S deficiency reduced BNF in pea (*Pisum sativum* L.) and lucerne (*Medicago sativa* L.) as a consequence of decreased ferredoxin and leghemoglobin concentrations as well as reduced ATP supply. Besides the direct impact of P, K and S in these aspects of carbon and N metabolism, it is generally accepted that their main effect on BNF is mediated by responses of host plant growth (Almeida et al., 2000; Høgh-Jensen, 2003; Varin et al., 2010). In this sense, when nutrient deficit reduces plant growth, an N-feedback is triggered that down-regulates nodule development and activity. This mechanism seems also responsible for the regulation of BNF when other stresses, such as drought, salt, toxic metals and pathogen attack, are involved (Lea et al., 2007).

The effects of P, K and S availability on plant legume growth and BNF are therefore biologically interesting and agronomically relevant, and a range of direct and indirect effects have been identified. However, several processes remain unclear and no attempts have been made to quantitatively consolidate the fragmented information on the effects of nutrients on BNF related traits. We compiled a data set on the effects of nutrient deficiency on shoot mass, nodule mass and number, nitrogenase activity and the concentration of N, P, K and S in shoots and nodules. Our aims were (1) to compare the relative sensitivity of these traits to nutrient deficiency and (2) to probe for nutrient-specific patterns in trait responses.

2. Method

2.1. Data sources

We compiled papers searching the Web of KnowledgeSM (Thomson Reuters, 2013) database for “nitrogen fixation + phosphorus/potassium/sulphur” with alternative formats. Some of the papers were also obtained searching in the reference lists of those found in the Web of KnowledgeSM database. We included both field and controlled environment experiments. We excluded studies with non-cultivated species, where plants were not inoculated with the specific symbiotic rhizobium, where nutrient supply was confounded with other sources of experimental variation, where N rate or source could distort the interpretation of the results, or where P, K or S rate was reported as toxic. Only experiments which established P, K and S treatments at early plant growth stages were considered; experiments with an abrupt withdrawal of nutrients in late stages or where plants received differential rates of nutrients to relief deficiencies were excluded. We retrieved 124 papers, and the final database that satisfied our inclusion criteria consisted of 36 experiments on P, 15 experiments on K and 12 experiments on S (Table 1). We focused on traits that

are relevant to plant and rhizobia growth and function, and are often reported in the literature, including shoot mass, nodule mass and number, nitrogenase activity (estimated by the acetylene reduction activity test, ARA) and the concentration of N, P, K and S in shoots, roots and nodules. The estimation of BNF through ARA was selected because it was the most abundant in the retrieved papers. Some authors noticed some problems of this assay related to an acetylene-induced decline in nitrogenase activity over the time (Michin et al., 1983). To account for this, we only considered determinations done with less than 60 min incubations. In general, nutrient stress was higher in controlled conditions due to a better control of nutrient provision. This was the main difference we detected between growing conditions; no attempt was made to use this as a criterion to data classification in the analysis.

2.2. Statistical analysis

To account for differences between growing conditions (e.g. field, pots, etc.), species and other sources of variation, all traits were normalized as the ratio between the actual value for each trait and the maximum in the experiment. If secondary sources of variation were included in the experiment (e.g. soil moisture), the ratio was calculated for each level of the secondary variable. The ratios were ln-transformed before analysis (Hedges et al., 1999) but untransformed data are presented for easier interpretation. The normality and residual distributions were tested.

To compare the relative sensitivity of these traits to nutrient deficiency, we carried out pair-wise comparisons of traits for their responses to P, K and S deficiency; hence, data points where traits in both x and y axis were equal to 1, often treatments with no nutrient deficiency, were excluded from statistical analyses. The null hypothesis was that both traits in a pair (e.g. nodule mass vs. shoot mass) were equally responsive to nutrient deficit. Graphically, the null hypothesis is represented by scatter plots aligned with the $y=x$ line. Deviations of data from the $y=x$ line were calculated. Statistically, a t -test ($P < 0.05$) returning no significant deviations from $y=x$ supports the null hypothesis, significant positive deviations indicated that trait “y” is less responsive than trait “x”, and significant negative deviations indicate that trait “y” is more responsive than trait “x”. To probe for nutrient-specific patterns in trait responses, we used an F-test to compare traits deviations in response to P, K and S deficiency. When F-test was significant, Least Significant Difference (LSD) at the 0.05 level was calculated. Normality, t - and F-tests were all performed with the R program (R Development Core Team, 2009); SigmaPlot (version 11.0, Systat Software Inc., San Jose, CA, USA) was used to draw box plots.

3. Results and discussion

3.1. Shoot and nodule growth

Fig. 1 shows that nodule mass is more sensitive to nutrient deficit than shoot mass as most data points are in the right area below the $y=x$ line. The patterns for P, K and S were similar. For P and S, we hypothesize that this differential sensitivity is related to the greater concentration of nutrients in nodules compared with that in shoots or roots (Table 2) which may indicate a greater nutrient need to maintain high nodule growth rates. Qiao et al. (2007) provides direct evidence to support this hypothesis, as the critical P concentration for peak nodule growth of 5 mg P g DM^{-1} compares with the critical concentration of $1.5 \text{ mg P g DM}^{-1}$ for maximum shoot growth in soybean (*Glycine max* (L.) Merr.). Similar thresholds were proposed for white lupinus (*Lupinus albus* L.), which lie between 3.1 and $1.1 \text{ mg P g DM}^{-1}$ for shoots and 6.5 – $3.3 \text{ mg P g DM}^{-1}$ for nodules (Schulze, 2006). Tang et al. (2001) reported

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