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Importance of nickel in biological nitrogen fixation for soy farming.

MAIS INTEGRIDADE

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Introduction

Soy (*Glycine max* L.) is a legume of Asian origin and cultivated in several parts of the world. It is an ancient crop that has become a staple food, directly or indirectly, for billions of people in both the Eastern (center of origin) and Western hemispheres.

Soy is a two-dimensional crop that contains about 40-42% high-quality protein; between 20 to 22% oil and 20 to 30% carbohydrates. Due to these characteristics, it has become the main source of protein for humans and animals either in the form of whole grains or crushed in the form of oil or flour (Pimentel et al., 2006; Gonçalves et al., 2018; Peiretti et al., 2019; Narayanan and Fallen, 2019). The protein quality of soy is similar to that of meat, dairy products and eggs (Mendes et al., 2004; Lodhi et al., 2015).

According to the data in Figure 1, both the sown area and the productivity of the soy crop have been expanding rapidly since the 1976/77 harvest. For the 2019/20 harvest, the sown area was 36.8 million ha, while the national average yield was 3,373 kg ha^{-1}.

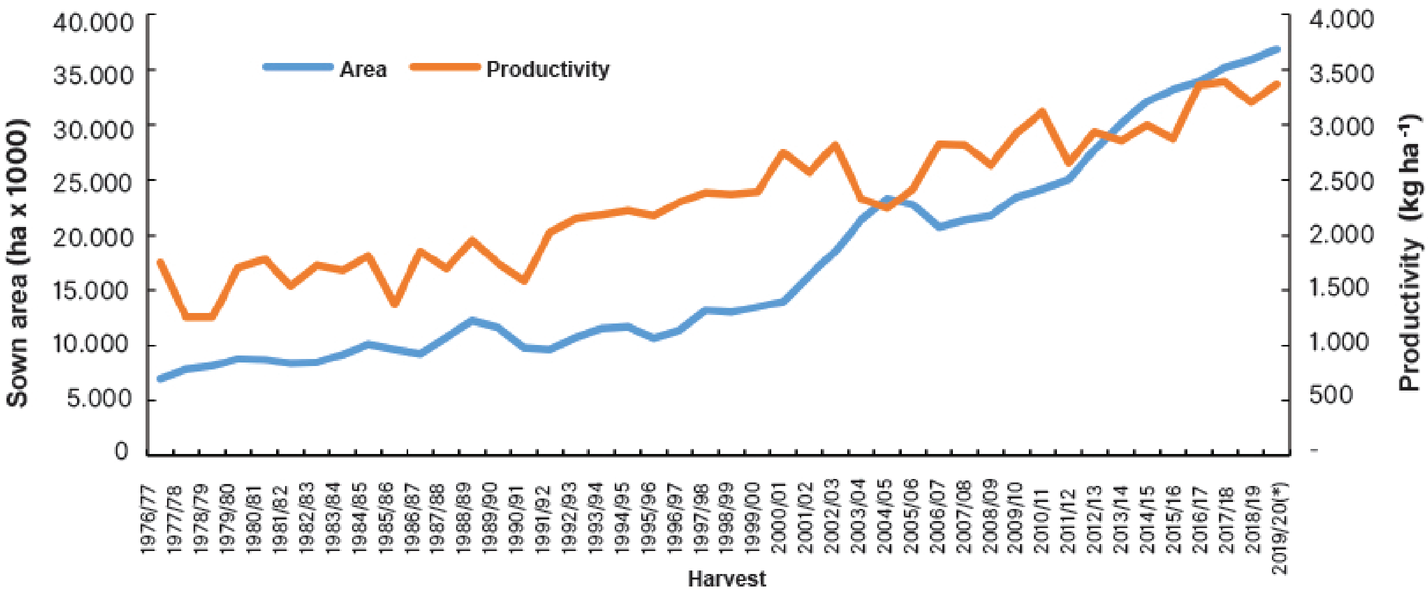

Figure 1. Historical series of the sown area and productivity of the soy crop in Brazil.
Source: (CONAB, 2020)

Once the relevance of the soy crop is known, it is essential to understand the factors that are directly related to the productivity of this crop. In this context, it is known that, among other factors, soy yield is often associated with the total uptake of nitrogen (N) and, ultimately, the total uptake of this element is dependent on the amount of N that is biologically fixed and/or absorbed from the soil solution (Santachiara et al., 2017).

Nitrogen and biological nitrogen fixation (FBN) in soy

High N uptake is a requirement for soy cultivars, especially those with high yields (Santachiara et al., 2017). In this sense, reports in the literature show that approximately 80 kg ha^{-1} of N are needed to produce one ton of soy (Salvagiotti et al., 2008). Although N is abundant in the atmosphere (78%), this huge amount is not available to plants, animals or humans (Coskan and Dog, 2011; Yang et al., 2019). Therefore, FBN is a process by which plants, associated with a microorganisms, convert atmospheric nitrogen (N_2) into ammonia (NH_3), which is readily available for plant growth (Yang et al., 2017).

However, under high yield conditions, N from the soil and FBN may not be sufficient to sustain uptake rates during the soy production period, so it would not meet the N demand needed to achieve the maximum attainable yield (Salvagiotti et al., 2009). Results show that the total N fixed through FBN varies between 300 and 400 kg ha^{-1}, an amount that is insufficient to support high yields (Santachiara et al., 2017; Ciampitti and Salvagiotti, 2018). Situations of high productivity and/or low FBN efficiency could negatively affect the N balance and the carbon (C) balance, which would therefore affect the health and sustainability of the soil in the long term (Córdova et al., 2019).

This problem could be overcome with applications of inorganic N to the soil through coating or incorporation, however, the design of such a strategy must also deal with the often observed reduction in FBN when inorganic N is applied (Salvagiotti et al., 2008). Furthermore, the amount of N fixed through FBN is negatively correlated with N uptake in the soil, so that any extra kg ha^{-1} of N absorbed from the soil solution can result in a reduction of 1.4 kg ha^{-1} N-derived from FBN (Santachiara et al., 2017). Furthermore, the use of nitrogen fertilizers has a high economic and environmental cost, which would certainly make soy farming unfeasible.

Biological nitrogen fixation may be insufficient to provide sufficient N for high yields and still susceptible to biotic and abiotic factors, but the key role FBN has in advances in production and long-term soil sustainability is the consensus (Córdova et al., 2019).

The aforementioned facts suggest that there is a greater chance of increasing total N uptake through increased FBN efficiency than by increasing soil solution uptake (Santachiara et al., 2017). In this context, knowledge of the process and techniques that enhance biological nitrogen fixation in intensive soy farming systems is essential to obtain high yields.

Initially, it is necessary to understand that there is no obligation to establish a symbiosis between the two organisms (soy crop and N-fixing bacteria), especially if the environment in which they are found does not have limitations as to the availability of nitrogen (N) (Câmara, 2014) or presents edaphoclimatic factors that limit the good development of the bacteria. In this context, the deficient supply of nutrients such as molybdenum (Mo), cobalt (Co) and nickel (Ni) will negatively affect soy FBN. Based on what was previously mentioned, this material will discuss the importance and the role of Ni in soy crop FBN.

Nickel

To facilitate the understanding of Ni in agriculture and especially in soy farming, this topic was subdivided into: essentiality of Ni, hydrogenase and urease.

Essentiality of Nickel

The first report on the essentiality of Ni for living beings was made in 1975, in this study it was demonstrated that the urease enzyme had two Ni atoms in its structural composition (Dixon et al., 1975). Still, eight years later, in 1983, when studying the soy crop in a nutrient solution, Eskew et al. (1983) found necrosis at the tip of leaflets due to the accumulation of urea in toxic concentrations and suggested that nickel, as a component of urease, would be necessary to prevent the accumulation of toxic concentrations of urea. Ni essentiality was also suggested by Eskew et al. (1984), these authors stated that Ni plays a fundamental role in superior plants and that the importance is general due to the similarities in the responses of soy and cowpea to Ni deficiency. After these pioneering studies, other functions of Ni were discovered and studied and finally Ni was added to the list of essential elements for plants.
Nickel is the 28th element on the periodic table. It is a silvery white metal found in various oxidation states (ranging from -1 to +4). However, the divalent oxidation state (Ni^{2+}) is the most common in natural systems (Denkhaus and Salnikow, 2002). This element is essential for plants, animals and humans (Sreekanth et al., 2013).

The concentration of Ni in the soil depends on the source material and the formation process (Ureta et al., 2005). On the other hand, the availability of this element in the soil is mainly altered by pH, which can be indirectly altered by base saturation (Macedo et al., 2020).
At pH <6.5, the Ni compounds present in the soil are relatively soluble, while at pH >6.7, most Ni exists as insoluble hydroxides (Sreekanth et al., 2013). In Brazil, there is no determination of critical levels for available Ni in agricultural soils to boost fertilizer recommendation. Consequently, there is no recommendation of a specific extractor to determine the availability of Ni in the soil (Rodak et al., 2015).

Ni affects several physiological processes in plants, which include enzymatic activities and therefore plays vital roles in a wide range of morphological and physiological functions, from germination to productivity (Van Assche and Glijsters, 1990; Sreekanth et al., 2013).

Among the fundamental roles played by Ni, the importance of Ni for hydrogenase and urease stands out.

Hydrogenase

During the (FBN) process, by-products such as H_2 are released (Polacco et al., 2013; Macedo et al., 2020). The H_2 released in the FBN process will be free in the nodular environment and may, among other ways, compete with N_2 for nitrogenase, since this enzyme has binding sites that can receive N_2 and H_2. Then, the released H_2, by competing with N_2 for nitrogenase, may decrease the efficiency of the FBN process (Figure 2).

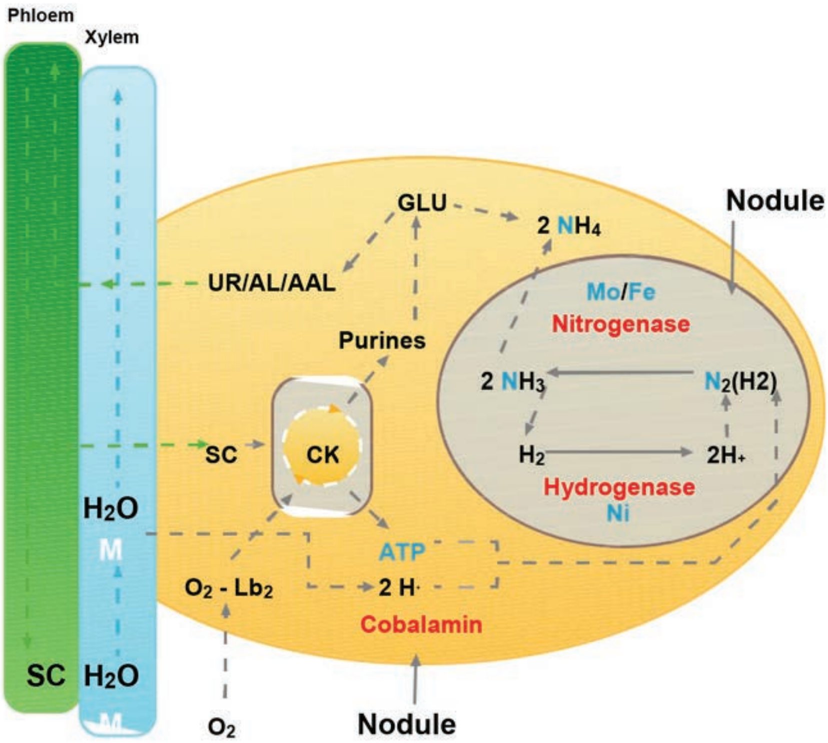

Figure 2. Schematic diagram demonstrating interactions between nutrients and biological nitrogen fixation (FBN) in soy. The dashed arrows in phloem and xylem indicate the transport directions, either of water (H_2O) and nutrient (M) in the xylem or sucrose (SC), ureides (UR), allantoin (AL) and allantoic acid (AAL) in the phloem. When absorbed by the roots and transported to the nodule, water is hydrolyzed to form energy in the form of H^+, and along with ATP from sucrose respiration, they provide part of the substrate for FBN. For ATP production in the Krebs cycle (CK), the presence of oxygen (O_2) is necessary, which is transported inside the nodule by the leghemoglobin enzyme (Lb2). This enzyme is synthesized from cobalamin, which has the element cobalt (Co) as a constituent. With the entry of nitrogen (N_2) into the bacteroid and in the presence of ATP and H^+, the enzyme nitrogenase breaks the triple bond of N_2, producing two molecules of ammonia (NH_3) and H_2. This H_2 can compete with N_2 in nitrogenase, which can cause the inactivation of this enzyme and the paralysis of the FBN. However, through the hydrogenase enzyme, which is composed of two nickel atoms, H_2 will undergo hydrogenation whose product is two H^+, which will be used as an energy source by nitrogenase. It should be noted that nitrogenase is an enzyme that contains molybdenum and iron, essential elements for its functioning. By breaking N_2 down into NH_3, these two ammonia molecules diffuse out of the bacteroid where they are protonated to NH_4^+, which is enzymatically converted to glutamine (GLU) and subsequently to ureides (UR), allantoin (AL) and allantoic acid (ALA) to be transported from nodules to leaves by the phloem. It is worth mentioning that it is estimated that 90% of the nitrogen from the FBN is transported to the shoot in the form of ureides, for this reason, we will only address the metabolism of ureides in this article.

SC – Sucrose; H_2O - Water; M – Nutrients; Ni – Nickel; Co – Cobalt; Mo – Molybdenum; P – Phosphorus; Fe – Iron; N – Nitrogen; Lb2 – Leghemoglobin; ATP – Adenosine triphosphate; CK – Krebs Cycle; UR – Ureides; AL – Allantoin; AAL – Allantoic acid; GLU – Glutamine; NH_4^+ – Ammonium: NH_3 – Ammonia.

Another possible pathway, and perhaps the best alternative, is for the hydrogen gas produced to be re-oxidized by the hydrogenase enzyme, which will recover a certain amount of energy used for the previous reduction by nitrogenase (Gonzalez-Guerrero et al., 2014). Thus, hydrogenase catalyzes the oxidation of molecular hydrogen (H_2) into protons and electrons (Brazzolotto et al., 2016). Therefore, the efficiency of nitrogen fixation depends immediately on the hydrogenase activity, since the oxidation of hydrogen supplies the energy (ATP) necessary to reduce N in ammonia. This hydrogen recycling has been associated with significant increases in plant productivity in certain symbiotic systems, such as soy (Albretch et al., 1979).

However, hydrogenase biosynthesis is a complex process that involves at least 15 accessory proteins, some of which participate in the insertion of an essential nickel atom into the active site of the enzyme (Ureta et al., 2005). In this context, Ni is essential for H_2 recycling to occur (Freitas et al., 2018).

Thus, low levels of available Ni in the soil affect hydrogenase activity and therefore the performance of FBN (Ureta et al., 2005). The facts mentioned above are highlighted by Seregin and Kozhevnikova (2006), according to these authors, Ni^{2+} deficiency was shown to decrease hydrogenase activity in the nodules. Furthermore, the presence of Ni may have favored the hydrogenase activity, recovering more H_2, increasing the energy efficiency of the process and, therefore, optimizing the reduction of N_2 and the entire FBN process. Thus, it is considered that there is a positive feedback between the activities of hydrogenase and nitrogenase, in order to keep the FBN constant and efficient (Lavres et al., 2016).

Therefore, an alternative to supply Ni to plants and consequently improve the FBN process is through seed treatment (TS). Positive results for the use of this technique have already been demonstrated by Lavres et al. (2016), according to these authors, the presence of Ni in the seeds stimulated the FBN process, probably due to the increased hydrogenase enzyme activity. Still, Milléo et al. (2009), observed that the use of Ni through TS or foliar application in the vegetative phase contributed positively in an analogous way for the productivity of the soy crop, but the use of this element in both phases increased productivity by over 4.7%.

Urease

The main means of transport of nitrogen in soy from the nodules to the shoot is in the form of ureides (King and Purcell, 2005) (Figure 3). However, when increasing the concentration of ureides in the shoot of the plants, the FBN is significantly reduced, in the phenomenon known as "*feedback effect*" (King and Purcell, 2005; Fagan et al., 2007). In this context, once in the leaves, ureides can be converted into urea, through the purine degradation pathway and then metabolized by urease (Zrenner et al., 2006). The urea is a small neutral organic compound, formed by two molecules of ammonia (NH3) and one of carbon dioxide (CO_2) (Wang et al., 2008).

However, the urea molecule, in its original form, cannot be used by living organisms and must be broken down to be used. Furthermore, as previously discussed, the accumulation of ureides and later of urea in plants is something that must be avoided, since, among other factors, it will decrease the FBN process by the "*feedback effect*". Thus, two different types of enzymes are capable of degrading urea: urea amidase and urease. Thus, urease is essential for urea to be used by living organisms and it is estimated that the spontaneous degradation of urea has a half-life of 520 years to generate ammonia and carbamate, while the half-life of urea catalyzed by urease is 20 milliseconds (ms) (Callahan et al., 2005). Making urease one of the fastest hydrolases known.

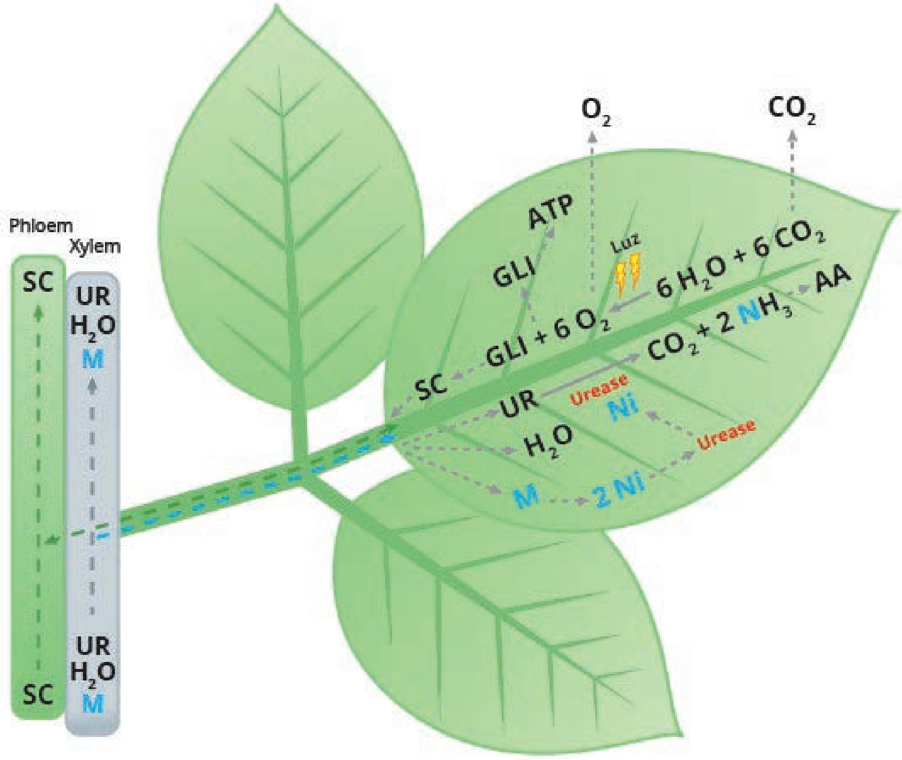

Figure 3. Schematic diagram demonstrating ureide metabolism and photosynthesis in soy leaves. After being transported from the no dules to the leaves, nickel is used to synthesize urease, the enzyme responsible for breaking ureides (UR) into two molecules of ammonia (NH_3), which will later be metabolized to synthesize amino acids and other products that contain nitrogen. However, nickel deficiency can cause the accumulation of ureides in the leaves, which consequently induces a *feedback effect*, i.e., the production of signals for nitrogenase in the nodules to reduce the activity, which consequently will reduce the FBN. Thus, adequate nutrition with nickel is essential for the FBN process and the metabolism of ureides and nitrogen in the leaf to remain active. Furthermore, for the activity of this process, the production of glucose (GLI) by photosynthesis is essential, which is used for energy production (ATP) and sucrose (SC), which will be transported to different parts of the plant, such as the nodules, where it will be a source of energy (ATP) for FBN.

SC – Sucrose; H_2O - Water; M – Nutrients; Ni – Nickel; Co – Cobalt; P – Phosphorus; N – Nitrogen; Lb2 – Leghemoglobin; GLI - Glucose; UR – Ureides; NH_3 - Ammonia; AA - Amino acids; CO_2 - Carbon dioxide; O_2 - Oxygen.

Urease is responsible for the hydrolysis of urea into two molecules of ammonia and one of carbon dioxide (Polacco et al., 2013). In plants, urease plays a role in the assimilation of urea derived from ureides or arginine (Polacco and Holland, 1993).

This enzyme is a metalloenzyme that uses nickel ions at its active site, which is essential for its activity (Dixon et al., 1975). Therefore, they consist of a dimer of homotrimers in which each active site has two nickel ions, totaling six active sites per active protein (Dixon et al., 1975; Zambelli et al., 2011). In other words, a urease subunit comprises two Ni^{2+} ions crucial for the catalytic process (Seregin and Kozhevnikova, 2006).

The urease pathway is, therefore, another biological reaction in which Ni plays an important role (Freitas et al., 2018), and the supply of this micronutrient, as shown earlier, is essential for the NBN process in soy crops.

Understanding the importance of nickel in biological nitrogen fixation and nitrogen metabolism in plants, ICL went to great lengths to develop Up! Seeds and Tônus, two products that provide physiological stimuli and nutrition, containing the micronutrient nickel.

Discover Up! Seeds

Product developed to provide physiological stimuli and nutrition focused on the initial stages of the crop, providing greater rooting and stimulation of biological nitrogen fixation. It has proven compatibility with inoculants, not altering the survival of diazotrophic bacteria (Rhizobia).

Advantages and Benefits

- Greater efficiency in the absorption of nitrogen starting in the germination process.
- Deep root system: greater tolerance to dry spells and efficiency in nutrient extraction.
- Ease of operation and uniform distribution over the seeds.
- Ideal pH: favoring the establishment of nitrogen-fixing bacteria.
- Spray mixture compatibility

Discover Tônus

It stimulates and increases the efficiency of the Biological Nitrogen Fixation (FBN) process until the end of the crop cycle. Tônus provides nutritional and physiological stimuli that act on the longevity and renewal of plant nodules to maintain FBN up until grain filling.

Advantages and Benefits

- It provides the continuous formation of young and strong nodules, through modulation of the hormonal balance;
- It makes nitrogen fixation much more efficient, providing more energy for the plant to grow;
- Rapid transformation of nitrogen supplied by the nodules into heavier proteins and grains;
- Maintains energy supply to the nodules;
- It reduces the formation of ethylene in the plant, preventing premature death of the nodules;
- It provides essential elements to keep the nodules physiologically active.

Meet the authors

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