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Reappraisal of the central role of soil nutrient availability in nutrient management in light of recent advances in plant nutrition at crop and molecular levels

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ABSTRACT

The concept of soil nutrient availability is still widely viewed within the framework of crop yield responses to fertilizer applications as the intermediary variable linking the rate of application of a single nutrient to the absorption of this nutrient by plants according to the pioneer work of Boussingault (1855), von Liebig (1855), and Mitscherlich (1924). For interpreting the huge variability of crop yield responses to increasing fertilizer applications, agronomists and soil scientists have focused on soil nutrient dynamics in order to estimate the quantity of each nutrient available for plant uptake. This linear approach considering "available nutrient in soil" as an external factor to which plants respond does not correspond to the reality for three main reasons: (i) the root absorption capacity is deeply feed-back controlled by the plant growth capacity itself and, therefore, does not depend univocally on soil nutrient availability; (ii) interactions among different nutrients in soils and plants imply that the availability of one nutrient for plants depends of the availability of others, requiring a more integrated approach; and (iii) the plant itself influences nutrient dynamic processes in soils through interactions with microbial communities in its rhizosphere. Consequently, soil nutrient availability cannot be only considered as a property of the external medium to which plants adapt, but also, and more importantly, as resulting of the functioning of the whole plant-soil-living organisms ecosystem. This review paper proposes an integrated and hypothesis-based vision of plant mineral nutrition based on several recent findings: (i) the corroboration and verification of hypotheses of regulation of plant nutrient uptake at the whole plant level by recent advances in the molecular physiology of plant nutrition, (ii) the physiological basis for interactions among different plant nutrients, and (iii) the increasing evidence of plant-soil interactions at the rhizosphere level.

1. Introduction

Plant mineral nutrition research has been dominated during the last two centuries by agronomists dealing with the determination of optimum fertilizer applications to crops to achieve the maximum yield potentially determined by climate and genotype. Jean-Baptiste Boussingault (1855) first identified the role of nitrate as the main source for the nitrogen (N) nutrition of plants. Justus von Liebig (1855) then established the Law of the Minimum: "*plants grow only to the extent allowed by the single nutrient that is most limiting*" and, later on, Mitscherlich (1924) established the Law of Diminishing Return in which the crop response to the addition of one nutrient decreases as the level of application increases. All these paradigms constituted the basis for plant nutrition and crop fertilization management around the world as soon as external fertilizer resources became available for agriculture through the industrial Haber-Bosh process for the production of N fertilizers and the mining industry for the production of phosphorus (P) and potassium (K) fertilizers.

Crop mineral nutrition has long been studied by empirical "rate-response" approaches linking the rate of fertilizer application with crop yield. For a better understanding of these rate-response curves, the concept of "soil nutrient availability" for plants was proposed in order to separate the whole effect of fertilization into: (i) the effect of application rates on soil nutrient availability and (ii) the effect of increasing soil nutrient availability on crop yield (de Wit, 1994). Soil nutrient availability was then considered as the pivotal variable and as an

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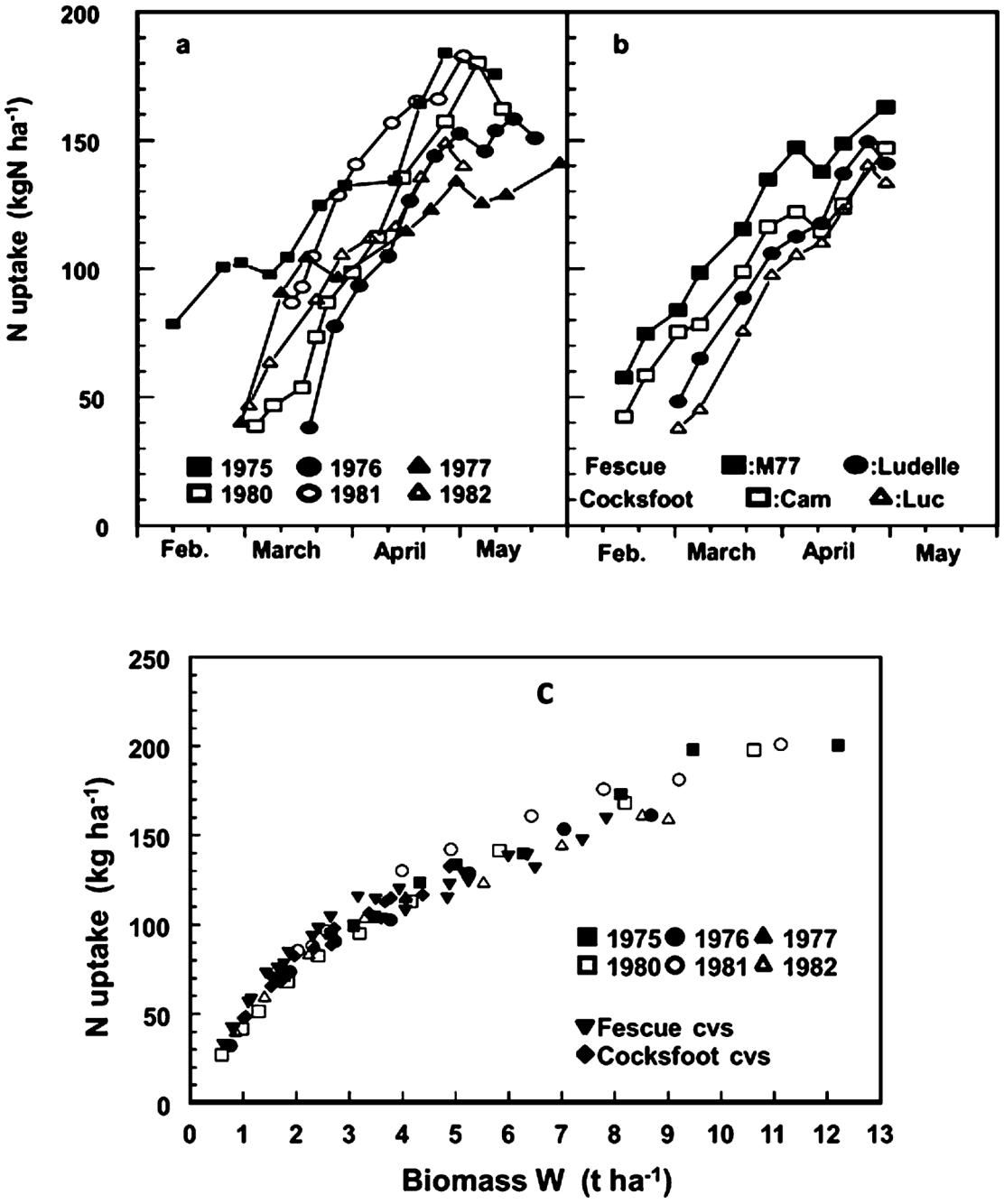

Fig. 1. Nitrogen uptake dynamics during spring of tall fescue receiving a non-limiting N fertilizer application in different years (a) and of different tall fescue or cocksfoot cultivars in the same year (b) along with the expression of N uptake in relation with aboveground biomass accumulation for all data (c). (After Lemaire and Salette, 1984a, b).

external factor to which plants respond. This approach has been dominated by soil physico-chemistry focusing on the interaction between the different nutrient elements and the soil mineral matrix for the determination of the "nutrient availability". Plant physiologists were then left with dealing with the relationship between "nutrient availability" and root absorption processes.

Over the last 30 years, studies on the dynamics of plant and crop nutrition (see recent review of Lemaire et al., 2019) based on allometry between nutrient uptake (N, P, and K) and above ground biomass accumulation by crops have resulted in a more integrated hypothesis of crop nutrient uptake in which the rate of nutrient uptake by plants is co-regulated by both the nutrient concentration in the root medium and the plant growth capacity itself (Devienne-Baret et al., 2000). This co-regulation of nutrient absorption has been experimentally established as a long distance signaling from shoots to roots (Ismande and Touraine (1994); Tourraine et al., 1994; Forde, 2002). So, if such a co-regulation occurs, it implies that "nutrient availability in soil" cannot be longer considered only as an external factor for plants, but as resulting also of the functioning of the integrated soil-plant system. Moreover, the analysis of interactions between the different nutrient elements (N, P, and K) as allowed by this approach indicates clearly that the availability of one given element for plants is in large part determined by the availability of other elements (see Lemaire et al., 2019), leading then to strong interactions between the different nutrients.

Research in plant physiology for understanding plant N mineral nutrition and the regulation of nutrient absorption processes by roots have been conducted by using very simplified experimental systems, such as excised roots or young germinating seedlings. This approach

allowed a precise characterization of the kinetics of *in planta* nutrient transport systems, that is to say the function describing their instantaneous transport activity over a range of external nutrient concentrations. In such a system, the availability of nutrient was considered an external factor for plants, which allowed a quantitative analysis of absorption in response to variations in nutrient concentration within the root medium (Rao and Rains, 1976). Although convenient for fast laboratory experiments, these experimental systems did not allow the unravelling of the regulatory mechanisms controlling the transport systems in intact autotrophic plants. More recently, molecular approaches allowed the identification of the different root membrane transporter proteins for the absorption of nitrate and ammonium, and of P, K, and other mineral elements (Nacry et al., 2013) and demonstrated that the expression of genes coding these proteins were feed-back regulated by plant shoot signals (Gansel et al., 2001; Chen et al., 2016; Ohkubo et al., 2017).

In parallel with these advances in plant physiology, research in soil science progressed in the understanding of soil-plant-microbe interactions by going beyond the restricted physico-chemistry and static vision of soil nutrient availability. Tremendous progress has been made recently thanks to the dynamic analysis of the soil microbiome under various nutrition conditions (Stringlis et al., 2018), through the analysis of root exsudates for solubilization of different minerals (Voges et al., 2019; Dakora and Phillips, 2002; Sisó-Terraza et al., 2016), and the role of soil microbe communities for providing available nutrients to plants (Jacoby et al., 2017; Garcia and Kao-Kniffin, 2018). Plants and microbes associated within the rhizosphere are playing an important role in the availability of N, P, K and other nutrients for root absorption.

The overall objective of this review paper is to develop an integrated and hypothesis-based vision of plant mineral nutrition. More specifically, we wanted (i) to demonstrate how these different hypotheses of regulation at the whole plant-soil system are corroborated and verified by recent advances in the molecular physiology analysis of the different processes involved in plant nutrition, (ii) to present new evidence of the physiological basis for analyzing interactions among different plant nutrients, and (iii) to analyze the plant-soil interactions at the rhizosphere level for a more integrated view of the soil-plant-microbe system.

2. An integrated vision of the regulation of plant nutrient uptake at crop level

2.1. Evidence for a co-regulation of N absorption by both soil N availability and plant growth dynamics

Empirical studies demonstrated clearly that N uptake dynamics by different forage crop species is strongly controlled by aboveground plant mass accumulation (Lemaire and Salette, 1984a, b; Lemaire et al., 1985). As represented in Fig. 1, the large variation in N uptake (N) by perennial grasslands due to years, species, and genotypes is fully explained by the differences in the dynamics of aboveground biomass accumulation (W).

Greenwood et al. (1990); Lemaire and Gastal (1997), and Gastal and Lemaire (2002) showed that the relationship illustrated in Fig. 1c corresponded to an allometry between N uptake (N) and biomass accumulation (W):

$$N = aW^b \quad (1)$$

When Eq. 1 is drawn for different levels of soil N availability, it is possible then to illustrate the combined effect of both plant growth dynamics and soil N supply on crop N uptake (Fig. 2).

This representation allows the identification of two processes: (i) an increase in N uptake related to the increase in N application rate and (ii) an increase in N uptake associated to the biomass accumulation dynamics. So according to Fig. 1, any factor accelerating the rate of plant biomass accumulation rate increases *de facto* N uptake dynamics.

For each sampling date corresponding to a different growth stage (Fig. 2), it is possible to determine the minimum plant N uptake for achieving the maximum crop mass (W_c), which allows the determination of the critical N uptake (N_c) or the crop N demand (Lemaire et al., 2008):

$$N_c = a_c W_c^b \quad (2)$$

An equivalent relationship between plant N concentration and crop mass is obtained when the two members of Eq. (2) are divided by W. A factor 10 is then introduced as $\%N_c$ is expressed in g 100 g^{-1} DM and W in t DM ha^{-1}:

$$\%N_c = 10a_c W_c^{b-1} \quad (3)$$

As coefficient b is < 1, this equation represents the decrease of $\%N_c$ as crop mass increases and is called the critical N dilution curve.

As the two variables N_c and W_c are time dependent, the derivative of Eq. (2) allows the estimation of the daily N uptake rate or the daily crop N demand:

$$dN_c/dt = a_c b W_c^{b-1}\, dW_c/dt \quad (4)$$

So the critical daily N uptake is determined by the maximum crop biomass accumulation rate (dW_c/dt) under non-limiting N availability with a declining coefficient of proportionality as crop mass increases (W_c^{b-1}) as attested by the negative value of coefficient b-1. Devienne-Barret et al. (2000) integrated this feed-back regulation of N uptake rate by plant growth with its regulation by soil N availability by using the Michaelis-Menten formalism:

$$dN_c/dt = a_c b W_c^{b-1}\, [dW_c/dt] \times [V \times C/(K + C)] \quad (5)$$

where V and K are the coefficients of the Michaelis-Menten formula, and C is the concentration of nitrate in soil solution. Eq. (5) allows the formalization of the co-regulation of plant N uptake by both plant growth capacity and soil N availability. This co-regulation of plant N uptake implies that, at any moment, any increment of crop N uptake results from the addition of the two effects: (i) an increase in N uptake associated with an increase in crop mass (W) as stated with the first part of Eq. (5) and illustrated by the dark arrow in Fig. 2 and (ii) an increase in soil N availability as stated with the second part of Eq. (5) and illustrated by the red dotted lines in Fig. 2.

The consequence of this co-regulation of plant N uptake by both plant growth capacity and soil N supply is that the N supply in soil cannot be considered as univocally determining N availability for plants. As shown in Fig. 2, a fast-growing genotype should have a higher N uptake capacity than a slow-growing genotype not only in non-limiting N supply conditions, but also in low N supply conditions. So the feed-back regulated nature of N absorption by roots disqualifies *de facto* any linear approach of crop response to external modifications of soil N supply. The plant N nutrition dynamics must therefore be considered as a whole auto-adaptive system for the interpretation of the genotype-environment-crop management interactions.

2.2. Extension to P, K, and S nutrition and to multi-nutrient analysis

The allometric relationship between crop N uptake and biomass accumulation, as expressed in Eq. 1, has been successfully extended to the P and K nutrition of grasslands (Salette and Huché, 1991; Duru and Thellier, 1997). The critical P and K uptake curves can be expressed as follows:

$$P_c = a_p W^b \quad (6)$$

$$K_c = a_k W^b \quad (7)$$

As shown in Fig. 3, the critical P and K curves depend highly on the crop N supply. Phosphorus and K uptake dynamics are not only

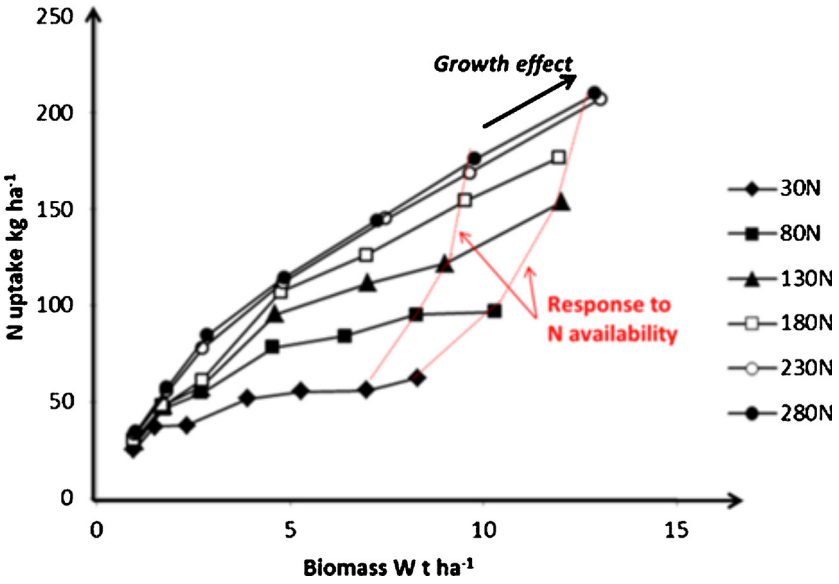

Fig. 2. Nitrogen uptake dynamics in relation with crop biomass accumulation for a maize crop having received different levels of fertilizer N applications. The dark arrow identifies the increase in N uptake associated with the increase in biomass while the red dotted lines identify the plant response to increasing soil N availability on each sampling date. (Data adapted from Plénet and Lemaire, 2000) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

determined by the quantity of above ground biomass accumulated by the crop, but they also depend on the N nutrition status of the crop as influenced by the N fertilizer supply.

It therefore appears that the availability of soil P and K for plants highly depends on the availability of N, demonstrating then strong N–P and N-K interactions. Moreover, as P and N uptake are both allometrically linked to crop mass, it is possible to obtain a direct relationship between plant P (%P) and N (%N) concentrations across different crop biomass and N supply levels for non-limiting P conditions (Fig. 4).

The result illustrated in Fig. 4 shows the close adjustment of %P and %N during crop biomass accumulation, whatever the crop N supply. This adjustment was possible because the P supply was close to optimum. In such a situation, it is then possible to determine a critical %Psh-%Nsh curve that allows the determination of a P nutrition index. Duru and Ducrocq (1997) used this index for natural grasslands and demonstrated that applications of P fertilizers on grasslands under limiting N nutrition can lead to an increase in the N nutrition status, while applications of N fertilizers under limiting P nutrition can lead to a deterioration of the plant P nutrition status. With arable crops such as wheat and maize, Ziadi et al., 2007, 2008 showed that the application of a high N fertilizer supply on wheat or maize crops under a limiting P soil supply provoked an increased P deficiency. Nitrogen and sulfur interactions have also been analysed by Reussi Calvo et al. (2011).

The above analysis demonstrates that: (i) the availability in soil of each individual element (N, P, K, and S) is under the control of both plant and soil, as attested by the existence of the strong allometry of

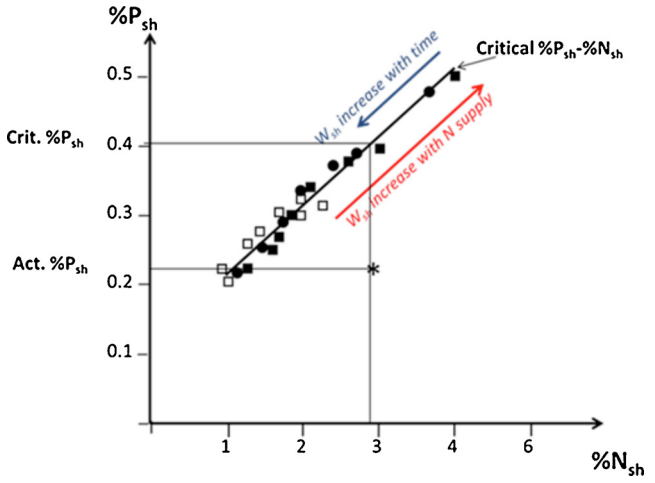

Fig. 4. Relationship between shoot P concentration (%Psh) and shoot N concentration (%Nsh) in grassland receiving a non-limiting P supply but a variable N fertilization supply: high (dark squares), moderate (circles), and low (open squares). The fitted relationship [%Psh = (0.091 × %Nsh) + 0.13]. provides a value the critical %Psh. The ratio of the actual %Psh under limiting P conditions to the corresponding critical %Psh value allows the calculation of the crop P nutrition index (PNI) whose value attests the degree of P nutrition limitation. (After Salette and Huché, 1991).

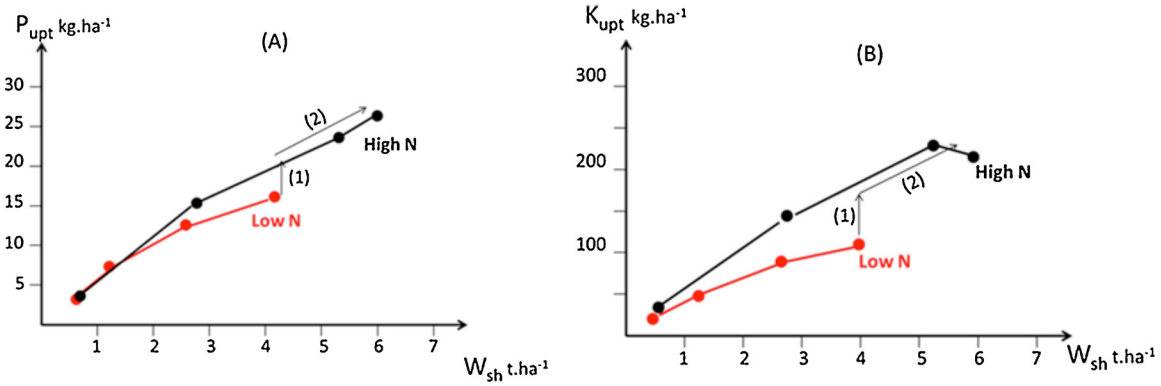

Fig. 3. Phosphorus (A) and potassium (B) uptake dynamics as a function of above ground biomass accumulation in grasslands for two levels of N supply. Two sources of P and K uptake variations can be identified: (i) the level of N supply and (ii) the level of biomass accumulation. (After Salette and Huché, 1991).

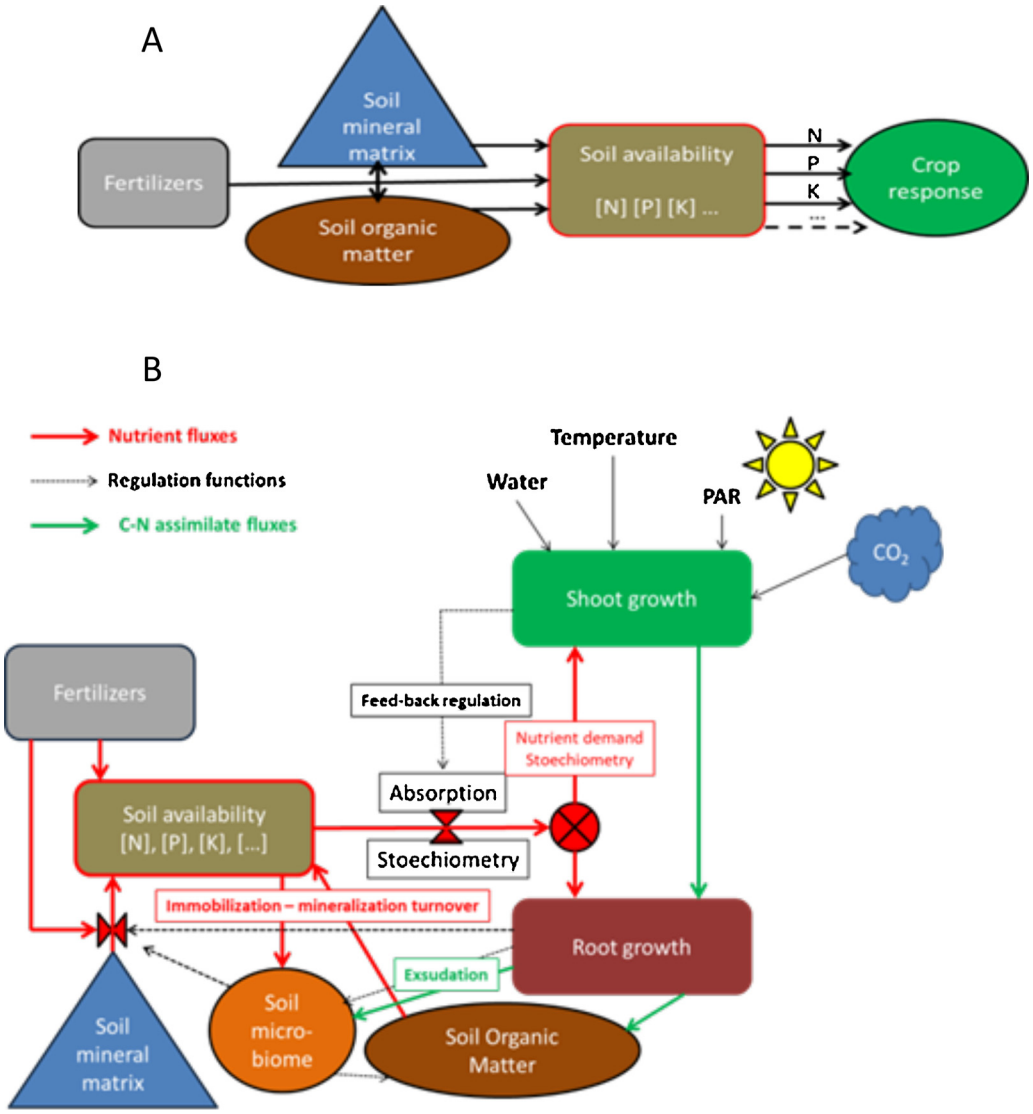

Fig. 5. Diagrams representing (A) the linear approach of crop response to fertilizer application* where nutrient availability** for plant is considered as an external factor driven by soil physico-chemical properties and soil organic matter dynamics; and (B) the integrated approach where nutrient availability is considered as an internal factor of the soil-plant-microbiome system and resulting from multiple interactions and feed-back loops between the different components. *Fertilizer application corresponds to mineral nutrient supply. **Nutrient availability indicates the amount of nutrients at a given time being immediately available for plant nutrition as a result of all contributing factors; it has therefore to be considered more as a flux than a stock.

each of these nutrients with plant growth dynamics and (ii) the availability of each element in soil depends also on the supply or the availability of the other elements. This very general observation requires the adoption of a more integrated vision of crop mineral nutrition based on the identification of the processes governing soil-plant interactions that control soil nutrient availability, as schematically represented in Fig. 5.

The initial paradigm driving past and current research in crop nutrition and fertilization is based on a linear approach. In this approach, available nutrients in soil, expressed either as a stock or a concentration, are considered as an external factor to which plants respond (Fig. 5A) and only the direct effect of fertilization on nutrient availability is taken into account. In fact, the fertilizer supply can indirectly affect some soil properties such as pH, redox potential, and the cation exchange capacity that affect nutrient availability and plant growth. These effects are implicitly included within Fig. 5A as resulting from interactions of nutrients with the soil mineral matrix. However, Fig. 5A does not correspond to the more complex reality for four main reasons: (i) root absorption capacity is deeply feed-back controlled by the plant growth capacity itself and, then, does not depend univocally on soil parameters, even if those parameters are important; (ii) interactions among different elements in soil and in plant imply that the availability of one element for plants depends upon the availability of others, requiring a more integrated approach based on stoechiometry; (iii) the plant itself influences nutrient dynamic processes in soil through interactions with microbial communities in its rhizosphere; and (iv) soil microbiome drives also nutrient availability either as providing nutrients or as competing for nutrients with plants through mineralization and immobilization processes.

Consequently, nutrient availability can be no longer considered as resulting only from static soil parameters such as stock or concentration, but as a dynamic variable resulting from the functioning of the whole soil-plant-microbiome system. This new representation allows the identification of three important research areas for the elaboration of a fully integrated approach of the control of nutrient availability for plants in agro-ecosystems: (i) the physiological and molecular control of root absorption dynamics; (ii) the physiological basis for analyzing interactions among different plant nutrients; and (iii) the analysis of the plant-soil interactions at the rhizosphere level for a more integrated view of the soil-plant-microbe system. These research areas are discussed within the next three sections with the identification of underlying biological and molecular processes.

3. Molecular control of plant N absorption dynamics

The past 20 years have seen a tremendous breakthrough in our understanding of the mechanisms governing N acquisition by plants. This occurred first in the model species *Arabidopsis thaliana*, where

molecular studies of N uptake systems provided a strong support to the hypothesis of co-regulation of root N uptake by both external N availability and the plant growth dynamics (see section 1.1).

3.1. Physiological and molecular characterization of root N uptake systems

Plants acquire N from the soil predominantly in the form of nitrate (NO_3^-) or ammonium (NH_4^+) through the activity of dedicated transport proteins located in the plasma membrane of root cells. In almost all species investigated to date, root NO_3^- or NH_4^+ uptake systems can be classified as either High-Affinity or Low-Affinity Transport Systems (HATS and LATS, respectively) (Nacry et al., 2013; von Wittgenstein et al., 2014). HATS ensure most of the N uptake at low external availability of NO_3^- or/and NH_4 ions ($< 0.2-1$ mM), whereas LATS become predominant above 1 mM. In *Arabidopsis*, the NO_3^- HATS and LATS are encoded by genes of the *NRT2* and *NRT1* (recently renamed *NPF*) family, respectively (Nacry et al., 2013). The NH_4^+ HATS are encoded by the *AMT1/2* genes (Yuan et al., 2007). The molecular identity of the NH_4^+ LATS still remains elusive.

Functional analysis of knock-out mutants for NRT2 and AMT1/2 transporters in *Arabidopsis* has led to a very detailed knowledge of the molecular structure of the HATS (Nacry et al., 2013). Root high-affinity NO_3^- uptake is predominantly ensured by NRT2.1 that can accounts for up to 75 % of the whole HATS activity. The NH_4^+ HATS activity relies on the AMT1.1, 1.2, 1.3 and 1.5 transporters. The NO_3^- LATS is less well characterized, but involves the NRT1.1(NPF6.3) transporter. Although differences may occur as compared with *Arabidopsis*, the same general molecular organization of the NO_3^- and NH_4^+ uptake systems was reported in many species, including crops (Garnett et al., 2013; von Wittgenstein et al., 2014).

3.2. Signaling mechanisms ensuring the co-regulation of root N uptake by external N availability and plant growth

The root N uptake machinery is highly plastic, because the expression of both NO_3^- and NH_4^+ transporter genes is dramatically affected by changes in the external concentration of these ions, and by changes in the N demand of the whole plant for growth (Nacry et al., 2013). Three major regulations have been documented: (i) local stimulation by the supply of NO_3^- or NH_4^+, (ii) systemic regulation by shoot-to-root signals of the N status of the whole plant, and (iii) stimulation by shoot-to-root signals of the photosynthetic activity (see Fig. 6).

The local stimulation of the expression of root N uptake systems by their substrate is best known for NO_3^-, and is often referred to as a "NO_3^- induction" or "Primary NO_3^- Response" (PNR) process. It corresponds to a marked and fast (within a few hours) dose-dependent increase in the expression of many NO_3^- utilization genes (transporters, enzymes), following NO_3^- provision to the plant (Medici and Krouk, 2014). From a functional viewpoint, the PNR allows the plant to dramatically accelerate its NO_3^- uptake rate as soon as NO_3^- is becoming available. Because this regulation is local, this also allows the plant to express NRT transporters specifically in roots in contact with NO_3^-. Collectively, these responses play a major role in optimizing root N acquisition in response to both temporal and spatial changes in the external NO_3^- availability, thereby allowing the plant to rapidly exploit transient bursts of nitrification in the areas of the soil where they occur.

One key point is that the PNR results from the action of NO_3^- as a signal molecule, and not as a nutrient (Wang et al., 2004). This unraveled the existence of specific NO_3- sensing systems, allowing the roots to perceive where and how much NO_3- is present in the external medium. The main NO_3- sensor identified to date is the Arabidopsis NRT1.1(NPF6.3) NO_3- transporter, which displays an unusual dual transport/sensing activity for NO_3- (Gojon et al., 2011).

Despite this initial positive effect, the supply of NO_3^- or NH_4^+ at high concentration results on the longer term (several days) in a feedback repression of root N uptake systems (Nacry et al., 2013). Conversely, a decrease in NO_3^- or NH_4^+ availability leads to the upregulation of these systems, allowing a compensatory stimulation of N uptake efficiency (Lejay et al., 1999). These responses are controlled by whole plant signaling of the shoot N status, as evidenced by "split-root" experiments where two parts of the root system are subjected to different N treatments. For instance, N starvation treatment on one portion of the root system results in the increased expression of the main NO_3^- HATS gene *NRT2.1* in the other untreated portion still fed with NO_3^- (Gansel et al., 2001). The interpretation is that *NRT2.1* reacts to signals coming from the shoot, which informed the N-fed roots of the N deficiency experienced by the other organs. These signals modulate root N acquisition for matching the N demand of the whole plant, which is primarily determined by its growth rate (Ismande and Touraine

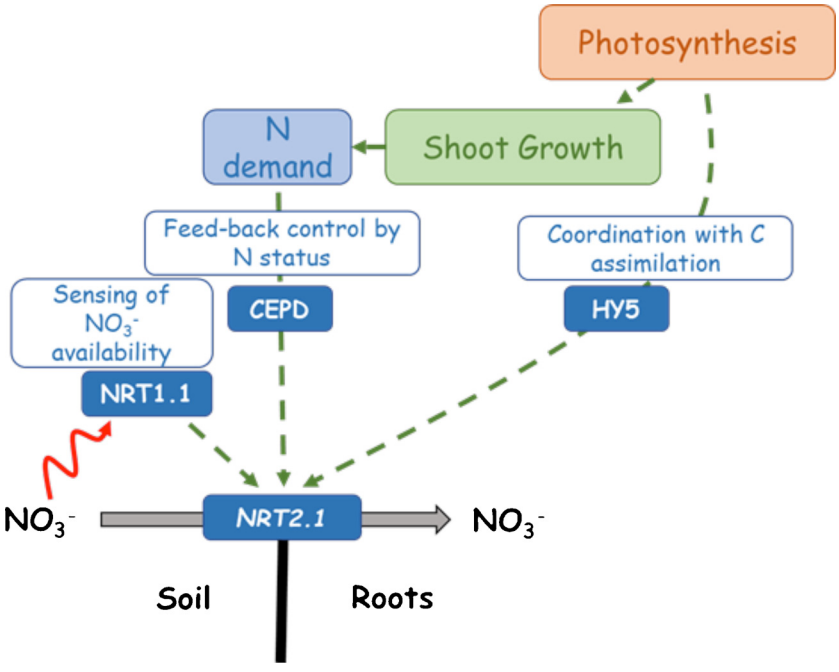

Fig. 6. Schematic representation of the molecular mechanisms ensuring co-regulation of root nitrate uptake by external nitrate availability and growth of the shoot in Arabidopsis thaliana. External nitrate availability is sensed by the NRT1.1 transporter/sensor. Shoot-to-root signaling of N demand generated by shoot growth is ensured by mobile CEPD proteins. Shoot-to-root signaling of photosynthetic activity is ensured by the mobile HY5 transcription factor. NRT1.1, CEPD and HY5 are regulators of the expression of the NRT2.1 gene, encoding a major root nitrate uptake transporter.

(1994)). This feed-back regulation of N uptake corresponds to the empirical mechanism described in the first part of Eq. 4 as discussed in section 1.

Molecular mechanisms underlying this whole plant signaling pathway have recently been identified in *Arabidopsis* (Ohkubo et al., 2017). Briefly, when N-starved, roots export small peptides (the 15-amino acids long CEPs) to the shoot via the xylem. In the shoots, the CEP peptides are perceived by two specific leucine-rich repeat receptor kinases (named CEPRs for CEP Receptors), which are themselves regulated by the N status of the plant (upregulated by N deficiency). This in turn triggers the expression of glutaredoxin proteins (named CEPD for CEP Downstream), which are subsequently transported down by the phloem to the roots where they activate expression of the *NRT2.1* gene.

Finally, the upregulation of root N transporters by signals from photosynthesis also participates in the control exerted by growth on N uptake. Indeed, both root NO_3^- and NH_4^+ uptake rates are strongly dependent on light conditions (Gastal and Saugier, 1989; Delhon et al., 1996). This is due to the production of photosynthates, as the stimulation of root NO_3- uptake by light is abolished in CO_2-free air, and the negative effect of darkness can be suppressed by sugar supply to the roots (Delhon et al., 1996). This was fully confirmed at the molecular level by the observation that several *NRT* and *AMT* genes are upregulated in the roots by illumination of the shoot only in presence of CO_2, and are sucrose-inducible (Lejay et al., 1999, 2008). Most importantly, this could not be explained by an indirect effect of photosynthesis through activation of the N demand regulatory mechanisms, because the transporter genes responding to photosynthesis are not the same as those responding to the whole plant signaling of N status (Lejay et al., 1999; Nacry et al., 2013; Lejay et al., 2008). This indicates the occurrence of specific shoot-to-root photosynthesis signals targeting root N transporter genes to coordinate N uptake with C assimilation. One such signal is the HY5 transcription factor, which is synthesized in the shoot in response to light and photosynthesis, and transported down to the roots where it is able to directly stimulate *NRT2.1* transcription after binding to the promoter of this gene (Chen et al., 2016).

Collectively, the three above regulations explain how both external N availability and plant growth act to co-regulate root N uptake systems. They allow the plants to react to changes in the soil environment and to maintain N homeostasis in their tissues (see Box 1). Noteworthy, it is now possible to position precise molecular regulators in the schematic representation of an integrated approach of crop nutrition (Fig. 6, to compare with Fig. 5). Although best documented in *Arabidopsis*, these mechanisms are of general significance, as similar regulatory patterns for the expression of root N transporters have been reported in other species (Buchner and Hawkesford, 2014).

3.3. Open questions on the effect of increasing atmospheric CO_2 on the N nutrition of plants

Despite the fact that the regulation of root N uptake by plant growth has been firmly established by ecophysiological, physiological, and molecular studies, intriguing observations aroused from the investigation of the expected positive effect of elevated CO_2 concentration (eCO_2) on photosynthesis and growth of C3 species. Indeed, meta-analyses from a large number of FACE (Free-Air − CO_2-Enrichment) field studies have concluded that the increase in biomass production of most C3 plants in response to eCO_2 is associated with a decreased concentration of N in plant organs, including seeds (Taub and Wang, 2008; Loladze, 2014). Furthermore, although it is particularly pronounced for N, this decrease is also observed for many other mineral nutrients, thereby suggesting that the continuous increase in atmospheric CO_2 concentration will lead on the long term to a reduced nutritional quality of most plant edible products (Loladze, 2014; Uddling et al., 2018).

The reasons why the growth at eCO_2 leads to a significant decrease in N concentration in plant tissues are not understood (Taub and Wang, 2008; Uddling et al., 2018). One possibility is that eCO_2 alters the bioavailability of nutrients in the soil, through increased competition with microorganisms (Uddling et al., 2018). However, mechanisms intrinsic to the plants are also certainly involved, and the concepts detailed in the above sections may help putting forward at least two hypotheses. Firstly, the decline in N concentration in plants grown at eCO2 may directly result from the regulation of root N uptake by the N demand for growth. As a matter of fact, most C_3 plants grown under eCO_2 display the so-called “acclimation of photosynthesis to eCO_2 “, which results in a down-regulation of the photosynthesis machinery, leading to reduced concentrations of Rubisco in leaves (Taub and Wang, 2008). Because Rubisco accounts for up to one-third of the total protein content in photosynthetically active leaves, this suggests that the N

Box 1

Homeostasis in plant nutrition. How to estimate the nutrient status in plants and crops?

Homeostasis can be defined as the property of a plant to maintain as constant as possible some key internal variables for optimizing its growth and development. Concerning mineral nutrition, homeostasis corresponds to a set of feed-back mechanisms through which plants adjust the acquisition of different nutrients to their metabolic demand. This auto-adaptive property of plants results in the fine-tuning regulation of the internal concentration of nutrients in relation with the nutrient concentration of the external medium. It raises the question of how to estimate nutrient concentration in plants for evaluating their nutrition status by reference to an optimum nutrition. The nutrition status of plants is generally estimated through their nutrient concentration. Following Ulrich (1952), a critical plant nutrient concentration can be defined as the minimum plant concentration necessary to obtain the maximum plant growth rate. But as shown above (section 1), the critical concentration of the major nutrients (N, P, and K) decreases as plant mass (W) increases. Consequently, the actual plant nutrient concentration alone cannot be considered as a relevant estimate of the plant nutrition status. Plant nutrient concentration values have to be corrected from the general dilution effect by calculating nutrition indices as follows:

for N: $NNI = \%N_{act}/\%N_c$

for P: $PNI = \%P_{act}/\%P_c$

for K: KNI = with $\%K_{act}/\%K_c$

with $\%N_c$, $\%P_c$, and $\%K_c$ being the critical concentrations estimated by the critical dilution curves (e.g. Eq. 3 for N) and corresponding to the actual crop mass (W_{act}).

As reviewed in Lemaire et al. (2019), the dilution of nutrient with crop mass accumulation can be explained if we consider that plant mass is composed of two compartments: (i) a metabolic compartment (W_m) associated with plant growth processes and having a high N concentration ($\%N_m$) and (ii) a structural compartment (W_s) associated with plant architecture and having a low N concentration ($\%N_s$) with: $W = W_m + W_s$. So as postulated by Caloin and Yu (1984), W_m and W_s being retated with an allometry ($W_m = kW^{\alpha}$, with $\alpha < 1$), then plant N concentration should decline allometrically with crop mass (W) as expressed in Eq. 3. Homeostasis of N nutrition of plants would be achieved by maintaining $\%N_m$ as constant as possible during plant growth despite the ontogenic decrease in %N. This decline of plant N concentration with increasing crop mass is the reason why attempts to estimate the N nutrition status of plants or crops directly by their total N concentration failed.

demand is lowered in plants under eCO_2 as compared to ambient CO_2, thereby resulting in a down-regulation of root N uptake systems. Secondly, the empirical allometry reported between N and biomass accumulation (see Eq. 3) introduced a declining coefficient of proportionality between both variables as crop mass increases. As outlined in Box 1, the regulation of root N uptake by plant growth does not aim at maintaining the total N concentration in plant tissues constant, but at ensuring N homeostasis in the metabolic compartment ($\%N_m$). Because this is associated with an allometric decrease of the total plant N concentration as the plant grows, it suggests that reduced nutrient concentration of plants grown under eCO2 may simply be the predictable consequence of the rules depicted in section 1.1.

3.4. Coordination between plant responses to combined nutrient deficiencies

Various minerals interact in the soil based on their opposite charges. As a result, many of them become less mobile and available for plant nutrition with negative effects on plant growth and development. These interactions among nutrients exist in plants as well, and the interdependency between the different nutrient homeostasis is a general rule rather than the exception. Nevertheless, determining how this interaction between different nutrient homeostasis controls plant growth is only in its earliest stages of understanding (Bouain et al., 2019a).

Here we focus on recently published results on the interaction between nutrients, using the example of P and N, as well as interactions between P and metals such as iron (Fe) and zinc (Zn). These interactions manifest themselves at the morphological, physiological, and molecular levels. At the morphological level, several unexpected observations have been reported, such as the effect of inorganic P (Pi) and/or Fe deficiency on root system architecture. Remarkably, whereas primary root growth is inhibited by single Pi starvations, its recovery has been observed under combined Pi and Fe deficiencies (Ward et al., 2008). This observation indicates that the plant response to a combined nutrient stress cannot be predicted from its response to a single stress. Similarly, the plant response to a combined nutrient stress is not simply the addition of its responses to each individual stress. Several genes acting at the interface of the P and Fe homeostasis to control primary root growth have been identified, mainly in *Arabidopsis* (Bouain et al., 2019b).

Another intriguing finding on nutrient interaction was reported at the physiological level, in which important changes in the ionome *in planta* (involving many nutrients) were observed as a result of the altered availability of one or more nutrients in the medium. The biological relevance of ionome changes due to the absence of one or more nutrients remains poorly understood for plants. Whether this phenomenon is beneficial or detrimental for plants deserves further investigation. Finally, at the molecular level, a combined nutrient stress was recently shown to modulate (i.e. enhance or repress) the plant response to the deficiency of one of the nutrients, such as the interdependency of a Pi deficiency signaling on the presence of N in the medium (Medici et al., 2019). This result provides a possible explanation for the strong N–P interaction observed in field conditions as shown above (see Fig. 3a). The manner in which plants detect, make sense of, and adapt to various nutrient signals such as P, N, and Zn are fundamental biological questions that need to be addressed in order to fully appreciate the regulation of mineral nutrition in plants.

Phosphorus in the form of Pi can influence the bioavailability and mobility of metals (e.g. Fe and Zn) in the soil. Plants have evolved highly sophisticated mechanisms to co-regulate P and Zn homeostasis (i.e. uptake, transport, storage, and remobilization). Our understanding of how plants respond to Pi deficiency is more advanced than how they sense and respond to Zn deficiency. Specifically, a complete Pi starvation signaling pathway has been identified in plants (for further review: Briat et al., 2015). In contrast, two master regulators of the Zn starvation response have been identified in plants: TFs bZIP19 and bZIP23 (Assunção et al., 2010). Since the 1970s, the interaction between Pi and Zn homeostasis has been recognized in many plant species. This raises an important question regarding how deficit-Zn signals can induce the Pi transporters that presumably cause a further accumulation of Pi in the shoots, despite the presence of a sufficient Pi concentration in the medium (Marschner and Cakmak, 1986). This observation paved the way for the discovery of new pathways that regulate Pi acquisition and accumulation in plants. Indeed, thanks to the recent development of high-throughput phenotyping technologies and system biology approaches a new mechanism controlling Pi homeostasis in a Zn-dependent manner has been discovered in plants (Khan et al., 2014; Pal et al., 2017; Kisko et al., 2018). These results open perspectives for improving Pi transport and accumulation in plants and crops by modulating the Zn deficiency signaling (Bouain et al., 2019a).

The interaction between P and N homeostasis takes place in the shoots and roots, and their deficiency has a dramatic effect on the growth capacity of these two organs. A genetic screen in *Arabidopsis* aimed at identifying plants that display sustained growth in N-deficit conditions resulted in the identification of the NITROGEN LIMITATION ADAPTATION (NLA) gene as an important component in controlling plant adaptability to N-deficit conditions. NLA encodes a RING type E3 ubiquitin ligase. Interestingly, NLA and PHO2 (a ubiquitin-conjugating E2 enzyme) cooperatively control the trafficking of Pi transporters and, thereby, Pi transport and accumulation (Lin et al., 2013). This strongly supports the idea that Pi accumulation in the shoots is N-dependent. The connection between N and P homeostasis in roots has also been demonstrated (Cui et al., 2019). More recent studies have outlined the existence of a strong interdependency between the Pi deficiency signaling pathway and the availability of N in the medium. These results indicate that plants do not respond to Pi deficiency if N is limiting in the medium (Medici et al., 2019). This process is conserved in crops such as rice (Hu et al., 2019). All these molecular processes for co-regulation of N and P homeostasis corroborate perfectly the empirical N–P relationships as described in Fig. 4 and the necessity to develop a more integrated approach of nutrients availability for plants as expressed in Fig. 5B.

In this section, data on P interactions either with N, Zn or Fe were examined out of many other nutrient interactions reported in the literature, which are often studied two-by-two (e.g. P–S, Fe-Zn). It is important to pursue the effort in determining how plants make sense of and adapt to various nutrient signals. Developing a system level understanding of the regulation of plant mineral nutrition is of equal interest. This is key to start appreciating the mineral nutrition as a system (Bouain et al., 2019a). This future research direction will have important consequences for agricultural practices and biotechnology, in terms of adapting genotypes to particular agricultural conditions and decreasing our dependency on nutrient fertilizers.

4. How root-microbes interactions control soil nutrient availability for plants?

Plant mineral uptake is feed-back controlled by plant growth, as reported above. Nevertheless, this uptake heavily depends on the physico-chemical properties of the soil mineral matrix, which determine the equilibrium among different mineral forms more or less usable by plants (see Fig. 5B). In addition to soil physico-chemical properties, the actual mineral availability for plants, representing the pool of minerals that will be taken up by the plants, either directly through root cells and/or indirectly by symbiotic micro-organisms associated with the roots, is strongly affected by living organisms found in the soil and their interconnections with soils and plants as described in Fig. 7.The microbiome and the micro- and macro-fauna interact in multiple trophic ways, leading to the modification of nutrient availability for plants. Conversely, the roots, by their exudates, play an active role in the shaping of the microbiome and, therefore, on soil biocenosis. Plants and soil organisms are also affected by the physico-chemical properties of the soil, which they contribute to modify in a

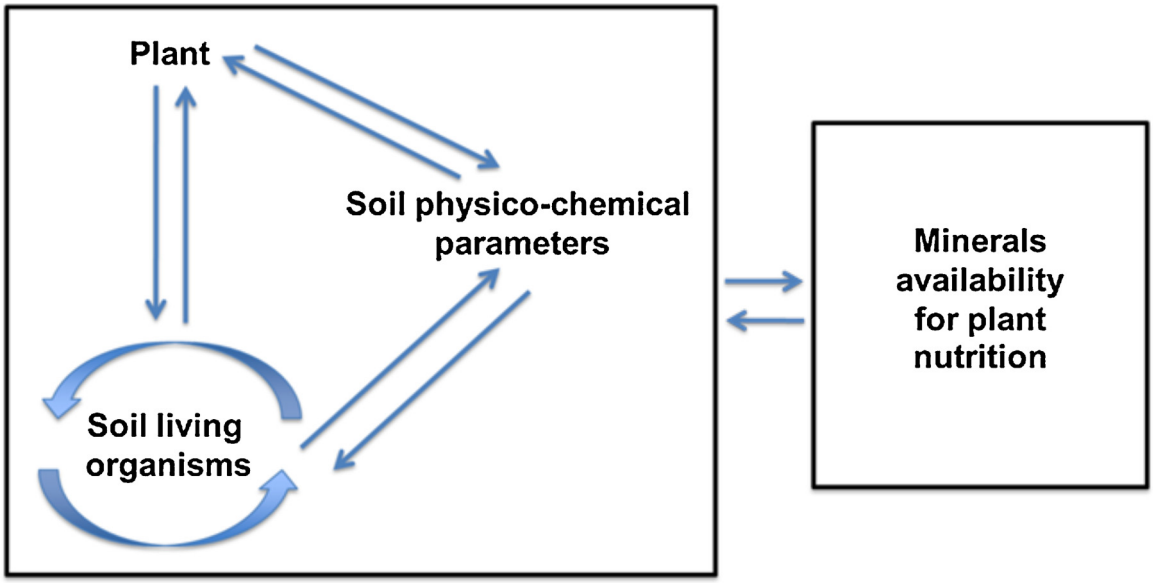

Fig. 7. Schematic representation of the various parameters controlling soil nutrient availability. The composition of soil living organism communities is determined in part by the competition for nutrients between them. These communities, in particular the microbiome, are also shaped by root exsudates, and, conversely, they play an active role in providing nutrients to plants. Both plants and soil living communities depend upon the physico-chemical properties of a given soil but, in return, they influence these properties. This tripartite equilibrium determines the availability of nutrients for plant nutrition, which in a feed-back loop will influence this trophic equilibrium.

feedback loop. It is also important to keep in mind that the uptake of minerals by plants will influence, in return, all the various equilibriums mentioned above.

4.1. Plant-microbe interactions to facilitate plant nutrition

4.1.1. Importance of mycorrhiza for plant nutrition

In nature, mycorrhizal symbiosis can be considered as the rule because only 8% of plant species are truly non mycorrhizal (Brundrett and Tedersoo, 2018). It is well known that most species of agricultural interest form exclusively endomycorrhizas with fungi belonging to the *Glomeromycotina* subphylum to produce the so-called arbuscular mycorrhizas (AM). Two plant families (*Brassicaceae* and *Chenopodiaceae)*, however, are non AM species.

Plants and fungi can take up only free orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) (denoted Pi) from the soil solution. Because Pi represents only a tiny fraction of soil total P, P is often limiting for plant growth. Furthermore, because a zone of depletion is rapidly created around the absorbing organs, the Pi uptake will depend strongly upon the ability of the species to explore new zones containing more Pi in solution. Consequently, mycorrhizal symbiosis (discovered more than 50 years ago) improves plant P nutrition (Smith and Read, 2008). The low diameter of hyphae (10 µm on average) combined to their length, which can represent up to 1 m of fungal filaments per mm of root length (Allen, 2007), explains the better P nutrition of mycorrhized plants. This effect was nicely demonstrated by measuring the uptake of ^{32}P supplied specifically to external AM hyphae, either in the field with clover (Jakobsen et al., 2001) or in controlled conditions with maize (Sawers et al., 2017). In both experiments, the amount of ^{32}P in plants was strongly related to the length of hyphae colonizing the labelled soil, but not to the length or the proportion of roots colonized. In addition to the better soil exploration, the hyphae of AM species could increase Pi availability by complexing cations linked with Pi through the release of low molecular weight organic anions, such as citrate, as recently shown in axenic conditions with the model AM species *Rhizophagus irregularis* (Zhang et al., 2016). If displayed by other AM species, this property will add a new capacity to the mycorrhizal root system to access the mineral P fraction usually unavailable for hyphal or plant uptake.

Remarkably, besides these effects of AM increasing the capture of Pi from the soil solution, Smith et al., 2003, 2004 demonstrated that the Pi uptake through the mycorrhizal pathway (via the P transporters of external hyphae) can provide up to 100 % of Pi entry into endomycorrhizal plants (Facelli et al;, 2010; Smith et al., 2004). It therefore dominates the plant pathway (via the P transporters of epidermal cells), irrespective of the effect of mycorrhizal symbiosis on plant growth and P accumulation of mycorrhizal when compared to control plants. This could be explained by the expression of the plant Pi transport systems localized in the epidermal cells which is more or less negatively regulated in AM roots. Conversely, the absence of epidermal Pi transporters is compensated by the expression of new Pi-transport systems specifically induced by AM symbiosis and localized at the plasma membrane of root cortex cells containing arbuscules (Harrison et al., 2002; Rausch et al., 2001). Thus, Pi ions absorbed by the hyphae far from the root are transported into the arbuscules where they leave the fungal cytosol by a yet unknown mechanism (Plassard et al., 2019) to be taken up by mycorrhizal-induced plant P transport systems in the common apoplastic space of mycorrhizal roots. Finally, at the whole plant level, those findings suggest that a mycorrhizal plant could take up Pi mainly through the fungal cells and not plant cells. Cropping practices that favor the growth of hyphae in soils, therefore, appear essential for the development of an efficient and sustainable agriculture. As well, those findings on the importance of mycorrhizal plants for P uptake suggest that the classical approach relating soil Pi availability measured with chemical extractants to plant uptake must be revisited.

In addition to P, AM fungi have been shown able to take up ^{15}N-nitrate or ^{15}N-ammonium and to transfer ^{15}N to the root tissues in simplified controlled conditions (Guether et al., 2009). However the effect of AM symbiosis on the N nutrition of the host is not that clear, as reported by Corrêa et al. (2015). From their analysis of the literature (55 experiments), only 36 % and 25 % of the experiments reported positive or neutral to positive mycorrhizal response for N, whereas the other experiments (39 %) reported no effect, or negative effects. A possible explanation for these contrasted results could be that the relationship between N availability and the mycorrhizal effect on plant N nutrition might not be linear but curvilinear, with positive effects only

at intermediate N levels because the fungus and the plant will be limited by C and N, respectively. The plant will benefit from increased N uptake by the fungus that will increase plant growth and photosynthesis, resulting in more C availability for the fungus. In contrast, at low N, the fungus may retain N, becoming a competitor for the plant. At high N levels, both the fungus and the plant become limited for C or other elements and the negative AM effect may result from a too high demand in C required to assimilate N or a retention of the other limiting nutrient. Therefore, N fertilization appears as an important parameter to be controlled for benefitting from endomycorrhizas, in particular to improve P nutrition. This point emphasizes the importance to consider plant nutrition as a whole by taking into account interactions across different nutrients and particularly N and P as illustrated in sections above.

4.1.2. Iron nutrition as a case study of plant-microbiome interactions

An important part of the C fixed by leaves through photosynthesis is secreted by roots in the rhizosphere under the form of various organic molecules (Bais et al., 2006), nurturing a huge microbial community at the root-soil interface, known as the root microbiome (Bulgarelli et al., 2013). Although the microbiome contains soil-borne pathogens, it also hosts mutualistic microbes helping plants to acquire water and nutrients.

Plants can modify their root environment in different ways and, as a consequence, the soil and rhizospheric microbiome will adapt and change its composition (Bulgarelli et al., 2013). This has been well documented for iron nutrition. Plant genotypes with varying efficiencies for iron uptake have been reported to affect the soil microbiome. Plant genotypes that deplete the rhizosphere for iron led to a counter-selection of specific fluorescent pseudomonads more adapted to a scarce iron environment and beneficial for plant health (Robin et al., 2008). Plants secrete organic molecules in the rhizosphere as one of their responses to iron deficiency, independently of their genotype. Among these molecules, a particular class of phenolic compounds, the coumarins, has recently received a wealth of attention. Their synthesis and their secretion by a specific root transporter in the rhizosphere are up-regulated in response to iron deficiency (Rodríguez-Celma et al., 2013; Fourcroy et al., 2014; Schmid et al., 2014;), but down-regulated in response to Pi deficiency (Chutia et al., 2019). These molecules act by increasing the solubility of iron and its delivery to the plant uptake system (Fourcroy et al., 2016), but they have also an allopathic effect on soil microorganisms, contributing to reshape the root microbiome in response to iron deficiency (Stringlis et al., 2018; Voges et al., 2019). The example of iron nutrition perfectly illustrates the relationships between plant nutrition and the soil microbiome composition, and their interactions. A key issue for the future will be to understand how the choice of cultivated genotypes and their fertilization shapes the soil microbiome in order to favor its positive effects on plant nutrition while avoiding negative effects.

4.2. Interactions between soil living organisms and their impact on plant nutrition

4.2.1. N mineralization and N availability to plants

It is well known that microorganisms are directly involved in the mineralization of organic N compounds resulting in the production of mineral N sources such as ammonium or nitrate. However, bacterial grazers, mainly protozoa and nematodes, feed permanently on microbial populations, creating the microbial loop. This microbial loop will cause a shift in the composition of the soil microbial community that can strongly influence the flow of mineral nutrients in soils. In agreement with this hypothesis, a recent meta-analysis showed a positive effect of the presence of bacterial feeders on soil N mineralization that was increased by 80 % compared to situations without bacterial feeders (calculated from 220 observations published between 1977 and 2014). Also, plant biomass was significantly increased (+ 20 %) as well as N accumulation in shoots (+ 59 %) and roots (+ 28 %) (Trap et al., 2016). Two main pathways are proposed to explain the effects of bacterial grazers on increased N mineralization and plant growth: (i) a direct pathway due to the excretion of nutrients by the grazers and (ii) an indirect pathway involving the stimulation of microbial activity and its positive effects on root growth. Nutrient excretion is considered to be due to the strong stoichiometric homeostasis and low C assimilation efficiency of grazers (Trap et al., 2016). Thus, in order to compensate for the C losses due to respiration and to maintain their stoichiometry, a large part of the N and also of P ingested by the bacterial feeders is released as mineral (ammonium) or organic forms (amino acids). Estimations of the proportion of N excreted to N ingested ranged from 30 (Clarholm, 2002) up to 60 % (Griffiths, 1994), showing the importance of the microbial loop for improving mineralized N availability in soils.

Besides the effect of the microbial loop, a strong increase of mineral N availability to plants was demonstrated through the combined effect of bacterivores and AM symbiosis on plant growth and photosynthesis (Koller et al., 2013). In short, these authors observed that AM hyphae alone were not able to forage N from ^{15}N-labelled raw organic matter, confirming the poor ability of AM hyphae to mineralize organic N. As expected, addition of bacterivores only with hyphae, but not with roots, increased significantly the amount of plant ^{15}N, confirming their positive effect on N mineralization. But surprisingly, addition of bacterivores to both hyphae and roots increased by a factor 5 on average the amounts of ^{15}N in the AM plant, and also plant photosynthesis and root growth. Koller et al. (2013) proposed a conceptual framework to explain their results (Fig. 8). Hence, this experiment demonstrated that the action of microbivores is essential for the plants to benefit from N contained in a complex source via endomycorrhizal fungi.

4.2.2. Plant P use from organic P

Soil P reserves consist of insoluble mineral P but also of organic P (Po) that could represent the main part of soil total P. To be used by plants and all other organisms, the orthophosphate group must be released from its ester link by phosphatase enzymes. If the capacities of AM fungi to access and to take up more Pi than the plant itself are well established (see section 4.2.1), their abilities to mineralize organic P (Po) and especially phytate, which is considered as the most abundant but recalcitrant source of Po in soils, have been recently questioned in many studies. The main outcome of these studies is that AM fungi display poor capacities to mineralize phytate but are able to recruit on their hyphae phytate-mineralizing bacterial populations (Hara and Saito, 2016; Zhang et al., 2018; Wang et al., 2019). Remarkably, the hyphae-bacterial communities are significantly different from those found in the bulk soil, suggesting a selective effect of the AM fungal cells on its microbiome.

However, in controlled conditions, the amounts of plant P gained from phytate addition in the hyphal compartment inoculated with phytate-mineralizing bacteria could be low or equal to those measured without bacteria. Conversely, the amounts of bacterial P increased, indicating a competition between the bacteria and the AM fungus for the Pi released from phytate, especially when Pi availability is extremely low (Wang et al., 2016; Zhang et al., 2016). This competition is suppressed when a mineral P fertilization is brought to the hyphal soil. Hence, the outcomes of AM hyphae and organic P mineralizing bacteria interactions on plant P nutrition from organic P are complex and still difficult to predict, and constitute a major challenge to improve P plant nutrition in the future.

As for N, grazing of organic P-mineralizing bacteria hosted by the AM hyphae could improve plant Pi availability from the Po source. So far, we do not know what is the effect of grazing upon these bacteria. However, Irshad et al. (2012) have studied the grazing of *B. subtilis*, a phytate-mineralizing bacterium, by nematodes brought in the rhizosphere of Pine seedlings associated with an ectomycorrhizal fungus and grown with phytate as the sole source of P. They found that the presence of nematodes increased by a factor greater than 3 the total

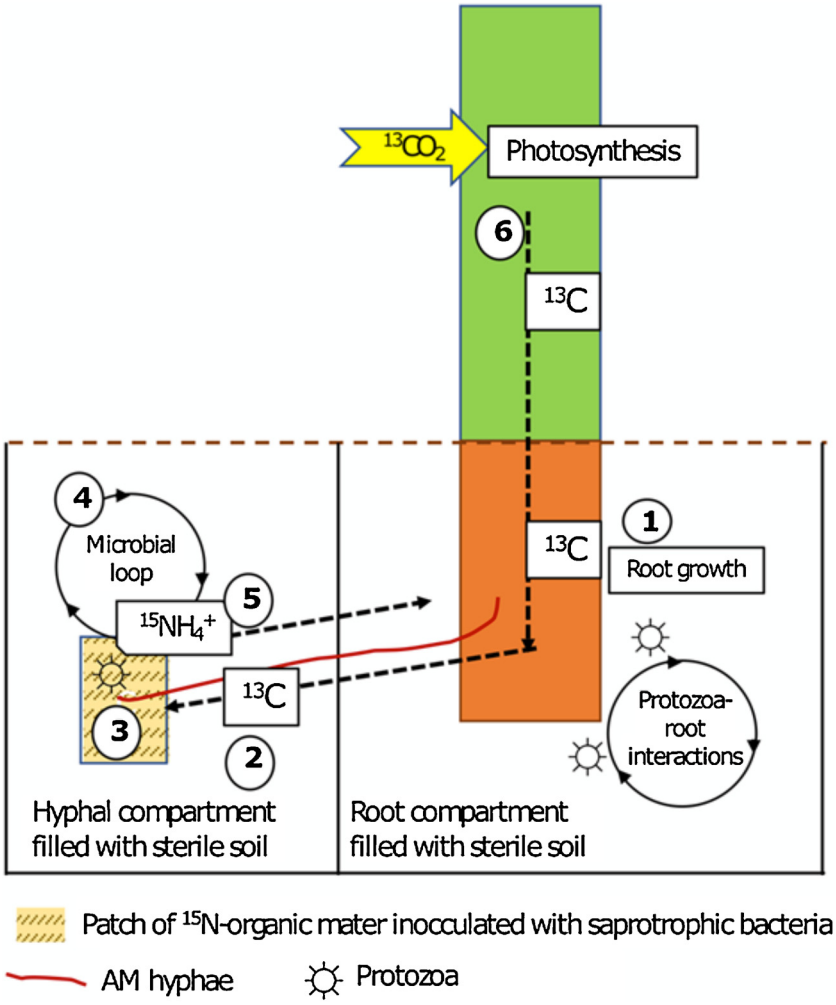

Fig. 8. Possible interactions between protozoa, AM fungi, and roots resulting in an increased plant biomass and 15N accumulation, as observed in the study by Koller et al. (2013). 1/ Addition of protozoa to the soil will stimulate photosynthesis and ^{13}C fixation from the $^{13}CO_2$ supply, and the ^{13}C-carbon flow towards the root; 2/ this increased C flow will also enhance the foraging activity of the AM fungus and 3/ of saprotrophic bacteria able to mineralize ^{15}N in the ^{15}N-organic matter patch; 4/ the protozoa feeding on the mineralizing bacteria (the microbial loop) will release ^{15}N-NH4+; 5/ this ^{15}N-NH4+ will be taken up by the AM fungus and transferred towards the plant; 6/ this additional N will stimulate plant photosynthesis and growth, inducing a positive feedback leading to the increase of ^{13}C allocation to the root and fungal cells (adapted from Koller et al., 2013).

amount of plant P compared to the one measured in mycorrhizal plants and *B. subtilis* only. Although obtained in simplified conditions, these results highlight the importance of microbivores to increase plant P nutrition from recalcitrant organic P source via the bacterial populations. Hence, these interactions should also be studied for AM plants, as they constitute promising approaches to improve plant nutrition through soil organisms engineering, which should contribute to decrease the use of mineral fertilizers.

4.3. Influence of soil physico-chemical parameters on plant-microbiome interactions related to plant nutrition

The effect of mycorrhizal symbiosis may vary according to abiotic conditions such as soil pH or N and P fertilization. There are very few studies reporting the effect of soil pH. In a long-term experiment, liming and P fertilization were manipulated in order to obtain pH values in water ranging from 4.5–7.5, and Olsen P concentrations varying between 8 and 30 mg /kg soil (Wang et al., 1993). The root colonization of oat did not vary much among different pH values but was 20–30 % in low P soil and 10 % or less in high P soil. Potato roots had higher levels of colonization in low P soil (up to 40 %) and also 10 % or less in high P soil. In contrast to its low effect on root colonization, pH had a great effect on spore production with no spores at pH 4.5, 100 at pH 5.5 and 600 at pH 6.5 and 7.5. These results suggest that the maintenance of the AM inoculum does not depend only on the production of spores. In contrast to the effect of pH, numerous studies have reported the effects of P and N fertilization. A negative effect of P fertilization has been repeatedly shown to decrease the intensity of AM colonization but more importantly the growth of the external hyphae (Sawers et al., 2017). This was also shown in a meta-analysis across independent field studies, with a decrease of root AM colonization of 30 % and 23 %, under P and N fertilization, respectively (Treseder, 2004). This trend was confirmed by another meta-analysis (Hoeksema et al., 2010) that showed a greater plant response when plants are P-limited rather than N-limited.

The plant/microbiome interactions involved in iron nutrition that we reported above (section 4.1.2) have been shown to be dependent upon the physico-chemical properties of the soil on which plants are grown. The effect of overexpressing the iron storage protein ferritin on increasing the iron content of plants, leading to the counter-selection of specific fluorescent pseudomonads synthesizing pyoverdins with a high affinity constant for ferric iron, is variable with the type of soil (Robin et al., 2006). The organic matter and phosphate contents of the soils seem to be key determinants of the amplitude of this effect (Vansuyt et al., 2000). Concerning coumarins, secreted by roots in response to iron deficiency and being active in shaping the root microbiome, their chemical nature varies with the pH of the growing solution, changing the ratio between coumarins that aremore efficient to mobilize iron from the soil and coumarins being more efficient as allelochemicals (Sisó-Terraza et al., 2016).

Agricultural practices used to modify physico-chemical properties of soils should therefore also be considered as a mean to facilitate expression of desired plant characteristics, and a way to shape the soil microbiome in order to optimize plant mineral nutrition.

5. Conclusion

The estimation of soil nutrient availability, as resulting only from the fertilizer supply and soil attributes and expressed either as a stock or as a concentration, is not sufficient for determining alone plant nutrient uptake dynamics and for the prognosis of crop yield responses to fertilizer applications. Several reasons for a more systemic approach have been proposed: (i) plants are a key driver of the soil nutrient availability through the auto-regulation of their own capacity for nutrient uptake in relation with their own growth capacity, which leads to the maintenance of their nutrient homeostasis during crop growth as expressed in the so-called “nutrient dilution curves”; (ii) interactions and associations of plants with fungi, bacteria and other soil living organisms play a strong role in the availability of nutrients in soils; (iii) plants are able to modify the physico-chemical properties of the soil matrix either directly by root exudates or indirectly through the soil microbiome, leading to changes in the soil nutrient availability; and (iiii) the availability of one nutrient for plants highly depends on the availability of other nutrients as well demonstrated for N and P, and for P and Zn and Fe. Consequently, the traditional approach of crop fertilization management based only on crop yield responses to fertilizer application and the chemical assessment of nutrient availability is no longer adequate. The more complex and integrated understanding of soil nutrient availability that we proposed in this paper provides the basis for a more reasoned use of mineral fertilizers in future agriculture.

The integration of all regulatory feed-back loops at the level of the crop-soil-microbiome system, and their expression within the resulting crop nutrient dilution concept, allows the formulation of an integrated crop nutrition diagnosis. This physiologically-based crop nutrition diagnosis should be more accurate and more precise than a crop prognosis based only on a soil diagnosis of nutrient availability. This crop nutrient diagnosis makes it possible to quantify directly the degree of satisfaction of plant nutrition for each element by using relevant N, P, K or S nutrition indices. As a consequence, the management of crop fertilization through the monitoring of crop nutrition status diagnoses should lead to the application of fertilizers only when and where necessary, therefore avoiding the excess of nutrient flows within the environment.

Authors contributions

J.F. Briat, conceptualization of the whole paper and co-writing §4. A. Gojon: conceptualization and writing §2. C. Plassard: conceptualization and co-writing §4. H. Rouached: conceptualization and writing §3. G. Lemaire: conceptualization and coordination of the whole paper, writing §2.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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