



# New paradigms and approaches for improved soil N supply synchrony with crop N demand in sustainable agroecosystems

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**Abstract** Nowadays, intensive cropping systems are increasingly dependent on mineral nitrogen (N) fertilizers, which contribute to global warming, hydrosphere pollution, and ecosystem eutrophication. Therefore, the traditional approach of optimizing crop N nutrition based on the crop's response to fertilizer applications must be reexamined. A new paradigm is proposed for crop N nutrition that merges recent advances in two complementary research areas. The availability of soil N to plants depends on interactions among different functional groups of plants and microbes, that contribute synchronizing the soil N supply with fluctuating plant N demand and favor also the closure of the N cycle and reduces environmental impacts. Moreover, the co-regulation of plant N uptake by soil N availability and plant growth enables feedback control of root N absorption by

plant N demand. Therefore, soil N availability cannot be considered only a soil characteristic, but also a function of crop growth capacity. The allometry between crop N uptake and crop biomass accumulation enables determination of the crop's N nutrition status (Nitrogen Nutrition Index, NNI). Based on these recent advances, we propose a new approach to breeding crops and designing agroecosystems that integrate the ability of soil–plant systems to mobilize natural N sources and close the N cycle in various contexts. We also propose using NNI to phenotype the capacity of crop species and genotypes to acquire soil N resources and to evaluate cropping system managements in providing N resources to crops. This new paradigm represents a promising, groundbreaking approach to develop more resource-efficient agriculture.

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## Introduction

Crop improvement has been achieved by breeding for high yield potential and by removing soil limitations to plant mineral nutrition through fertilization and combined pesticide use. However, intensive agricultural systems exacerbate technological dependency and inefficiencies in crop production (Vitousek

et al. 2009; Liu et al. 2013). This has important environmental consequences: (1) water quality, such as eutrophication of freshwater and marine ecosystems (Giles 2005; Beman et al. 2005), as well as groundwater pollution; (2) air quality, including nitrogen (N) oxides and ammonia; and (3) greenhouse gas emissions, such as nitrous oxide ( $\text{N}_2\text{O}$ ), which contribute to climate change (Ramos 1996; Stulen 1998). These impacts are all linked to the use of synthetic fertilizers via N cascades across agroecosystems (Galloway and Cowling 2002). In 2018, the synthetic N fertilizer supply chain was estimated to be responsible for 1.13 Gt of  $\text{CO}_2$  equivalent emissions, representing approximately 11% of global agricultural emissions and 2% of total greenhouse gas (GHG) emissions (Menegat et al. 2022). Cassman et al. (2002) showed that N use efficiency (NUE, kg N harvested per kg N applied) remains low (0.20–0.50) for maize, wheat, and rice in some North American and Asian agroecosystems, while higher values (0.45–0.90) are obtained for wheat in Europe (Quemada and Lasaletta, 2024). In regions with highly intensified agricultural systems and a low yield gap, reducing major crop species' dependence on synthetic N fertilizer applications is necessary. This can be achieved by increasing their ability to capture N resources from their environment, thereby reducing their environmental footprint while maintaining or increasing yield potential. However, in regions with less intensive agriculture and a high yield gap, such as Sub-Saharan Africa, crop yields remain low due to deficient soil nutrients and limited access to fertilizers (Fischer and Connor 2018). In these situations, small amounts of mineral fertilizer, together with enhanced crop capacity to capture soil N resources, could improve crop yields with minimal environmental risk (Connor and Minguéz 2012; Falconier et al. 2023). Thus, improving NUE in cropping systems is necessary in both intensive farming systems, to reduce environmental impacts, and in smallholder farming systems, due to relatively high fertilizer costs and limited access.

To improve the efficiency of agroecosystems in terms of N, this paper 1) analyzes the limitations of current approaches for crop fertilization management and plant breeding, 2) summarizes advances in ecology and crop physiology that are transforming our understanding of the N cycle through the plant-soil-microbes system, and 3) proposes alternative strategies in three areas -breeding, fertilization, and

management practices- to improve crop N nutrition while reducing environmental impacts.

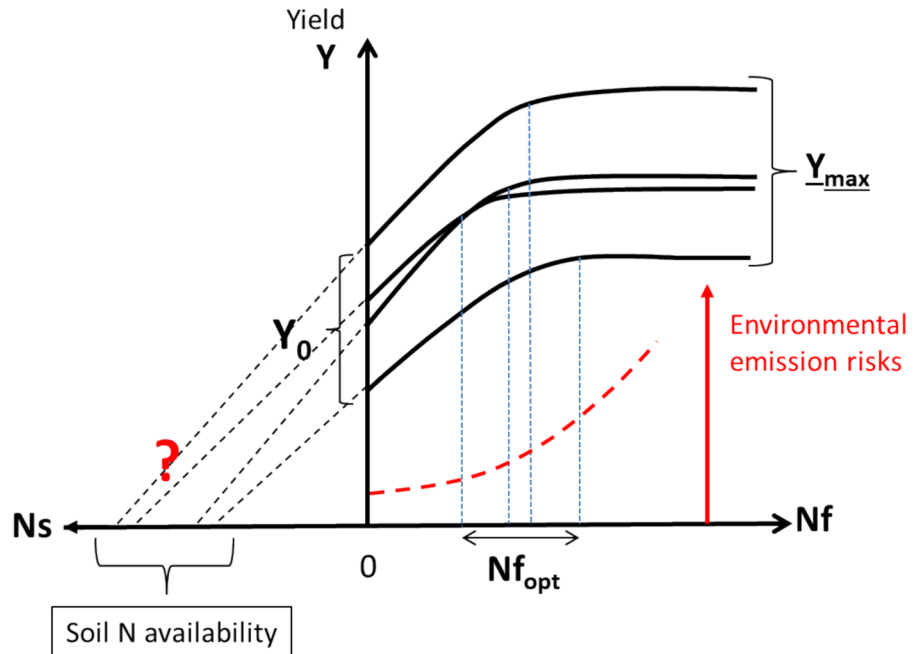
### The limits of the prognosis approach for optimizing N fertilizer application to crops

Until now, the paradigm guiding crop mineral nutrition and fertilization implied analyzing the effect of various soil nutrient availability on crop yield in response to variations in external resource factors.

For a mobile nutrient such as N, the timing of fertilizer application is important for matching crop N demand with soil N availability and reducing the risk of N losses to the atmosphere and/or the hydrosphere. Determining the optimal N fertilizer application rate ( $\text{Nf}_{\text{opt}}$ ) to achieve maximum yield ( $\text{Y}_{\text{max}}$ ) has long relied on statistical analyses of experimental response curves, such as the one in Fig. 1. However, there are important uncertainties due to variations in both the soil N supply ( $\text{N}_s$ ) and the maximum achievable yield ( $\text{Y}_{\text{max}}$ ) as a function of weather, genotype, soil N mineralization dynamics, and previous cropping management (Cui et al. 2010). Thus, the determination of  $\text{Nf}_{\text{opt}}$  cannot be generalized to conditions beyond those of the experiments (Bramley et al. 2013).

To overcome the large uncertainty in the optimal application of N fertilizer, the “mineral N balance sheet method” was developed (see Machet et al. 2017). This method estimates the optimal N application rate,  $\text{Nf}_{\text{opt}}$ , as the difference between the crop's N requirements to reach a given target yield ( $\text{Y}_{\text{max}}$ ) and the soil's N supply. Soil N supply was then estimated by using (i) a measure of the quantity of soil mineral N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) present at the start of the crop growth period (Rémy and Hébert 1977) and (ii) a model that estimates the amount of mineral N provided by the net mineralization of soil organic matter during the crop growth period. This model also estimates inorganic N losses by lixiviation and atmospheric emissions ( $\text{N}_2\text{O}$  and  $\text{NH}_3$ ) (Meynard et al. 1997). Using this method in France reduced the tendency to over-fertilize, resulting in economic gains (Machet et al. 2017). However, despite this progress, the uncertainty of this “prognosis” approach remains too high (Ravier et al. 2016, 2020), especially as the environmental footprint of cropping systems becomes a major issue (Meynard et al. 2002). The risk of  $\text{NO}_3^-$  leaching and  $\text{N}_2\text{O}$ -emission depends on

**Fig. 1** Schematic representation of response of crop yield ( $Y$ ) to fertilizer N application rates ( $N_f$ ). Optimum  $N_f$  ( $N_{f_{opt}}$ ) depends on both, (i)  $N_s$ , the soil N supply, and (ii) the maximum yield ( $Y_{max}$ ). So  $N_{f_{opt}}$  is highly variable according to genotype-environment-management conditions. The corresponding  $Y_0$  is the yield obtained without N fertilizer. Environmental risks for nitrate lixiviation and  $N_2O$  emission are represented as being more than proportional to  $N_f$  (see text below). Source: redrawn from Lemaire and Ciampitti (2020)



$NO_3^-$  concentration and on its residence time in the soil. The environmental risk then increases drastically with  $N_{f_{opt}}$ , as illustrated in Fig. 1. Therefore, determining  $N_{f_{opt}}$ , even with a high precision, to avoid excess N application is not sufficient for reducing environmental risks. It is also necessary to reduce the dependency of crops to N fertilizers (i.e., to decrease  $N_{f_{opt}}$  necessary for a given  $Y_{max}$ ).

The approach that considers plant N demand and soil N supply as independent variables does not account for the complex interactions between plant and soil microbes that determine N availability in the plant root environment (Fig. 2); this is a key variable for understanding crop N nutrition (see Stuart-Grandy et al. 2022; Fontaine et al. 2024).

### A renewed vision of the N cycle within agroecosystems

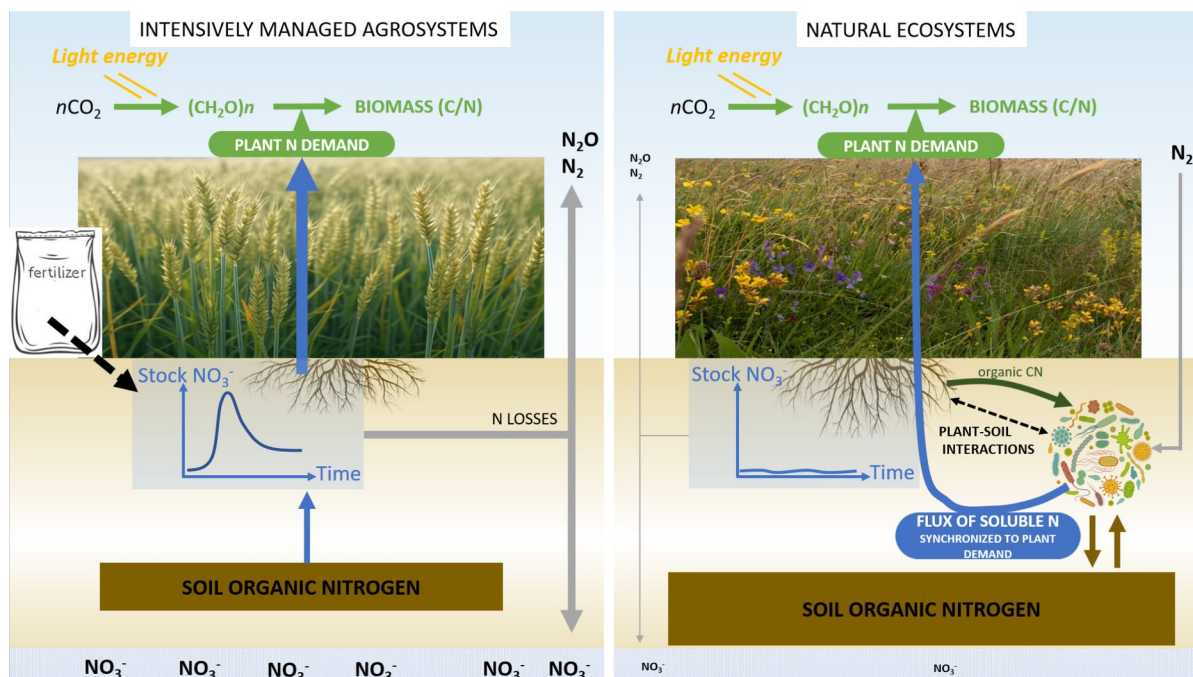
The goal of this section is to present two important concepts that are key to understanding the processes and mechanisms that govern N flows within the plant-soil-microbe system. The first concept is the "N dilution curve," which was developed over the last 30 years (see Lemaire and Gastal 1997). It is based on the co-regulation of plant N uptake by soil N supply and plant

growth rate. This concept emerged from ecophysiology and plant physiology and has been adopted in agronomy and crop science to optimize N application, prevent excess N, and minimize N deficiency. It has also been used to develop more universal approaches for diagnosing N requirements for various crops. The second concept is "synchrony" (Fontaine et al. 2024), which is based on knowledge of plant-microbe interactions within the rhizosphere and detritosphere. This concept has emerged more recently. It provides information on ecological processes that enable N to be mobilized and retained naturally in agroecosystems. We believe that integrating these two concepts within the same framework will accelerate the development of sustainable agroecosystems.

First, we present the concept of "synchrony," then we develop the concept of the "crop N dilution curve," and finally, we demonstrate how these two concepts converge to implement new approaches and methods for managing sustainable crop N nutrition and fertilization.

The concept of "synchrony": Feeding plants from N flows controlled by soil-plant-microbes' interactions

For years, the availability of mineral nutrients in the soil has only been considered as an external factor



**Fig. 2** Illustration of the differences in plant nitrogen (N) nutrition in today's intensive cropping systems compared to biodiverse natural ecosystems. In intensively managed crops, plant N nutrition relies on the creation of mineral N pool of sufficient size to meet the annual crop N need. Crop N need is calculated on the basis of expected yields, which are often optimistic. This leads to excess mineral N quickly converted

in nitrates that are lost through leaching and denitrification. In diversified ecosystems, plants feed on flows of soluble N generated by soil organisms without stock accumulation. Various plant-soil interactions contribute to synchronize the supply of soluble N with plant demand, thus strongly reducing mineral N stock and losses

to which plants responded. In the case of N, the use of external fertilizers has been the norm in modern agriculture to match crop demand with soil availability, without considering the fluxes of N controlled by soil-plant-microbe interactions. However, major advances in our understanding of soil N availability for plants as a dynamic process resulting from multiple interactions within the plant-soil-microbe system have been made in the last few decades. This knowledge, drawn from various disciplines, including ecology, biogeochemistry, and soil microbiology, is synthesized here to be made available to scientists and practitioners involved in agricultural transitions.

#### Root microbiomes and plant nutrition

All higher organisms live in association with a large number of microorganisms, collectively known as the microbiome. Each organism harbors a specific microbiome, and the "megastructure" formed by the

organism and its microbiome is referred to as a holobiont (Berg et al. 2016). The microbiome of an organism can differ from organ to organ. The development of metagenomics methods has promoted a global approach to the root microbiome (Nwachukwu and Babalola 2022). A PubMed search using these two terms (<https://pubmed.ncbi.nlm.nih.gov/?term=root+microbiome>) yields 92 results in 2014 and 999 results in 2024, revealing a tenfold increase in scientific output in this rapidly growing field. In 2012, a seminal paper defined the core Arabidopsis root microbiome (Lundberg et al. 2012).

These microbes, which are predominantly bacteria and fungi, live inside (endosphere) or outside (episphere) of plant root tissues. They play a crucial role in plant nutrition by increasing the availability and uptake of mineral nutrients by roots (Bulgarelli et al. 2013; Hacquard et al. 2015; Alegría Terrazas et al. 2016). The rhizosphere is a specific zone of soil (1–10 mm) that surrounds the roots and is the location

of these nutrient exchanges. The rhizosphere microbiome is shaped by the plant's deposition of root exudates, mucilage, and dead plant cells (Hinsinger et al. 2009). The most studied rhizospheric microorganisms for their role in plant nutrition are mycorrhizae (Van der Heijden et al. 2015) and rhizobium bacteria. Root nodulation by rhizobia is a well-known symbiotic process that provides legumes with atmospheric N (Downie 2014). Additionally, mycorrhizal fungi are associated with the roots of over 80% of plant species (van der Heijden et al. 2015). These fungi regulate nutrient and carbon cycles by providing up to 80% of the N and phosphorus (P) that plants require. In return, they obtain carbohydrates and lipids from the host plant (Rich et al. 2017).

The root microbiome is shaped by the complex interactions among plants, microbes, and environmental factors, including climate, soil, and cultivation practices (Dastogeer et al. 2020). Mineral nutrition is particularly important in influencing the composition and function of the root microbiome, as well as crop productivity and quality (Jacoby et al. 2017). Variations in the nutritional status of plants (e.g., deficiency, satiety, or toxicity) can modify some metabolic pathways and ultimately affect the secretion of exudates, which can modify the composition and function of the rhizosphere microbiome. A well-documented example of microbiome reshaping is the plant's response to iron deficiency (Lemanceau et al. 2009; Harbort et al. 2020), which is relevant to N mineral nutrition. Recently, it was demonstrated that the developmental program of root nodules in legumes requires the iron sensor BRUTUS A, which integrates iron and nodulation cues. Symbiotic nodules cannot form without iron, even under conditions of sufficient light and low N (Ren et al. 2025). Iron is also a cofactor of several enzymes, including nitrate reductase, nitrite reductase, and glutamate synthase, which are involved in the reductive assimilatory pathway of nitrate (Marschner 1995). Under iron deficiency conditions, nitrate assimilation decreases in plants (Alcaraz et al. 1986; Borlotti et al. 2012), and nitrate uptake by roots diminishes concomitantly (Iacuzzo et al. 2011). Furthermore, nitrate leads to rhizosphere alkalization, decreasing Fe solubility and inhibiting the activity of root apoplast ferric chelate reductase. This essential membrane protein is necessary for Fe uptake by roots (Nikolic and Römheld 2003). Iron deficiency leads to a severe decrease

in crop productivity and quality. Therefore, improving plant iron nutrition is of a great economic interest (Briat et al. 2015), which is an essential co-factor for optimal N nutrition.

#### *Ecological synchronization of the N supply by soil biota with fluctuating plant N demand*

In modern agriculture, crop N nutrition is based on creating and managing mineral N pools large enough to meet crop needs (Fig. 2). However, studies of natural ecosystems, such as old grasslands and forests, demonstrate that plants in these systems rely on N fluxes rather than stocks (Fontaine et al. 2024). These fluxes are controlled by diverse functional groups of soil microorganisms, which are being better understood through the use of isotopic tools in conjunction with soil DNA/RNA sequencing methods (Trap et al. 2017; Malik et al. 2019; Bernard et al. 2022; Wu et al. 2023). These microorganisms' activities continuously circulate N between plants, different organic and mineral N pools in the soil, and the atmospheric N compartment (Grandy et al. 2024). This movement is fueled by the energy-rich carbon (C) originating from photosynthesis and deposited in the soil by plants (Udvardi and Poole 2013; Henneron et al. 2020a; Gunina and Kuzyakov 2022).

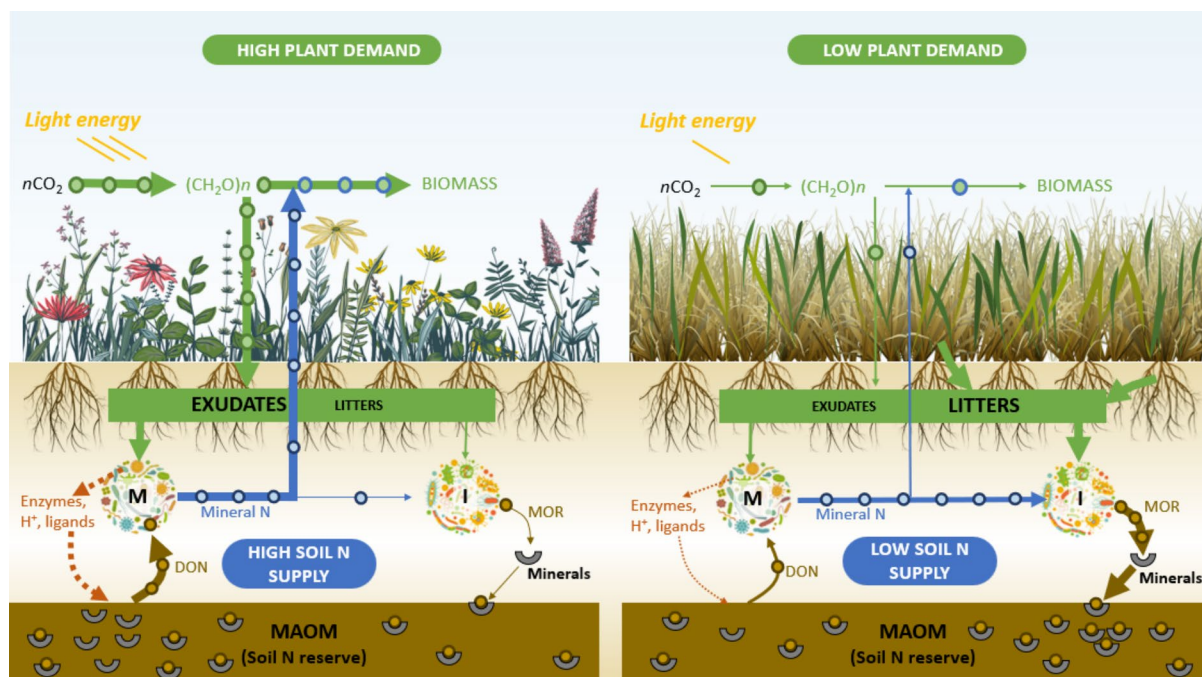
Studies of ecosystems also show that soil fluxes that supply plants with available N (soil supply) can adjust to the fluctuating plant demand over time and space. For instance, a study comparing twelve grassland plant species with contrasting growth rates revealed that gross soil N mineralization in the rhizosphere of each species was proportional to its nutrient demand (Henneron et al. 2020b). A literature review indicates that increased plant photosynthesis and nutrient demand under elevated CO<sub>2</sub> levels increases both gross N mineralization and plant N uptake (Kuzyakov 2019). In general, plant-soil synchrony, or synchronization between the supply of soluble N by soil biota and the demand for N by plants, can explain how diverse natural ecosystems produce large amounts of biomass, sometimes equivalent to that of high-input annual crops (Gilmanov et al. 2003; Glover et al. 2010; Loges et al. 2018). This occurs despite the fact that the pool of mineral N in the soil of these ecosystems is close to zero (Tilman et al. 1996; Leimer et al. 2015; Helfrich et al. 2020). However, our understanding of the processes leading to

plant-soil synchrony is limited. Here, four ecological systems that contribute to this synchrony have been described.

- (1) Synchrony based on mineral-associated organic matter (MAOM). This synchrony system (Fig. 3) is promoted by plant species that acquire resources (Grime 2001). These species are characterized by rapid growth, high tissue turnover and rhizodeposition (Henneron et al. 2020a) and produce litter with chemistry conducive to decomposition- e.g. low content of lignin and condensed tannins, and low C/N ratio (Hobbie 2015). Many domesticated crop species belong to this functional group (García-Palacios et al. 2013; Tribouillois et al. 2015). Plant rhizodeposits and litter are used as energetic C sources by two decomposers groups with contrasted role on soil N cycle due to different strategies of N-acquisition (Fig. 3): a group of microbes mineralize MAOM and release mineral N

(M-microbes) and a group of microbes immobilize mineral N and release small organic N-rich residues that bound to soil minerals to form MAOM (I-microbes) (Perveen et al. 2014; Malik et al. 2019; Bernard et al. 2022). The activities of M- and I-microbes, combined with the heterogeneous distribution of organic matter of contrasting quality (C/N ratio), create hotspots of N immobilization and mineralization and diffusion of hundreds of kilograms of mineral N per hectare and per year between these hotspots (Schimel and Bennett 2004; Booth et al. 2005; Schimel and Hättenschwiler 2007).

By exploring the soil space with their root systems associated with mycorrhizal fungi, the plants can short-cut the diffusion of mineral N toward I-microbes and uptake the mineral N they need to grow (Jingguo and Bakken 1997; Kuzayakov and Xu 2013; Bergmann et al. 2020). Furthermore, mineralization and immobilization fluxes may adapt to the



**Fig. 3** Illustration of the synchrony system based on mineral associated organic matter (MAOM-synchrony) and its response to a change in plant N demand (seasonal change, plant phenology). DON=dissolved organic nitrogen. DON is released from MAOM due to the activity of protons, ligands and enzymes released by M-microbes. MOR=microbial organic residues.

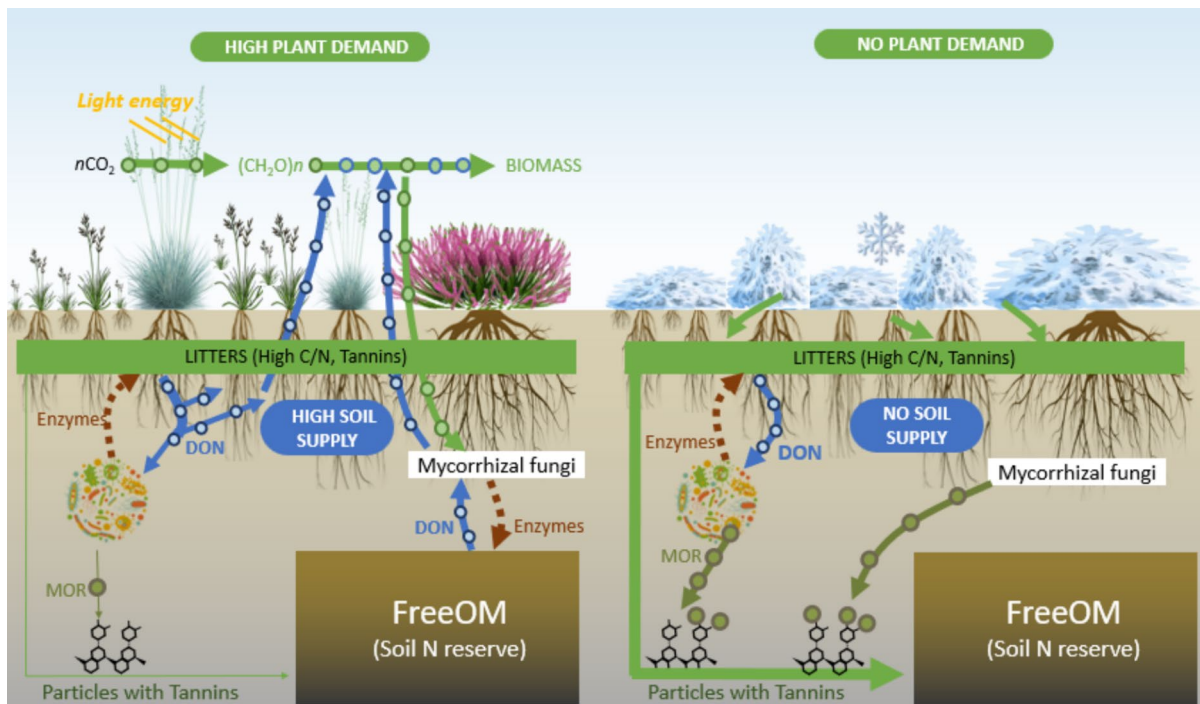
MOR are N-rich compounds released during turnover of microbial biomass. The release of MOR by I-microbes combines with soil minerals to form MAOM. M-microbes also build MOR and MAOM, but their net effect is a decrease in MAOM pool. For clarity we have not represented the release of MOR by M-microbes

demand of the plants (Perveen et al. 2014; Henneron et al. 2020b). As plant demand increases, the greater uptake of mineral N by plants reduces N immobilization by I-microbes, as well as their use of plant-derived carbon (C). Consequently, more energy is available to M-microbes stimulating their mineralization activities and their release of mineral N from MAOM. Conversely, when plant demand decreases, the mineral N “left over” by the plants is rapidly immobilized by the I-microbes, which increases their populations and N storage in the MAOM. This plant-soil synchrony simultaneously satisfies plant demand for N while maintaining a low concentration in the mineral N pool and reducing the risk of losses. Reactive soil minerals such as clays also play an important role in retaining N in this synchronous system by fixing small organic compounds of microbial origin that would otherwise leach out.

- (2) Synchrony based on particulate organic matter free of soil minerals (FreeOM). This synchronous system (Fig. 4) is promoted by resource-

conservative plant species (Grime 2001) characterized by slow growth, low tissue turnover and rhizodeposition (Lambers and Poorter 1992; Henneron et al. 2020b), litter with high C/N ratio and high content of lignin and condensed tannins (Hobbie 2015). This litter chemistry slows down microbial decomposition of litter that consequently accumulates to form organic layers covering mineral soil. Moreover, condensed tannins of plant litters bind small organic compounds of microbial origin to form nutrient organic reserve called FreeOM. This chemical fixation implies that, contrary to MAOM-based synchrony, FreeOM-based synchrony can establish in soil with coarse minerals with low reactivity (e.g., sandy soils).

The C/N ratio of litters and FreeOM is so high relative to decomposer biomass (strong N limitation) that microbial N immobilization dominates over microbial N mineralization. To compensate for the lack of mineral N, plants have developed the capacity to absorb



**Fig. 4** Illustration of the synchrony system based on organic matter free of soil minerals (FreeOM-synchrony) and its response to a change in plant N demand (seasonal change). DON=dissolved organic nitrogen (N). MOR=microbial

organic residues. MOR are N-rich compounds released during turnover of microbial biomass. The developed representation of a molecule represents a condensed tannin that combines with a MOR, for example a protein

soluble organic N such as amino acids (Schimel and Bennett 2004; Chapman et al. 2006) released by the activity of decomposer exoenzymes. Plant-decomposer interactions can synchronize the soil's supply of soluble organic nitrogen with plant demand. During periods of high plant demand, plants uptake soluble organic N, which limits decomposer growth and directs their investment toward the solubilization of litter and FreeOM into soluble organic N, thereby increasing the soil supply (Sinsabaugh et al. 2005; Liu et al. 2023). When plant nutrient uptake diminishes, the increased availability of soluble organic N to decomposers stimulates their growth, turnover and formation of FreeOM. In addition, conservative plant species may actively control the depolymerization of FreeOM to satisfy their nutrient demand during the growing season. Indeed, conservative woody plants associate with ericoid or ectomycorrhizal fungi which have large enzymatic abilities (Miyachi et al. 2020). These capacities allow the fungi to depolymerize FreeOM and supply the plant with organic N in exchange for energetic C (Trap et al. 2017; Lu and Hedin 2019). By modulating their supply of energy-rich carbon to mycorrhizal partners, plants can adjust the supply of soluble organic nitrogen to meet their needs.

- (3) Synchrony in leguminous plants. This is probably the best-known synchrony system. In root nodules, rhizobia supply plants with ammonia originating from the reduction of atmospheric  $N_2$  in exchange for energy-rich carbon (C) provided by plant roots, forming a stable, reciprocal reward strategy (Warembourg and Roumet 1989; Udvardi and Poole 2013). Given the dependency of nodules to energetic C, conditions that enhance photosynthesis and plant demand, such as increased light intensity, lead to increased microbial  $N_2$  fixation (Lawn and Brun 1974). Conversely, factors that reduce photosynthesis also reduce microbial  $N_2$  fixation (Lawn and Brun 1974). Photosynthesis modulates nodule number and growth as well as nitrogenase activity (Udvardi and Poole 2013), leading to a fast (hours) synchrony between plant demand and microbial  $N_2$  fixation. It is interesting to note that  $N_2$  fixation is also regulated according to the concentration of mineral N in the soil, with  $N_2$  fixation by Rhizobia reducing when mineral N accumulates in soil (Guinet et al. 2018). This accumulation can occur when the regulatory capacity of synchronization systems based on soil organic matter has been exceeded (e.g., strong local herbivore N excretion, extreme climatic events that strongly reduce plant N demand). Therefore, synchronous systems can interact to reinforce the overall synchrony between N demand of plant communities and soil supply of available N.
- (4) Synchrony based on a common market of nutrients. Plants and soil microorganisms require nutrients in specific ratios (Elser et al. 1996), but these ratios differ from those of soil organic and inorganic reserves. Consequently, despite the action of synchrony systems described above, some mineral nutrients accumulate in the rhizosphere while others remain deficient (Turpault et al. 2005; Fay et al. 2015; Dieffenbach and Matzner 2000). In ecosystems with high plant diversity, this asynchrony is reduced through the redistribution of nutrients between plants with complementary needs and nutrient-acquisition strategies (e.g., leguminous plants versus plants that stimulate the release of nutrients from soil organic matter or rock) (Fontaine et al. 2024). Mycorrhizal fungi play a key role in this process by forming hyphal networks that facilitate nutrient and carbon exchange (Beiler et al. 2010; Wipf et al. 2019). These fungi trade nutrients not only with their host plants in exchange of energetic carbon but also with other symbionts connected to other plants, creating a dynamic nutrient market. This market benefits both fungi and plants (Wipf et al. 2019). Indeed, the capacity of mycorrhizal fungi to trade the various soil-acquired nutrients against energetic C is promoted while the plants need diverse nutrients and in specific proportion is better satisfied.

Globally, soil organic reserve-based synchrony systems (MAOM and FreeOM) regulate the primary sources of nitrogen (N) for plants in natural ecosystems. Recycled N accounts for nearly 90% of the annual demand for N by terrestrial plants (Cleveland et al. 2013). Next are the synchrony systems in leguminous plants, which regulate 9% of the annual demand. However, these global averages conceal significant disparities based on plant type and biome.

For instance, N fixation by rhizobia could provide up to 100% of the N for legumes but less than 1% for deciduous broadleaf forests (Cleveland et al. 2013). The redistribution of recycled N or N fixed by rhizobia between plants (marker-based synchrony) can significantly impact N uptake depending on the functional group of the plant and the soil conditions. For instance, research has shown that 15–40% of the aboveground N in grasses comes from legumes in grasslands (Høgh-Jensen and Schjoerring 2000; Ouyang et al. 2016; Hammelehle et al. 2024).

The capacity of ecosystems to simultaneously sustain several services such as biomass production, water epuration and soil carbon storage (ecosystem multi-functionality) depends on the health of synchrony systems. Degraded synchrony systems generate both periods of excess soluble N, which can lead to loss by leaching and denitrification, as well as periods of nutrient deficiency that limit plant production (Myers et al. 1994; Crews and Peoples 2005; Fontaine et al. 2024). Healthy synchrony systems promote biomass production by alleviating N limitations to plant growth, closing the N cycle by preventing the accumulation of mineral N in the soil, and building soil organic matter from N retained in the soil or fixed by legumes. Asynchrony between soil supply and plant demand is common in agroecosystems, leading to increased nutrient losses, soil impoverishment and reliance on synthetic fertilizers to maintain productivity. Despite the degradation of synchrony in agroecosystems, the majority of nitrogen in crops comes from sources other than current-year fertilizer (Gardner and Drinkwater 2003; Yan et al. 2020). This suggests that although soil biophysical processes generate significant N flows, they are not well utilized by agricultural systems.

The concept of N dilution: Co-regulation of plant N uptake by soil N supply and plant growth rate

Despite the existence of mechanisms that synchronize soil N supply with plant demand, plant N demand is often not fully satisfied. This can occur in degraded synchrony systems, such as in agroecosystems due to the alternation of bare soil and vegetation cover. It can also occur due to strong spatial and temporal variations in nutrient availability or demand caused by exogenous factors, such as extreme climatic fluctuations.

Lemaire and Salette (1984a, b) demonstrated that in situations with high soil N availability (i.e., high levels of fertilization), the dynamics of N uptake by a grass stand are determined by the dynamics of aboveground mass accumulation ( $W$ ), regardless of the source of variation in  $W$ , such as weather conditions or differences among species and genotypes. In situations of low N availability, smaller N uptake- $W$  relationships are observed. Therefore, crop N uptake appears to be limited by both soil N availability and plant growth, as suggested by the allometric relationship between crop N uptake ( $N$  in  $\text{kg}\cdot\text{ha}^{-1}$ ) and  $W$  (in  $\text{t}\cdot\text{ha}^{-1}$ ):

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

The coefficient  $a$  (N uptake for  $W=1\text{t}\cdot\text{ha}^{-1}$ ) reflects the limitation of N uptake by soil N availability, while coefficient  $b$  is the ratio between the relative N uptake rate ( $dN/Ndt$ ) and the crop relative growth rate ( $dW/Wdt$ ), reflecting the limitation of N uptake by plant growth.

This equation can be modified for expressing the N dilution process, i.e. the decline in plant N concentration (%N in  $\text{gN}\cdot 100\text{g}$  of dry matter) as crop mass increases (Greenwood et al. 1986; 1990):

$$\%N = a/10W^{b-1} \quad (2)$$

The coefficient “ $a$ ” in Eq. (1) represents the quantity of N accumulated in aboveground biomass when the crop mass reaches  $1\text{t}\cdot\text{ha}^{-1}$ , and then coefficient “ $a/10$ ” of Eq. (2) corresponds to the plant N concentration (%N) for this same crop mass. The coefficient “ $b$ ” represents the ratio between the relative rate of N uptake ( $dN/Ndt$ ) and the relative rate of biomass accumulation ( $dW/Wdt$ ). As  $b < 1$ , N accumulation increases less rapidly than crop biomass accumulation in relative terms:  $dN/N = b(dW/W)$ , leading to the decline in %N as plants get bigger (see Greenwood et al. 1990; Lemaire and Gastal 1997).

#### *Molecular physiology of N uptake co-regulation by external N availability and internal nutrient status*

The co-regulation of crop N uptake by plant growth and soil N availability can be interpreted as the result of several physiological and molecular processes that regulate root N absorption (Fig. 5).

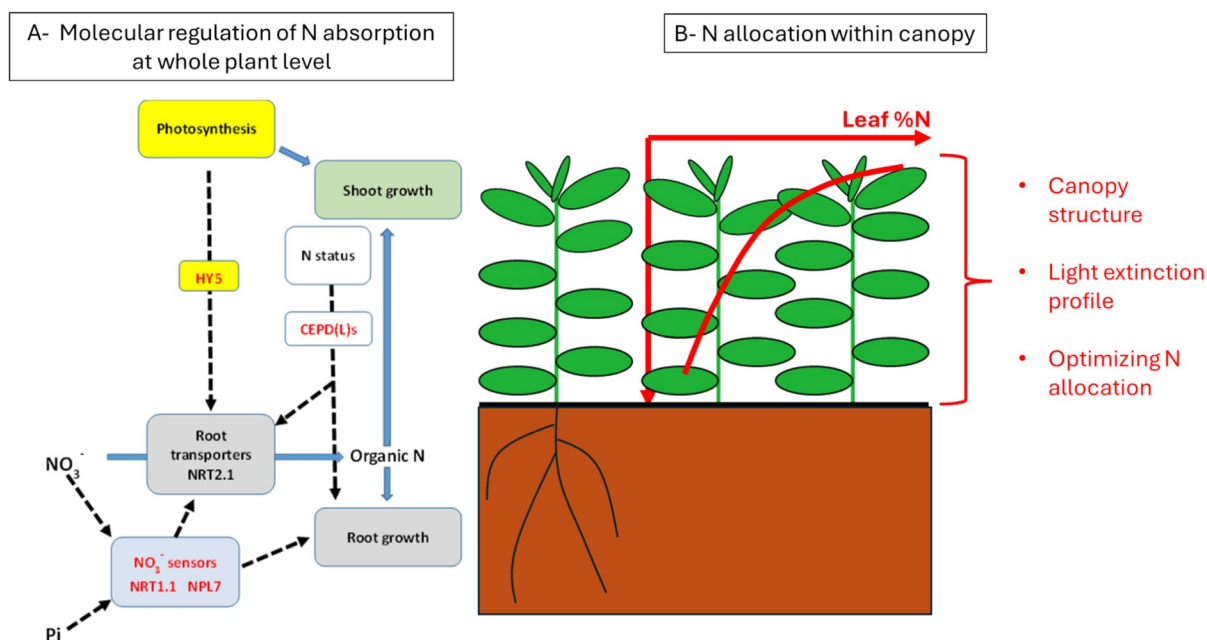
Root N uptake is controlled by the complex interaction of several regulatory pathways that integrate information about external soil N availability and the plant's internal nutrient status (Nacry et al. 2013; Delgado et al. 2024). Often, these pathways coordinate the modulation of protein transport systems that absorb nitrate or ammonium from the soil solution, as well as the size and architecture of the root system, which drives soil exploration and foraging for these nutrients.

Regulation by external N availability is best known for nitrate. Plants can perceive the presence and amount of nitrate in their root environment through dedicated nitrate sensor proteins. The NRT1.1 transceptor and the NLP7 transcription factor are the most well-documented proteins, especially in *Arabidopsis thaliana* and rice (Krouk et al. 2010; Hu et al. 2019; Liu et al. 2022). These sensors trigger local signaling pathways involving calcium and phytohormone-dependent transduction cascades in root cells. These

cascades regulate key actors of nitrate transport, such as the NRT2.1 transporter, as well as root growth and development (Delgado et al. 2024).

Regulation by the internal nutrient status of the plant uncovers two different aspects, namely the control by the specific N status and the interaction with the acquisition of the other nutrients. Both are still only partially unraveled at the molecular level but are known to involve long distance signaling pathways integrating information from both roots and shoots (Nacry et al. 2013).

Regarding control by specific N status, the CEP/CEPR/CEPD(L) module was recently described in *A. thaliana* (Ohkubo et al. 2017; Ota et al. 2020). Upon N starvation, roots export short peptides named CEPs in the xylem, which are perceived by specific receptors (CEPRs) in the shoot. If the N status of the shoot is low, CEPRs trigger the induction of CEPD(L)s glutaredoxins, which are transported down to the roots and act as systemic signals upregulating root



**Fig. 5** Schematic representation of regulation of N uptake and allocation in crop. **A-** Molecular mechanisms ensuring co-regulation of root nitrate uptake by external nitrate availability and internal nutrient status. Nitrate availability is sensed by the NRT1.1 and NLP7 sensors. Shoot-to-root signaling of N demand associated with N status is ensured by mobile CEPD(L)s proteins. Shoot-to-root signaling of photosynthetic activity is ensured by the mobile HY5 transcription factor.

NRT1.1, CEPD(L)s and HY5 are regulators of the expression of the NRT2.1 gene, encoding a major root nitrate uptake transporter. NRT1.1 and CEPD(L)s are also regulators of root growth and development. Dashed arrows indicate sensing/signaling mechanisms. **B-** Regulation of N allocation within crop in relation with canopy structure and light extinction profile leading to the allometry between crop N uptake and crop mass and the N dilution process.

N acquisition. On the other hand, if the N status of the shoot is high, CEPD(L)s induction is prevented, and root N uptake is not upregulated. Interestingly, the CEP/CEPR/CEPD(L) module was shown to target not only root transporters (e.g. NRT2.1), but also lateral root growth and nodulation in legumes (Imin et al. 2013).

The most important example of interaction with other nutrients is probably the regulation of root N uptake by photosynthesis, which ensures coordination between N and C acquisition. Changes in shoot photosynthetic activity generally led to similar changes in root N uptake within a few hours (Gastal and Saugier 1989; Lejay et al. 2003). Recently, the mobile transcription factor HY5 was shown to act as a long-distance signal from shoot to root, upregulating NRT2.1 activity in response to photosynthesis (Chen et al. 2016). This demonstrates that, in addition to photosynthates' role as energy providers for root nutrient uptake, specific signaling pathways are also involved in maintaining acceptable limits of elemental stoichiometry in plant tissues. Other examples include (i) the interaction between nitrate and phosphate signaling pathways, which share common components in *A. thaliana* and rice, such as the NRT1.1 transceptor or the NIGT/HRS and NLP transcription factors (Medici et al. 2015; Hu et al. 2019), and (ii) the interaction between iron and N nutrition (see paragraph III-1).

In conclusion, as illustrated in Fig. 5A, plants have sophisticated systems for sensing N availability in the soil. However, root N acquisition is not solely regulated by these systems. It also depends heavily on internal signals that inform the roots whether additional N uptake is required to meet the nitrogen demand resulting from the plant's overall N status, growth potential, and the availability of other nutrients.

#### *N dilution process within crop canopy*

The physiological regulation of root N absorption by plant N demand, as described above, does not explain why crop N uptake is proportional to  $W^b$  and not  $W$ , nor why plants are unable to maintain a constant N concentration in their tissues (homeostasis) as crop mass increases. According to the model proposed by Caloin and Yu (1984), the allometry coefficient  $b$  reflects the ontogenetic decline in the proportion of metabolic tissues in plant shoots as they grow larger

(Greenwood et al. 1990; Lemaire and Gastal 1997). When growing in a dense canopy, plants compete for light, so proportionally more biomass is used to support structural tissues with low N concentrations that position leaf area within the well-illuminated layers of the canopy (Lemaire and Bélanger 2020). Furthermore, plants preferentially allocate N to well-illuminated leaf layers by recycling N from shaded leaves at the bottom of the canopy to new leaf areas growing at the top, thereby accelerating the N dilution process (Hirose et al. 1988; Lemaire et al. 1991). Therefore, coefficient  $b$  reflects the physical constraints that determine the light extinction profile within canopies and must be considered an emergent property at the canopy level (see Fig. 5B).

When soil N supply is maintained at the minimum necessary to achieve the maximum crop growth rate during the growth period, then it is possible to define the critical N uptake curve:

$$N_c = a_c W^b \quad (3)$$

Coefficient  $a_c$  represents the crop N demand for producing  $1 \text{ t}\cdot\text{ha}^{-1}$  of biomass. Similarly, it is then possible to determine a critical N dilution curve:

$$\%N_c = a_c / 10 W^{b-1} \quad (4)$$

with  $\%N_c$  as the minimum plant N concentration for achieving maximum biomass accumulation. The coefficient  $a_c/10$  represents  $\%N_c$  for producing  $1 \text{ t}\cdot\text{ha}^{-1}$  of biomass.

Critical N dilution curves have been determined for many crop species using experimental datasets that measure both  $\%N$  and  $W$  at various times during the growth period, with a wide range of N fertilizer applications (see, for example, Lemaire et al. 2008; Justes et al. 1994; Plénet and Lemaire 2000). Using a Bayesian approach, Makowski et al. (2020) proposed a method to estimate the confidence intervals of the two coefficients,  $a$  and  $b$ , of critical N curves (Eqs. 3 and 4). Large data sets can then be used to analyze the influence of genotype-environment-management interactions on critical N dilution curves, as well as the degree or genericity of these curves (Fernandez et al. 2022).

Preliminary analysis by Greenwood et al. (1990) showed that the coefficient  $a$  was clearly higher for C3 species as compared to C4, reflecting their difference in photosynthetic pathway, while coefficient  $b$  seemed

roughly similar. The dataset synthesized by Ciampitti et al. (2022) was reutilized to calculate new dilution curves (Fernandez et al. 2022) and this new analysis provides evidence that the ‘b’ coefficient could be not different of 2/3, the theoretical value reflecting the fact that N accumulation, in a dense crop canopy, scales with leaf area while W scales with canopy volume (Lemaire and Gastal 1997; Lemaire et al. 2007).

Several studies comparing values of coefficient “a” among genotypes of the same species (see Ciampitti et al. 2021a, b, for maize; Yao et al. 2021, for wheat; and Fernandez et al. 2021, for tall fescue) showed that, even if some variations can be detected, these differences remained of very low amplitude and then, a generic critical N dilution can be used at crop species level.

#### *Plant N status diagnosis: Nitrogen Nutrition Index (NNI)*

As demonstrated by Lemaire et al. (2008), Eqs. (3) and (4) allow one to determine the N nutrition status of a given crop by calculating a NNI as the relative distance of the data point  $N_{act}-W_{act}$  (where  $N_{act}$  and  $W_{act}$  are the measured values of crop N uptake and crop mass at a given time in a given condition) to the critical N uptake curve. The NNI can be calculated by using either Eqs. (3) or (4):

$$NNI = N_{act}/N_c = \%N_{act}/\%N_c \quad (5)$$

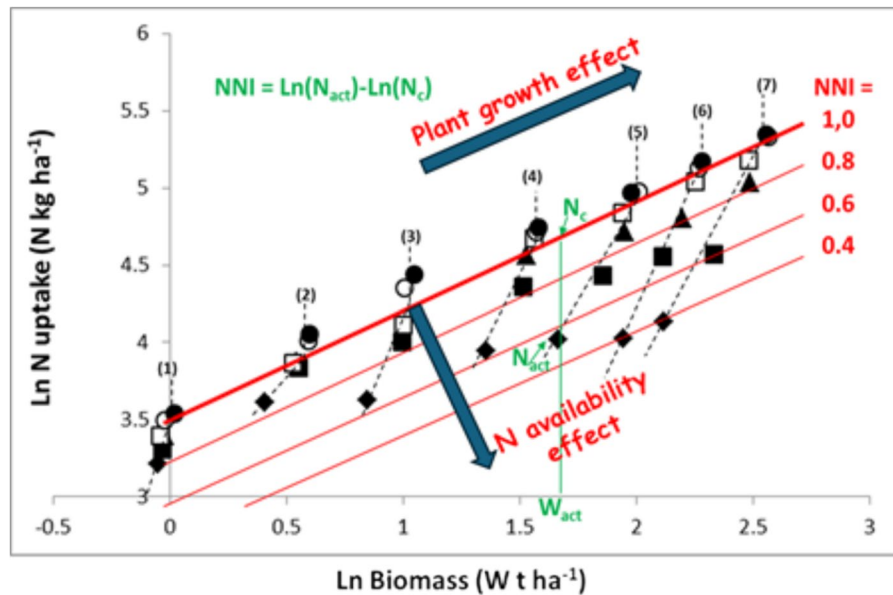
A NNI value above 1 indicates luxury N nutrition, while a value below 1 indicates N deficiency. The NNI provides a quantitative evaluation of the crop N status in a given situation, taking into account the soil N supply and the application of N fertilizer. For example, a value of 0.60 indicates that the soil N supply plus the application of N fertilizer allowed the plants to satisfy only 60% of their N demand. Figure 6 shows how the NNI changes for a maize crop that receives different rates of N fertilizer. On a log–log scale, the critical N–W relationship is a straight line, and plant N nutrition homeostasis is represented by parallel lines corresponding to NNI values less than 1. For higher N application rates, crops follow an N–W trajectory that is close to or slightly above  $NNI=1$ . For lower N application rates, crops describe an N–W trajectory with a declining NNI, which indicates more significant crop N deficiency as

the crop grows, and the available soil N is depleted. This example illustrates the capacity to use NNI to quantify crop N status during its growth cycle.

The Fig. 6 illustrates that crop N uptake depends on both (i) the N availability in the root environment, which results from the interaction between the soil microbiome and the N fertilizer application rate, and (ii) the plant growth capacity, which depends on weather and genotype conditions that determine crop N demand and the root system’s capacity to capture N in the soil. Therefore, the NNI can be used to phenotype cultivars in genotype–environment–management studies (Lemaire and Ciampitti 2020).

An important question emerges regarding the potential impact of climate change on critical N curves. Climate change is mainly caused by elevated levels of  $CO_2$  in the atmosphere and results in temperature increases and more frequent and severe water shortages. These factors are all known to affect plant nitrogen nutrition.

Elevated  $CO_2$  stimulates photosynthesis in C3 crops independently of temperature and water, resulting in higher biomass and yield (Ainsworth and Long 2021). However, this positive response to elevated  $CO_2$  is often strongly limited by N (Wang et al. 2013; Coskun et al. 2016). Furthermore, elevated  $CO_2$  leads to a general decrease of N, and therefore protein, concentrations in almost all organs of C3 crops, including fruits and grains (Taub and Wang 2008; Loladze 2014; Uddling et al. 2018). This decrease may result from more pronounced N dilution caused by a larger plant canopy (see above), but many studies have pointed out that this is probably not the main explanation (Wang et al. 2013; Feng et al. 2015; Gojon et al. 2023). Other mechanisms may be involved in the N dilution effect induced by elevated  $CO_2$ . (i) changes in the bioavailability of mineral N in the soil, caused by increased competition with microorganisms due to higher N immobilization (Uddling et al. 2018) or enhanced  $N_2O$  volatilization (Moser et al. 2018); (ii) leaf N acclimation, caused by the downregulation of RuBisCO concentrations in leaves (Taub and Wang 2008), which leads to a decrease in the critical plant N concentration; and (iii) impaired root acquisition of soil mineral N, caused by reduced plant transpiration (Houshmandfar et al. 2018) and/or the direct negative effects of elevated  $CO_2$  on the physiological processes of N uptake and assimilation (Bloom et al. 2010; Wang et al. 2013; Gojon et al. 2023; Cassan



**Fig. 6** Ln–Ln relationship between plant nitrogen (N) uptake and biomass (W) from the fourth leaf (4th) (1) until silage harvest stage (7) for a maize crop receiving different N fertilization rate: dark diamond (no N), dark square (30 kg N ha<sup>-1</sup>), dark triangle (80 kg N ha<sup>-1</sup>), open square (130 kg N ha<sup>-1</sup>), dark circle (180 kg N ha<sup>-1</sup>), open circle (230 kg N ha<sup>-1</sup>), and dark circle (280 kg N ha<sup>-1</sup>). Dotted lines (1) to (7) represent the plant N uptake-to plant W response under differ-

ent fertilizer N rates for each stage. The bold line represents the critical N uptake curve ( $N_c$ ) as determined for maize by Plénet and Lemaire (2000):  $N = 36.4 W^{0.66}$  corresponding to the N nutrition index (NNI) equal to 1. As soil N availability becomes limited for plant N uptake, this leads to a corresponding decrease in NNI.  $N_{act}$  = actual plant N concentration,  $N_c$  = critical N concentration, and  $W_{act}$  = current biomass. Source: data reinterpreted from Plénet and Lemaire (2000)

et al. 2023). A key point is that providing ample N supply to plants grown at elevated CO<sub>2</sub> generally allows both to reach the full stimulation of photosynthesis and prevent the decline in N concentration in tissues (Coskun et al. 2016; Halpern et al. 2018; Cassan et al. 2023). This has led to the controversial suggestion that increasing the supply of nitrogen fertilizers will be necessary to stimulate yield and maintain satisfactory protein concentrations in crops under future climate conditions. The above considerations illustrate that many aspects of the direct effect of elevated CO<sub>2</sub> on plant N status remain unclear, and further studies are necessary to analyze these points. For example, to our knowledge, no study has assessed the potential changes in the critical N curve or NNI in response to elevated CO<sub>2</sub>. Furthermore, the role of the root microbiome in plant responses to elevated CO<sub>2</sub> has certainly been under-evaluated. This is evidenced by the recent finding that elevated CO<sub>2</sub> stimulates plant biomass production and that the effect of root N acquisition on it dramatically depends on mycorrhizae (Terrer et al. 2021).

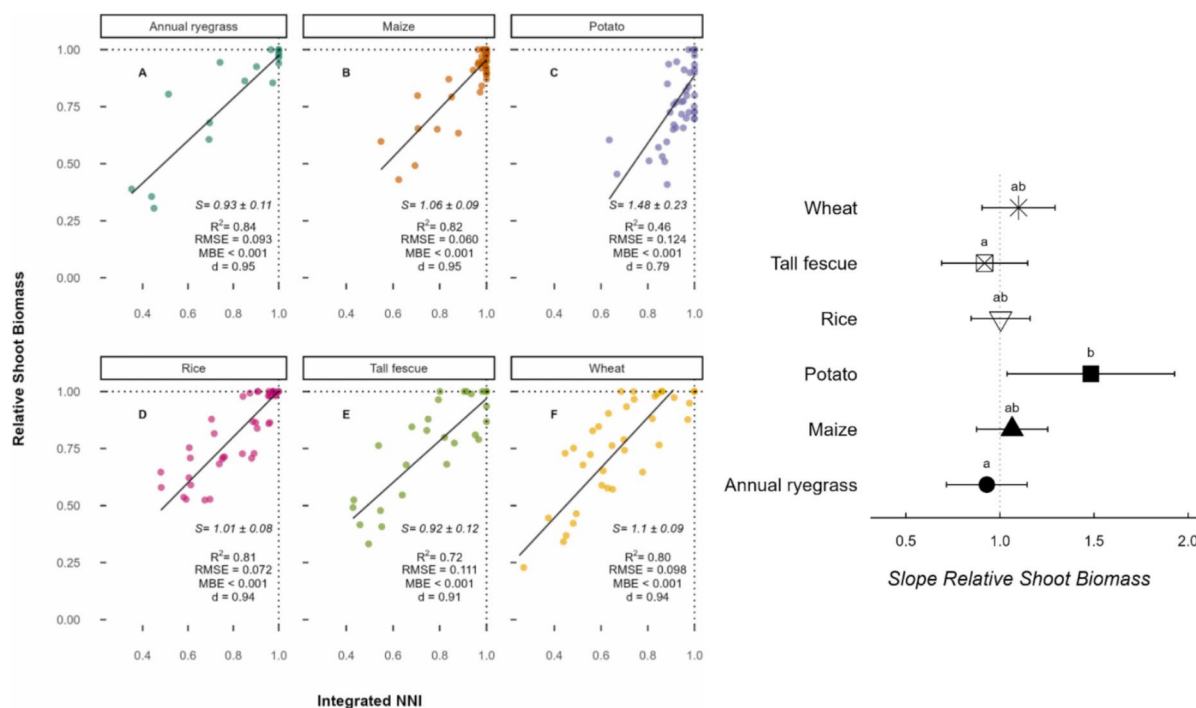
The effect of water deficiency on the critical N dilution curve has been studied in maize, wheat, and tall fescue (Ciampitti et al. 2021b); however, no significant differences were observed in the curves. As Kunrath et al. (2020) demonstrated, a soil water deficit results in lower soil N availability, causing drought-induced crop N deficiency. Wheat and maize crops exhibit different yield responses (neutral, negative, or positive) under adequate N supply at high temperatures (Sadras et al. 2022). According to N dilution, %N in plants should increase or decrease under rising temperature conditions. Depending on its components, climate change could affect plant N nutrition in various ways: (i) a simple effect on the intensity of N dilution associated with changes in crop mass; (ii) an effect on the critical N dilution curve; or (iii) an effect on soil N availability. Using NNI as a metric for crop N status should enable us to understand all the intricate effects of climate change on plant N nutrition and allow for more comprehensive modeling under different scenarios.

## Shoot biomass response to plant N deficiency

Several studies have shown that the reduction of shoot biomass can be directly related to the intensity of N deficiency experienced by a given crop during its growth period by expressing the relative biomass ( $W_a/W_{max}$ ) as a function of NNI where actual biomass ( $W_a$ ) and maximum biomass ( $W_{max}$ ) achievable under the conditions of the experiment with a non-limiting N application rate. Generic response curves have been proposed, as shown by Rodriguez et al. (2024), the slope of the linear relationship between relative biomass and the integrated NNI was close to 1.0 for several crops (wheat, rice, maize, tall fescue, and annual ryegrass, except for potato), suggesting a similar sensitivity to N deficiency, i.e. a decline in relative biomass ( $W_a/W_{max}$ ) roughly equal to the intensity of N deficiency ( $1-NNI$ ) as shown in Fig. 7.

## New approach for plant breeding and cropping system management

One of the grand challenges facing humankind is feeding a growing world population while preserving soil organic N for future productivity, reducing the use of mineral N fertilizers, and mitigating environmental impacts such as greenhouse gas emissions (e.g., nitrous oxide [ $N_2O$ ]) and eutrophication. Simultaneously achieving these objectives requires changing our approach to crop management at several levels. This section explores how new insights into the N cycle can inform plant breeding and agricultural practices, thereby enhancing the productivity and sustainability of agroecosystems. Some knowledge can inform the development of breeding programs or agricultural practices, while other knowledge, such as NNI, can evaluate the efficiency of tested solutions. Some proposals are operational and must be applied in different contexts (e.g., INN), while others must be tested in experiments considering all advantages and constraints, including technical feasibility and



**Fig. 7** **A** Relationships between relative shoot biomass (actual biomass,  $W_a$ /maximum biomass,  $W_{max}$ ) and the integrated NNI experienced by crop during its vegetative growth period (from seedlings to anthesis) for six crop species. **B** Com-

parison of the crop sensitivity to crop deficiency as  $b = d(W_a/W_{max})/d(NNI)$  across different crop species. Taken from Rodriguez et al. (2024)

economic relevance (e.g., a new breeding plan or agricultural practices to improve synchrony).

#### Plant breeding for soil N resource foraging and acquisition

Determining the crop NNI enables the distinction between crop traits associated with increased growth potential and those associated with increased capacity to satisfy the plant's own N demand through its effects on soil N availability, as previously demonstrated by Sadras and Lemaire (2014), Lemaire and Ciampitti (2020), and Ciampitti et al. (2022).

A new open database on N dilution across crops (Ciampitti et al. 2022) demonstrated that the critical dilution curves for wheat, oat, and many forage grasses were similar. Similar conclusion was documented when studying the effect of different maize hybrids grown in different regions around the globe, all reflecting a similar N dilution curve (Ciampitti et al. 2021a). Similar conclusion was documented for rice and tall fescue crops with similar N dilution within each crop (Ata-UI-Karim et al. 2017; Fernandez et al. 2021). However, other crops such as potato presented variation in the dilution curves as a result of combination of different genotype x environment x management interactions (Giletto et al. 2020; Bohman et al. 2023). Hence, the utilization of NNI as a diagnostic tool needs to consider potential effects of GxExM, mainly in those crops such as potato (Bohman et al. 2023) presenting variation in N dilution curves based on differences in genotypes.

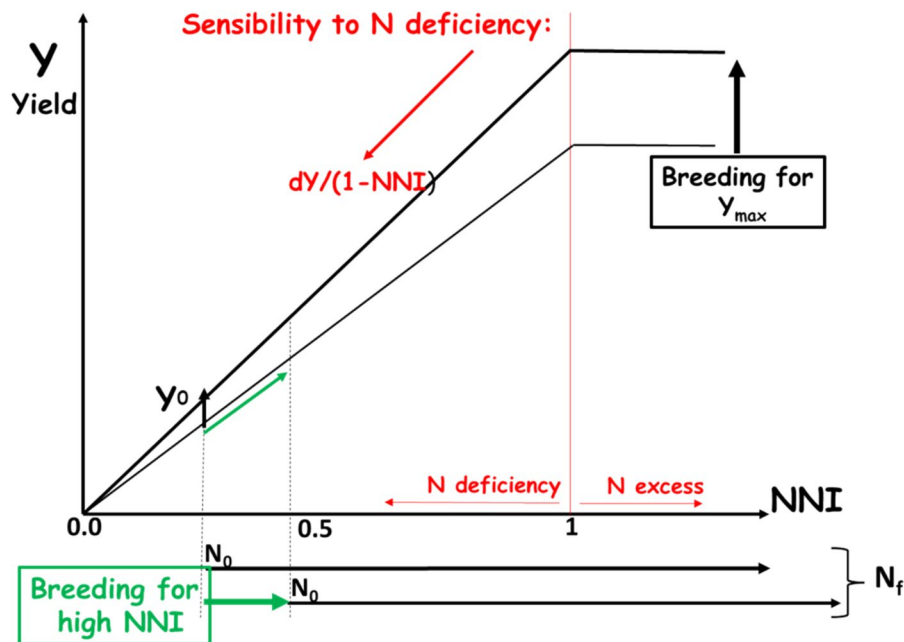
Figure 8 illustrates two strategies for crop improvement based on N gains:

- (1) Breeding for potential yield ( $Y_{max}$ ) in high N supply conditions. As shown by Coque and Galais (2007) breeding progress in  $Y_{max}$  also leads to a progress in  $Y_0$ , the yielding capacity in low N supply conditions. This genetic correlation is simply the illustration of the crop N uptake capacity regulation by crop biomass as presented above. But as  $Y_{max}$  increases, the slope of the  $Y$  vs NNI also increases (see Rodriguez et al. 2024). Therefore, the sensibility of crop to N deficiency [ $\Delta Y/(1-NNI)$ ] becomes greater, increasing then the dependency of the crop to N fertilizers: a higher  $N_f$  is required to reach  $Y_{max}$ .
- (2) Breeding for improving the intrinsic crop N uptake capacity, i.e. the ability of a crop to reach a greater NNI for  $N_f=0$  ( $NNI_0$ ). An increase in  $NNI_0$  should allow an increase in  $Y_0$  (see the green arrow in Fig. 7) and then a corresponding decrease of the  $N_f$  application necessary to reach  $Y_{max}$ , reducing then the fertilizer dependency (FD) of the crop.

These crop improvement strategies and the use of NNI as a relevant crop phenotyping index are discussed in more detail in Ciampitti and Lemaire (2024). Ranking genotypes based on their ability to achieve a high NNI under limited N conditions provides information about their capacity to meet their N demand through greater efficiency in using endogenous soil N resources (Ciampitti and Lemaire 2022). Significant differences have been reported across species (see Lemaire et al. 1996, for sorghum versus maize, and Lemaire and Gastal 1997, for tall fescue versus cocksfoot), yet differences among genotypes within a species remain unexplored.

Direct NNI measurement in field conditions is too labor-intensive to be used routinely in breeding programs. Recent studies have demonstrated the use of remote sensing techniques to phenotype crops under various N nutritional statuses (Chen 2015; Yang et al. 2020; Berger et al. 2020). Integrating new technologies will accelerate crop phenotyping for N status (e.g., Atefi et al. 2021; Pinto et al. 2023; Castilho et al. 2024). Recently, drones (e.g., Tanaka and Gilsum, 2025), satellites (Lapaz Oliveira et al. 2023), and other sources, such as proximal sensors mounted on farm equipment (Argento et al. 2025), have been utilized. Despite the rapid development of work measuring proxies of NNI, it is important to note that studying the accuracy of these tools requires large databases on NNI estimation for different crop species, which is the bottleneck of these promising technologies.

It is well-established that plants adapt to nutrient shortages or localized nutrient availability by altering their root system architecture to efficiently explore soil zones containing limited nutrients (Giehl and von Wirén, 2014). The signaling pathways involved in this root architecture remodeling have been well studied, particularly with regard to N nutrition (Jia and von Wirén, 2020). Therefore, a promising approach could consist in targeting root architecture in breeding



**Fig. 8** Representation of crop yield ( $Y$ ) response to crop NNI by a linear+plateau curve according to Rodriguez et al. (2024). An increase in  $Y_{max}$  (due to genetics, environment, or management, or all their combination) leads to an increase in  $Y_0$  (for  $N_f=0$ ). But the higher  $Y_{max}$  would imply a higher  $N_f$  for reaching  $NNI=1$ , and the higher slope  $dY/dNNI$  would increase the sensibility of crop to N deficiency, leading then to

a higher dependency of the crop to N fertilizers. The increase of the ability of crop to maintain a high NNI with  $N_f=0$ , would allow a more important increase in  $Y_0$  (see the green arrow) and would reduce the need of  $N_f$  for achieving a given  $Y_{max}$ , that should contribute to reduce the dependency of crop to fertilizers. Taken from Ciampitti and Lemaire (2024)

programs to develop crops with better capture of water and nutrients (Lynch 2022).

#### Plant breeding for microbiome optimization

The nutritional status of plants plays an active role in recruiting root microbiota by activating pathways that synthesize and secrete specific metabolites (see above). Therefore, it may be possible to influence the composition of a given microbiome by selecting the necessary genetic traits in plants to establish such microbiota (Cernava 2024). First, however, the plant genes involved in establishing the microbiome must be characterized. A similar approach has been successfully developed to prevent pathogen development using microbiota. Identifying and breeding specific M-gene haplotypes in rice plants enriched the rhizosphere with specific microbiome components, resulting in increased protection against pathogens. However, to our knowledge, a strategy

that improves plant nutrition has yet to be developed. A recent study on the genetic basis of reciprocal interactions between root architecture and the composition and diversity of specific microbial taxa in the maize rhizosphere lends credence to this approach. (Yu et al. 2021). This study shows that (i) root-derived flavones predominantly promote the enrichment of Oxalobacteraceae bacteria in the rhizosphere, which promote maize growth and N acquisition, and (ii) lateral root development coordinates interactions between the root system and flavone-dependent Oxalobacteraceae under N deprivation. We propose using NNI to phenotype the ability of different genotypes to recruit microbiomes that improve their N nutrition. This phenotyping must be carried out under conditions in which mineral N resource foraging and acquisition by roots are not limiting processes in order to distinguish it clearly from the previous strategy. For example, phenotyping can be done in shallow soils or pots.

## Cropping system management for enhancing plant-soil synchrony

A wide range of management approaches is currently being explored to restore soil health and agroecosystem functionality—including no or reduced tillage, organic farming, diversification, conservation and regeneration agriculture, and permaculture. However, these practices often lead to trade-offs between key functions, such as those between yield and greenhouse gas emissions (German et al. 2016; Shi et al. 2019), and between soil C storage and emission of N<sub>2</sub>O (Gregorich et al. 2005; Xia et al. 2018). One promising approach to overcoming these trade-offs is to focus on ecological systems that enhance the synchrony between soil N supply and plant N demand. These systems support a variety of vital functions in natural ecosystems:

- (i) to promote biomass production by alleviating the N limitation of plant growth
- (ii) to mobilize N from natural resources such as soil organic N and atmospheric N
- (iii) to minimize N losses by leaching and denitrification as well as greenhouse gas emission (N<sub>2</sub>O)
- (iv) to convert the excess of soluble N regarding to plant demand into soil organic N, contributing to N and C sequestration in soils. Integrating synchrony systems into agroecosystems is a promising strategy for sustaining or enhancing biomass production, reducing dependence on synthetic fertilizers, mitigating environmental impacts such as eutrophication and climate change, and conserving soil organic resources for long-term productivity. Understanding how and under what conditions these systems operate allows us to guide changes in agroecosystems to make them multifunctional.

Our review suggests that the types of synchronies to promote and the agricultural practices best suited to anchor them depend strongly on soil characteristics. In young or recently disturbed soils, where organic N reserves and mineral phases capable of stabilizing microbial residues are limited, practices that foster synchrony through leguminous plants may be more effective in enhancing agroecosystem multifunctionality than practices that rely on organic

reserve-based systems. As soils mature through mineral weathering and the accumulation of organic matter, synchronies based on organic reserves likely play a progressively greater role in supporting multifunctionality (Figs. 3 and 4). Therefore, management strategies that enhance these organic-based synchronies should be emphasized as soil development advances. Due to fine soil minerals' involvement in MAOM formation, the synchrony system induced by acquisitive plant species (Fig. 3) is inadequate for coarse-textured soils, such as sandy soils. Since most modern crops are acquisitive (Milla et al. 2015), they produce microbial residues that are inadequately stabilized in sandy soils (Fig. 4). This could explain the higher rates of carbon and N loss after land conversion in sandy versus clay-rich environments (Burke et al. 1989). Such soils call for alternative land uses—such as extensive grazing systems on heathlands—or the development of novel cropping systems incorporating conservative plant species, either alone or in combination with acquisitive crop types. For example, a new type of agroecosystem called agroprairie has recently been developed in order to associate annual crops with diverse functional groups of companion plants, including conservative plants (Bécu et al. 2025). Agroprairie is strip cropping of alternating narrow strips (approximately 50 cm) of diverse prairie communities with annual crops such as wheat. Depending on prairie species composition, the association can substantially improve wheat N nutrition and growth (Bécu et al. 2025).

In view of the species currently cultivated, one of the synchrony systems that is probably the most widely used in cropping systems is the synchrony system based on MAOM. These rely on the activity of N mineralizing and N immobilizing microbes that require a continuous supply of plant-derived energetic carbon (Fig. 3). This could explain why management practices that maintain permanent plant cover in annual cropping systems—such as cover cropping or relay cropping—promote N retention and soil organic matter accrual (Tonitto et al. 2006; Jian et al. 2020). However, the effectiveness of these practices may depend on the quality of plant residues. Specifically, cover crops must exhibit a sufficiently high C/N ratio to stimulate N immobilization by immobilizing microbes. Pure legume covers typically fail to meet this criterion, which may account for the substantial

N losses often observed under such covers (Crews and Peoples 2005).

In order to promote the beneficial role of synchrony systems in ecosystem multifunctionality, synthetic N fertilizers should be used sparingly, primarily in nutrient-poor soils. Excessive mineral N input can reduce plant carbon allocation to belowground processes and disrupt the balance between microbial community structure and plant N requirements. For example, mineral N fertilizer has been shown to decrease biological N fixation within days of application (Gordon et al. 2002; Guinet et al. 2018). However, to prevent long-term soil nutrient depletion, it is essential to maintain element mass balances as close to equilibrium as possible at the field scale. This implies that N removed through harvest must be offset by equivalent N inputs. To minimize disturbance to synchrony systems, these inputs should come from biological N fixation through legumes and/or the recycling of organic N sources, such as manure or compost.

#### Soil fertility: an emerging property of the plant-soil-microbes system

The concept of N dilution developed above has been extended to some other nutrients such as P, K or S (see the recent synthesis of Fontana et al. 2025). The concomitant dilution of N, P, K, and S in shoot mass during crop growth provides the possibility for assessing multi-nutrient plant status by calculating crop nutrition indices for P, K and S (PNI, KNI and SNI respectively). The critical values for P, K or S concentration in plant depends on the plant N status, then the P-, K-, S- nutrition diagnosis must be subordinated to the NNI estimation (Fontana et al. 2025). So, as underlined by Lemaire et al. (2019) an integrated plant-based diagnosis of multi-elements can be developed for considering interactions and stoichiometries among different nutrients. Hence, soil fertility cannot be estimated only by soil properties estimated through soil sample and nutrient-by-nutrient analysis, but as resulting also of multiple interactions between the plant, the soil and the microbiome (Briat et al. 2020).

Recent advances in synchrony call for a reassessment of the concept of soil fertility. Soil fertility is traditionally defined as a soil's inherent capacity to sustain plant growth and productivity by supplying

adequate quantities and proportions of nutrients. However, this definition overlooks the active role of plants in modulating N availability. Through at least four distinct mechanisms of synchrony, plants can influence the amount of soluble N they receive from soil microbes. In this paper, we have focused on the N cycle. However, synchrony systems regulate many other nutrients such as P, K, and S which are present in soil organic matter and in soil minerals and rocks. Consequently, the soil supply of various nutrients that sustains plant production should not be considered an intrinsic property of the soil alone. Rather, it should be understood as an emergent property arising from dynamic plant–soil and plant–plant interactions. Of course, soil characteristics such as mineral reactivity, CEC, pH, and water reserve remain important determinants of a soil's ability to support plant growth and productivity. However, the change in perspective on fertility that we suggest has important implications: depending on the functional composition of plant and microbial communities and their capacity to modulate N dynamics, the same soil can support markedly different levels of biomass production. This has been supported by several experimental studies (Chapman et al. 2006; Henneron et al. 2020b).

Furthermore, current diagnostic methods for soil fertility overlook the role of plants and fail to capture the true potential of plant–soil systems (Hansson et al. 2020; Legout et al. 2020), which can lead to misleading conclusions. For example, soil fertility is often inferred from the size of mineral N or "available" nutrient pools. Larger pools are interpreted as higher fertility (Qu et al. 2013; Chu et al. 2019). However, a large mineral N pool may simply indicate poor synchrony between soil N supply and plant N demand, leading to N losses and long-term soil impoverishment. Therefore, other diagnostic approaches must be developed to assess the ability of various soil–plant systems to mobilize N from natural reservoirs and remain fertile in the long term. Cropping or breeding plants without mineral N fertilization on selected soil types and evaluating plant N status using NNI would undoubtedly represent a groundbreaking promising diagnostic approach.

**Author contribution** All authors contributed to the study conception and design of the manuscript. Each author contributed more specifically to the different sections of the manuscript: Sections I and II (G. LEMAIRE); Section III-1 (S. FONTAINE and J.F. BRIAT); Section III-2 (G. LEMARE; A.

GOJON and I. CIAMPITTI); Section IV (all). All authors read and approve the final manuscript.

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