

REVIEW

Plant–soil synchrony in nutrient cycles: Learning from ecosystems to design sustainable agrosystems

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Abstract

Redesigning agrosystems to include more ecological regulations can help feed a growing human population, preserve soils for future productivity, limit dependency on synthetic fertilizers, and reduce agriculture contribution to global changes such as eutrophication and warming. However, guidelines for redesigning cropping systems from natural systems to make them more sustainable remain limited. Synthesizing the knowledge on biogeochemical cycles in natural ecosystems, we outline four ecological systems that synchronize the supply of soluble nutrients by soil biota with the fluctuating nutrient demand of plants. This synchrony limits deficiencies and excesses of soluble nutrients, which usually penalize both production and regulating services of agrosystems such as nutrient retention and soil carbon storage. In the ecological systems outlined, synchrony emerges from plant–soil and plant–plant interactions, eco-physiological processes, soil physicochemical processes, and the dynamics of various nutrient reservoirs, including soil organic matter, soil minerals, atmosphere, and a common market. We discuss the relative importance of these ecological systems in regulating nutrient cycles depending on the pedoclimatic context and on the functional diversity of plants and microbes. We offer ideas about how these systems could be stimulated within agrosystems to improve their sustainability. A review of the latest advances in agronomy shows that some of the practices suggested to promote synchrony (e.g., reduced tillage, rotation with perennial plant cover, crop diversification) have already been tested and shown to be effective in reducing nutrient losses, fertilizer use, and N₂O emissions and/or improving biomass production and soil carbon storage. Our framework also highlights new management strategies and defines the conditions for the success of these nature-based practices allowing for site-specific modifications. This new synthesized knowledge should help practitioners to improve the long-term productivity of agrosystems while reducing the negative impact of agriculture on the environment and the climate.

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KEYWORDS

agroecology, carbon nutrient coupling, conservation agriculture, ecosystem restoration, functional traits, multifunctionality, plant communities, plant nutrition, regenerative agriculture, rhizosphere, soil fertility, soil health, soil microbial communities, soil nitrogen cycling, sustainable intensification

1 | INTRODUCTION

One of the grand challenges of humankind is to feed a growing world population while preserving soil assets for future productivity, reducing environmental impacts such as greenhouse gas emissions, eutrophication, and biodiversity loss, all under more extreme climate conditions (Food and Agriculture Organization of the United Nations, 2017). Researchers and actors of the agricultural sector have driven many innovations to increase the efficiency of agricultural management practices (i.e., precision agriculture) (Ju et al., 2009) or transforming the cropping systems themselves (reduced tillage, rotation with permanent plant cover, crop diversification) in an attempt to mitigate the ongoing degradation of soil health, biodiversity, and the environment (Wezel et al., 2014). In this transformation of cropping systems, natural or semi-natural ecosystems such as grasslands and forests are increasingly being considered as benchmarks (Bardgett & Gibson, 2017; Bender et al., 2016; Glover et al., 2010). Indeed, these ecosystems can 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; Tilman et al., 2006), while maintaining natural assets such as soil organic matter (Glover et al., 2010; Jenkinson et al., 2004; Yang, Tilman, et al., 2018), high levels of biodiversity (Habel et al., 2013), and key regulating services such as water purification (Glover et al., 2010; Laurent & Ruelland, 2011) and carbon (C) storage (Bai & Cotrufo, 2022). However, effective guidelines for redesigning cropping systems based on natural systems remain limited (Malézieux, 2012; Pulleman et al., 2022).

The higher capacity of natural ecosystems to support multiple functions simultaneously such as high biomass production, maintenance of soil assets, and water purification (ecosystem multifunctionality) has previously been linked to characteristics such as higher plant diversity, higher root biomass, higher fungal/bacteria ratio, and the increased efficiency of particular functions, for example, improved soil exploration and resource uptake by roots (DuPont et al., 2014; Yang, Tilman, et al., 2018). However, ecosystems also show marked differences in their characteristics such as dominant plant traits (Joswig et al., 2022) and soil microbial diversity (Delgado-Baquerizo et al., 2018), which means that the type or level of characteristics required for sustainable agricultural production cannot be easily generalized and likely vary with pedoclimatic context. Moreover, ecosystem functioning results from numerous interacting organisms and functions involved in C and nutrient cycling (Figure 1). Therefore, the higher multifunctionality of natural ecosystems could reflect a greater coordination between species and between biogeochemical functions (i.e., a better ecosystem organization).

Here we advocate that the design of cropping systems should consider the fact that the productivity and sustainability of ecosystems are inextricably linked to the level of synchrony between the supply of soluble nutrients by soil and plant demand for those soluble nutrients. A low level of synchrony generates both periods of excess soluble nutrients with a risk of nutrient loss, soil impoverishment, and environmental pollution, and periods of nutrient deficiency limiting plant development (Crews & Peoples, 2005; Myers et al., 1994). In contrast, high synchrony promotes the conversion of light energy to biomass by alleviating the nutrient limitation of plant growth, the closure of nutrient cycles, and the conservation, or even accumulation, of soil organic nutrients (Crews & Peoples, 2005; Myers et al., 1994). Asynchrony between soil supply and plant demand is common in cropping systems, leading to increased nutrient losses, greenhouse gas emissions, and reliance on synthetic fertilizers to maintain productivity (Crews & Peoples, 2005; Fowler et al., 2013; Myers et al., 1994). Since plant demand and soil supply depend on a high number of organisms and processes that react differently to environmental factors (Figure 1), it is not surprising that the temporal variation in nutrient release from soil rarely coincides with the time course of plant demand in cropping systems (Myers et al., 1994). This raises the intriguing question of how multiple plant and soil processes can be coordinated to achieve a high level of synchrony in natural ecosystems (Bardgett et al., 2005), and to what extent this knowledge can be used to design sustainable agrosystems.

We propose here an integrated framework describing how to design sustainable agrosystems by copying the synchronized biochemical functioning of natural ecosystems. This framework is structured in two parts. By synthesizing the latest advances in ecology and biogeochemistry, we first explain how multiple plant and soil processes can be coordinated toward a synchrony between soil nutrient supply and plant demand in natural ecosystems. More specifically, we outline four systems of synchrony and discuss their relative importance in regulating nutrient cycles depending on the pedoclimatic context and the functional diversity of plants and soil microbes. The second part of the framework details how a high level of synchrony can be promoted in agrosystems. By using the knowledge from natural ecosystems, we identify the types of synchrony systems to be promoted according to the pedoclimatic context, and suggest combinations of practices that could anchor them in cropping systems. Compared to natural ecosystems, agrosystems are subject to strong constraints such as the need for a high production of harvestable biomass and export of nutrients in the products. Despite these constraints, better plant–soil synchrony in agrosystems is possible. By synthesizing the latest knowledge on “agroecological practices” (Wezel

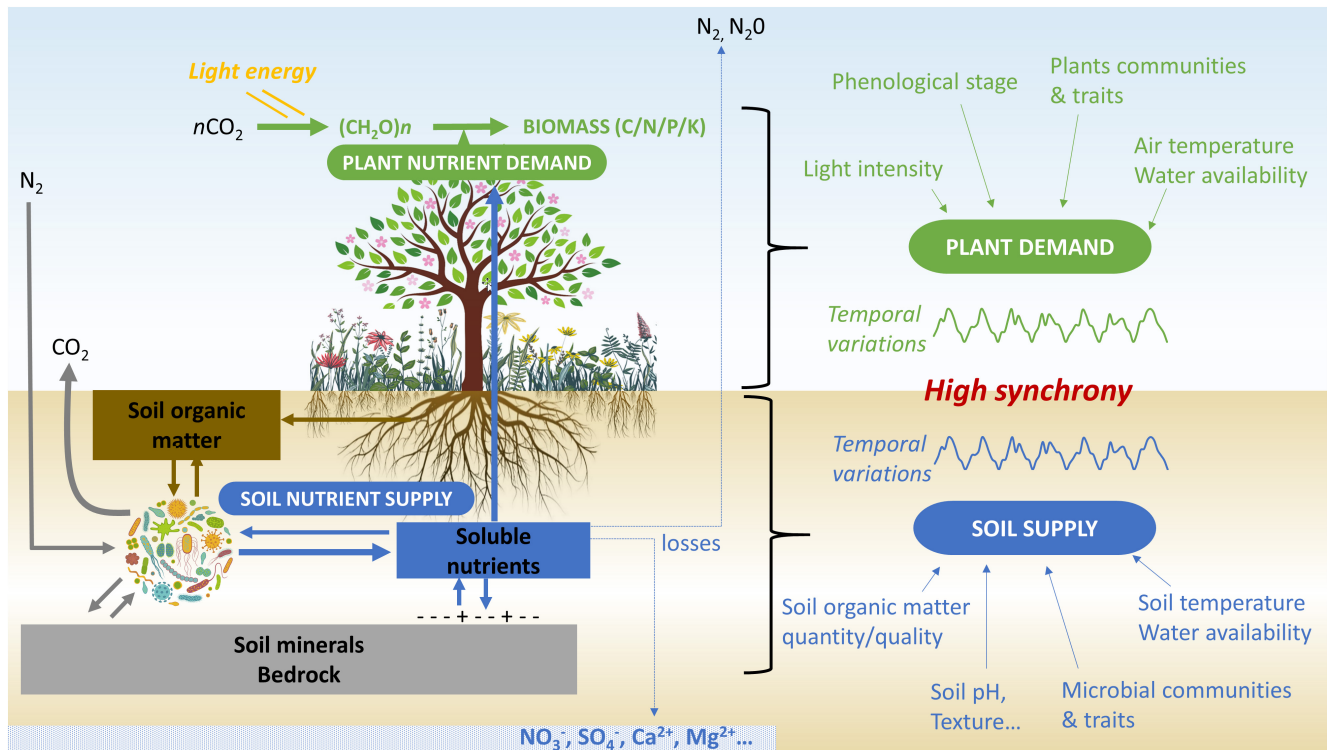


FIGURE 1 The plant–soil synchrony framework: the high level of synchrony between plant demand and soil supply characterizing natural ecosystems requires the coordination of numerous soil and plant functions. Plant demand corresponds to the amount of nutrients needed to convert the photosynthesis-derived carbon in biomass. It varies both over time and across species depending on multiple functions such as photosynthesis, organ formation and phenology, and factors such as the stoichiometric constraints of species and light intensity. Soil supply refers to the amount of soluble nutrients (mineral and organic), mainly released by soil biota comprising microbes and fauna. It varies over time and soil space depending on the prevalence of the various functions catalyzed by soil biota. Some functions increase soil nutrient supply (decomposition of soil organic matter—SOM, biological N_2 fixation and nutrient release from minerals), while others decrease it (nutrient immobilization in microbial biomass and soil organic matter). A fraction of soluble nutrients can also be adsorbed as ions on the electrically charged surfaces of soil minerals but it remains available for plant uptake. The factors controlling soil supply are mostly different from those controlling plant demand, raising the issue of the plant demand–soil supply synchrony.

et al., 2014), we show that some of the practices suggested as promoting synchrony (e.g., reduced tillage, rotation with permanent plant cover, crop diversification) have already been tested and shown to be effective in reducing nutrient losses and fertilizer use and/or improving biomass production and soil C storage. Our framework also highlights new management strategies based on the functional traits of plants and microbes, and defines the conditions for the success of these nature-based practices allowing for site-specific modifications.

2 | FOUR SYSTEMS OF SYNCHRONY

2.1 | Two synchrony systems based on soil organic nutrient reserves

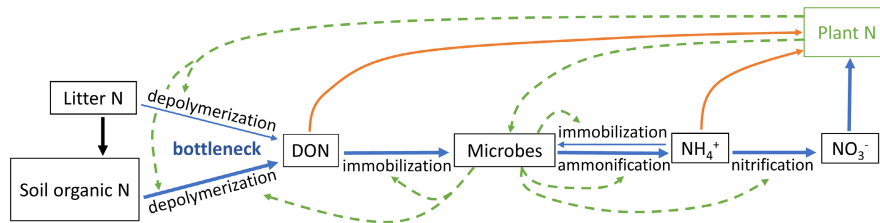
A significant part of plant nutrient uptake is obtained through organic matter recycling in natural ecosystems (89% for nitrogen, N, and 98% for phosphorous, P) (Cleveland et al., 2013) but also in fertilized cropping systems (50% for N) (Gardner & Drinkwater, 2003; Yan et al., 2020). The traditional view of nutrient cycling was that the

mineralization of soil organic matter to mineral nutrients is the major bottleneck restricting nutrient supply to plants (Box 1).

Over the last 20 years, however, progress in isotopic and molecular tracing of C and N fluxes has highlighted the capacity of plants to overcome this bottleneck (Henneron, Kardol, et al., 2020; Kuzyakov, 2019; Lama et al., 2020; Trap et al., 2017). Plants have been shown to exert an influence on all soil nutrient fluxes through a combination of processes altering the accessibility of soil resources and the activity of soil microbial communities (Bernard et al., 2022). These processes comprise rhizodeposition, nutrient uptake, litter chemistry, and mycorrhizal associations (Henneron, Kardol, et al., 2020; Sulman et al., 2017; Trap et al., 2017). Nevertheless, an apparent paradox remains regarding the synchrony between soil supply and plant demand. On the one hand, root activities such as rhizodeposition stimulate the microbial decomposition of soil organic matter and the release of soluble nutrients through the so-called rhizosphere priming effect (Henneron, Kardol, et al., 2020; Kuzyakov, 2019; Trap et al., 2017). These root activities are primarily fueled by photosynthesis-derived C. Therefore, an increase in plant photosynthesis and nutrient demand (Figure 1) induces an increase in root activities and nutrient

BOX 1 The dominant paradigm of nutrient (N taken as a model here) cycling, up the end of the 2000s.

The mineralization of soil organic N has long been considered as the major bottleneck restricting supply of N to plants (blue arrows in the Figure below, depolymerization being considered the limiting step in the mineralization process). Indeed, a large part of N present within plant litter is not released as mineral N during decomposition but incorporated and maintained into soil organic N for several decades to centuries (Balesdent et al., 1988; Knops et al., 2002; Mooshammer et al., 2014; Parton et al., 2007). Moreover, microbial mineralization of soil organic N was conventionally viewed and modeled as a process whose velocity is controlled by soil N content and environmental factors ($d/dt N = -k.N$), and not by the plant (Berardi et al., 2020; McGill, 1996). According to this paradigm, the soil supply of mineral N is decoupled from the plant demand and is the limiting process for plant growth in most ecosystems (soil supply \ll plant demand) (Vitousek & Howarth, 1991). This view was so pervasive that it continues to shape current-day vocabulary, with the concept of soil fertility still used to explain differences in plant communities and primary production between environments (e.g., plants from nutrient-rich vs. nutrient-poor soils) (Henneron, Kardol, et al., 2020; Hobbie, 2015; Jager et al., 2015). This view largely influences the representation of the nutrient cycle in models in ecology and biogeochemistry (Berardi et al., 2020; Daufresne & Hedin, 2005; Perring et al., 2008).



Although some support for these ideas can be found in studies of cultivated soils (Schimel & Bennett, 2004), research over these last two decades has deeply modified our knowledge on nutrient cycling, especially in natural ecosystems. A first revision of the classical paradigm was made in 2000s to include the ability of some plants and their mycorrhizal associates to uptake dissolved organic N and to compete for mineral N with microbes (Chapman et al., 2006; Schimel & Bennett, 2004)—represented by orange arrows in the figure. There is now a growing body of studies demonstrating the ability of plants to influence most soil N fluxes (Finlay et al., 2020; Henneron, Cros, et al., 2020; Subbarao et al., 2015; Trap et al., 2017)—represented by green dashed arrows in the figure. This calls for an overhaul of our vision of nutrient cycles (Daly et al., 2021; Grandy et al., 2022).

release from soil organic matter, suggesting a supply–demand synchrony. On the other hand, root activities are known to also accelerate microbial immobilization of mineral nutrients, and nutrient sequestration in soil organic matter (Henneron, Kardol, et al., 2020; Kallenbach et al., 2016; Nguyen et al., 2008; Schenck zu Schweinsberg-Mickan et al., 2012). This microbial immobilization reduces soil nutrient availability when plant demand increases, suggesting a supply–demand asynchrony. This apparent paradox can be resolved by considering two systems of synchrony where the antagonistic nutrient fluxes driving soil nutrient availability for plants (decomposition/nutrient release vs. nutrient immobilization/sequestration) are coordinated and coincide with the time course of plant demand. This coordination emerges from the interactions between different functional groups of plants and microbes, each of which trying to satisfy its own demand in carbon and nutrients (Figures 2 and 3). The two systems of synchrony are based on the two types of soil organic matter built by plant–soil systems, namely the mineral-associated organic matter—MAOM versus litter-based free organic matter—FreeOM, which are associated with two different nutrient cycles (Chapman et al., 2006; Sulman et al., 2017). These two nutrient cycles can co-occur and be interconnected but

their relative importance changes depending on plant functional diversity and pedoclimatic conditions (Figure 6).

2.1.1 | Synchrony based on mineral-associated organic matter (Sync-MAOM)

This synchrony system (Figure 2) is promoted by resource-acquisitive (Grime, 2001) plant species characterized by rapid growth, high tissue turnover, and rhizodeposition (Henneron, Kardol, et al., 2020), and litter with chemistry conducive to decomposition, for example, low content of lignin and condensed tannins, low C/N (Hobbie, 2015). Organic matter deposited by plants is rapidly decomposed by free-living soil decomposers that release smaller organic compounds characterized by lower-energy and higher-nutrient contents (Barré et al., 2016; Kallenbach et al., 2016). These compounds self-assemble, adsorb on soil minerals and also precipitate with metal cations (Fe, Al, Si), which further increases the cost to access them (secretion of exoenzymes and/or ligands) (Basile-Doelsch et al., 2020; Sutton & Sposito, 2005). Accumulating in soils over thousands of years (Balesdent et al., 2018; Syers et al., 1970),

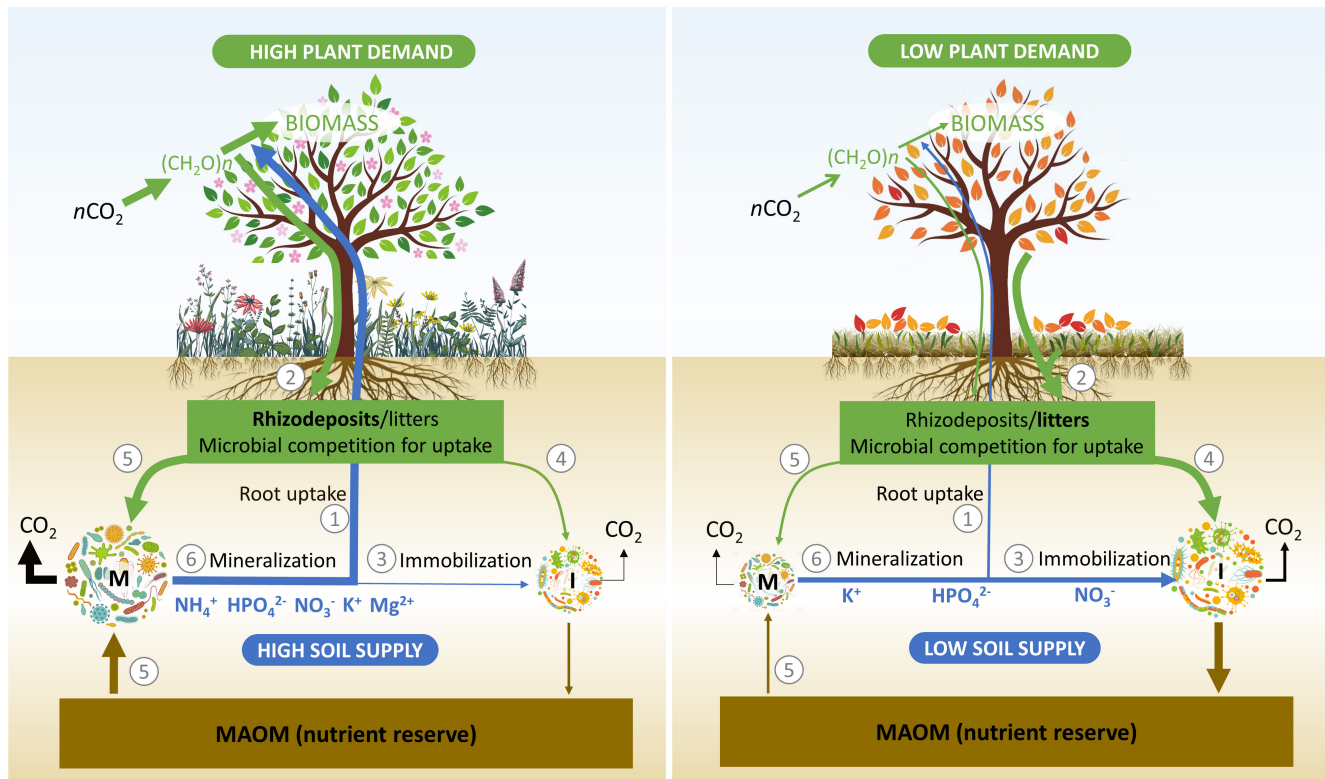


FIGURE 2 Synchrony between plant nutrient demand and soil supply of mineral nutrients through mineralization of mineral-associated organic matter (Sync-MAOM). This example describes the seasonal change in plant demand and soil supply, but the adjustment between plant demand and soil offer can be faster (within 24 h). The numbers illustrate the chronology of events in response to an increased (left panel) or decreased (right panel) plant demand. The letters M and I indicate the two functional types of microbes controlling the availability of mineral nutrients in soils (microbial mineralizers and immobilizers, respectively). Green, blue, and brown arrows describe flows of plant material, mineral nutrients and MAOM, respectively. For clarity, the mechanisms of MAOM decomposition such as the secretion of extracellular enzymes and ligands by microbes or roots are not represented. The synchrony presented here contributes to maintaining very low concentrations of soluble nutrients and hence low nutrient losses by leaching or denitrification (losses not represented).

these compounds constitute a large reservoir of MAOM (Lavalée et al., 2020).

Resource-acquisitive plants mainly absorb nutrients in mineral forms whose availability depends on the mineralization and immobilization activities (Daly et al., 2021; Sulman et al., 2017) of two broad functional types of microbes (Bernard et al., 2022; Perveen et al., 2014; Figure 2). It has recently been reported that these microbial types use, and compete for, plant rhizodeposits and litter as source of energy, but have different nutrient-acquisition strategies (Bernard et al., 2022; Malik et al., 2019). The C to nutrient ratio of plant material is often too high for microbial nutrient needs, implying that microbes have to find a complementary source of nutrients (Mooshammer et al., 2014). We refer to mineralizer microbes (M-microbes) as those able to acquire nutrients by decomposing MAOM through the secretion of exoenzymes and ligands, for example, some members from the *Tremellomycetes* class (Bernard et al., 2022; Yu et al., 2018). Their activities lead to net destruction of MAOM and release of mineral nutrients after excretion of excess nutrients and microbial turnover (Bernard et al., 2022; Perveen et al., 2014). The immobilizers (I-microbes) are not able to decompose MAOM and assimilate the nutrients they need from the

soil solution, for example, some members from the *Massilia* genus (Bernard et al., 2022; Liu et al., 2021). Their activities lead to the immobilization of nutrients and the formation of MAOM (Bernard et al., 2022; Malik et al., 2019; Perveen et al., 2014) through the release of small organic compounds that bind to each other and to soil minerals, as described earlier (Basile-Doelsch et al., 2020; Kallenbach et al., 2016).

These two microbial types characterized here according to their role on soil nutrient fluxes are consistent with ecological strategies, microbial traits, and microbial limitations previously described by microbiologists (Bernard et al., 2022; Sokol et al., 2022). M-microbes refer to slow-growing microbes characterized by high investment in resource acquisition and low carbon use efficiency (Malik et al., 2019). Their low carbon use efficiency, combined with the fact they have potentially unlimited access to MAOM nutrients, means that M-microbes are primarily limited by the availability of energy (rhizodeposits, litter, the MAOM compounds most accessible to M-microbes) (Bernard et al., 2022; Perveen et al., 2014). In contrast, I-microbes refer to fast-growing microbes characterized by low investment in resource acquisition, high carbon use efficiency, and limitation by nutrient availability.

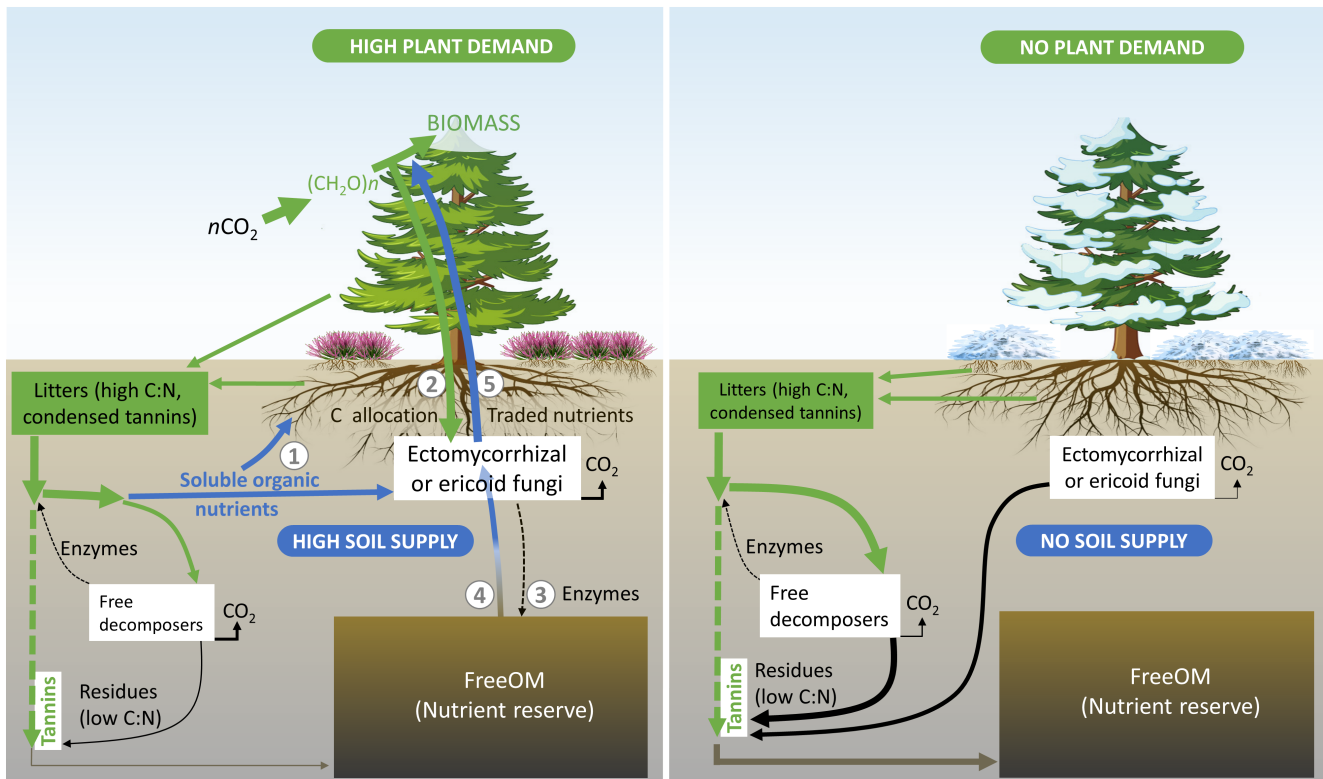


FIGURE 3 Synchrony between plant nutrient demand and soil supply of dissolved organic nutrient through depolymerization of free organic matter (Sync-FreeOM). This example illustrates the case of conservative woody plants associated with ectomycorrhizal or ericoid fungi. We describe the response of these ecosystems to seasonal changes including a long period of plant inactivity (e.g., alpine ecosystems). The numbers show the chronology of events in response to a high plant demand (left panel). Green, blue, and brown arrows describe flows of plant material, soluble organic nutrients, and FreeOM, respectively. Black arrows represent diverse microbial processes (enzyme activities, respiration, release of organic residues). The synchrony presented here contributes to maintaining very low concentrations of soluble nutrients and hence low nutrient losses by leaching or denitrification (losses not represented).

We suggest that the activities of M- and I-microbes constitute a supply chain of mineral nutrients (Figure 2, blue arrow) contributing to satisfy the plant and microbial nutrient demand, and to conserve nutrients in ecosystems. The heterogeneous distribution of roots, organic matter of contrasted quality, and communities of M- and I-microbes in soil create hotspots of nutrient immobilization and mineralization (Schimel & Bennett, 2004; Schimel & Hättenschwiler, 2007). Between these soil microsites, several hundred kilograms of mineral N and P per hectare are typically diffusing each year (Booth et al., 2005; Bünenmann, 2015; Wanek et al., 2019). These quantities exceed the yearly N and P requirements of most plant species. Plants efficiently compete for mineral nutrient uptake with I-microbes thanks to their longer lifespan and their root system that explores heterogeneous soil conditions with the help of mycorrhizal fungi (Bergmann et al., 2020; Korsaeht et al., 2001; Kuzyakov & Xu, 2013). Moreover, the two nutrient fluxes of the supply chain (mineralization and immobilization) may adjust to plant demand. Photosynthesis determines plant demand but also C rhizodeposition and nutrient uptake (Henneron, Cros, et al., 2020; Sulman et al., 2017). As a result, soil resource availability is continuously modified according to the plant demand with important consequences for M- and I-microbe activity (Figure 2). As plant demand increases, the greater uptake of mineral nutrients by plants reduces nutrient immobilization by I-microbes as

well as their use of plant material (Figure 2, left panel). At the same time rhizodeposition of energy-rich substrates is increased and the ligands present in rhizodeposits desorb organic matter from minerals making them more accessible to M-microbes (Jilling et al., 2018). More energy is available to M-microbes stimulating their decomposition activities and release of mineral nutrients from MAOM, producing the so-called rhizosphere priming effect (Fontaine et al., 2011; Henneron, Cros, et al., 2020; Perveen et al., 2014). Conversely, when plant demand decreases (Figure 2 right panel), the mineral nutrients “left over” by plants induce a rapid development of I-microbes. More I-microbes decrease the energy availability for M-microbes thus decreasing nutrient mineralization over immobilization.

Numerous studies support the existence of this synchrony system. A common garden experiment comparing 12 grassland plant species with contrasted photosynthetic activities reported that gross N mineralization (soil supply) adjusted to the demand of each of these species (Henneron, Cros, et al., 2020). Recent syntheses showed that enhanced plant photosynthesis and plant demand for nutrients under elevated CO₂ induce both an increase in gross N mineralization (Kuzyakov, 2019) and a decrease in soil organic matter stock (Terrer et al., 2021). Moreover, a decrease in plant photosynthesis in response to plant shading/cutting induces a reduction in soil organic matter mineralization (soil supply) within 24 h (Shahzad

et al., 2012; Tang et al., 2019), supporting the idea of a high-speed synchrony. In many ecosystems, the mineralization to immobilization ratio changes during the season in line with changes in plant demand; immobilization dominates during the winter (low demand) whereas mineralization dominates during spring–summer (high demand) (Schmidt et al., 2007; Yokobe et al., 2018). These functional changes have been shown to be correlated with changes in microbial community structure (Schmidt et al., 2007; Yokobe et al., 2018) supporting the idea of a synchrony driven by plant–microbe interactions. However, further studies are needed to fully demonstrate the role of the two microbial functional types M and I in this synchrony.

2.1.2 | Synchrony based on free organic matter (Sync-FreeOM)

This synchrony system (Figure 3) is promoted by resource-conservative plant species (Grime, 2001) characterized by slow growth (Lambers & Poorter, 1992), low tissue turnover, and rhizodeposition (Henneron, Cros, et al., 2020; Lambers & Poorter, 1992), and litter with high C/N ratio and high content of lignin and condensed tannins (Hobbie, 2015). This litter chemistry decreases the return on investment of decomposers (energy yield by decomposers once the investment in exoenzymes have been considered) (Malik et al., 2019) slowing down their activities and litter decomposition. Moreover, condensed tannins present in litter are able to complex small nutrient-rich organic compounds such as plant protein, exoenzymes, and residues of microbial necromass (Kraus et al., 2003) protecting them against decomposition and leaching. The accumulation of slowly decomposing litter complexing small nutrient-rich compounds contributes to the build-up of large reserves of organic nutrients, especially in heathland and cold ecosystems (Adamczyk et al., 2019; Clemmensen et al., 2013) but also in the root system of resource-conservative plants of some tropical regions (Abbadie et al., 1992). These organic matter forms are mainly free of soil minerals (FreeOM), accumulating in the organic layer and as particulate organic matter (Cotrufo et al., 2019) in the mineral soil (Figure 3) for decades–centuries (Clemmensen et al., 2013; Leifeld et al., 2009). Little mineral N is released by free-living decomposers in soils of this synchrony system because the C/N ratios of litter and FreeOM are high relative to decomposer biomass (Schimel & Bennett, 2004). To compensate for this lack of mineral nutrients, roots of conservative plant species and their associated mycorrhizal fungi have developed the capacity to absorb soluble organic nutrients such as amino acids (Chapman et al., 2006; Schimel & Bennett, 2004) released by the activity of decomposer exoenzymes, pre-empting this nutrient pool before its uptake by decomposers.

The plant–decomposer competition for soluble organic nutrients can help synchronize soil supply of soluble organic nutrients with plant demand for nutrients. During periods of high plant demand (Figure 3 left panel), plant uptake of soluble organic nutrients limits decomposer growth orientating decomposer carbon investment and activities toward the solubilization of litter into soluble organic

nutrients (high soil supply) (Liu et al., 2023; Sinsabaugh et al., 2005). When plant growth and nutrient uptake cease (Figure 3 right panel), the increased availability of soluble organic nutrient to free-living decomposers stimulates their growth, turnover and build-up of necromass, leading to the formation of FreeOM (low soil supply). Moreover, we suggest that conservative woody species may actively control the depolymerization of FreeOM in soluble organic nutrients to satisfy their nutrient demand during the growing season (left panel Figure 3). Indeed, recent studies have shown that these plants associate with ericoid or ectomycorrhizal fungi which have various enzymatic abilities (Miyachi et al., 2020) allowing them to depolymerize the FreeOM and supply the plant with nutrients in exchange of energetic C (Lu & Hedin, 2019; Phillips et al., 2013; Trap et al., 2017) in a stable reciprocal reward strategy (Kiers et al., 2011). Mycorrhizal fungi also have the capacity to inhibit or stimulate the activity of free-living soil decomposers and thus their release of soluble organic nutrients (Frey, 2019; Smith & Wan, 2019). By trading photosynthate-C against nutrients with their mycorrhizal partners, conservative woody species may modulate the rate of FreeOM depolymerization and nutrient supply to their needs.

Conservative herbaceous plants can also lead to the accumulation of FreeOM and take up soluble organic nutrients in the tropics as well as in temperate or cold environments (Abbadie et al., 1992; Leifeld et al., 2009; Näsholm et al., 2009). Endo-mycorrhizal fungi associated with herbaceous plants can help to satisfy plant nutrient demand by absorbing soluble organic nutrients released by the activity of free decomposers, with cascading positive effects on plant-to-fungi energy transfer. However, contrary to ericoid and ectomycorrhizal fungi, endo-mycorrhizae have no or little degradative capability (Frey, 2019). Therefore, it remains unclear whether these plants can control the release of nutrient from FreeOM and by which mechanisms they would exert their control. An increased mowing of conservative species has been shown to accelerate FreeOM decomposition and N cycling (Klumpp et al., 2009; Robson et al., 2010), suggesting that roots of conservative plants have some control over soil nutrient fluxes. Conservative herbaceous plants have been suggested to modulate nutrient fluxes by shaping the activity of free-living decomposers through their associations with endo-mycorrhizal fungi and endophytes (Binet et al., 2013; Frey, 2019).

2.2 | Synchrony based on inorganic nutrients retrieved from the atmosphere and minerals (Sync-Inorganic)

Aside from soil organic reserves, plants can access several other sources of nutrients for which supply–demand regulations can occur (Figure 4). A classic example is N uptake from the atmosphere by legumes which depends on the rapid transfer of photosynthates to root nodules where Rhizobia carry out the costly process of N₂ fixation (Udvardi & Poole, 2013; Figure 4). Given the dependency of nodules to plant C, conditions enhancing photosynthesis (plant demand) such as the increase in light intensity or atmospheric CO₂ usually lead to

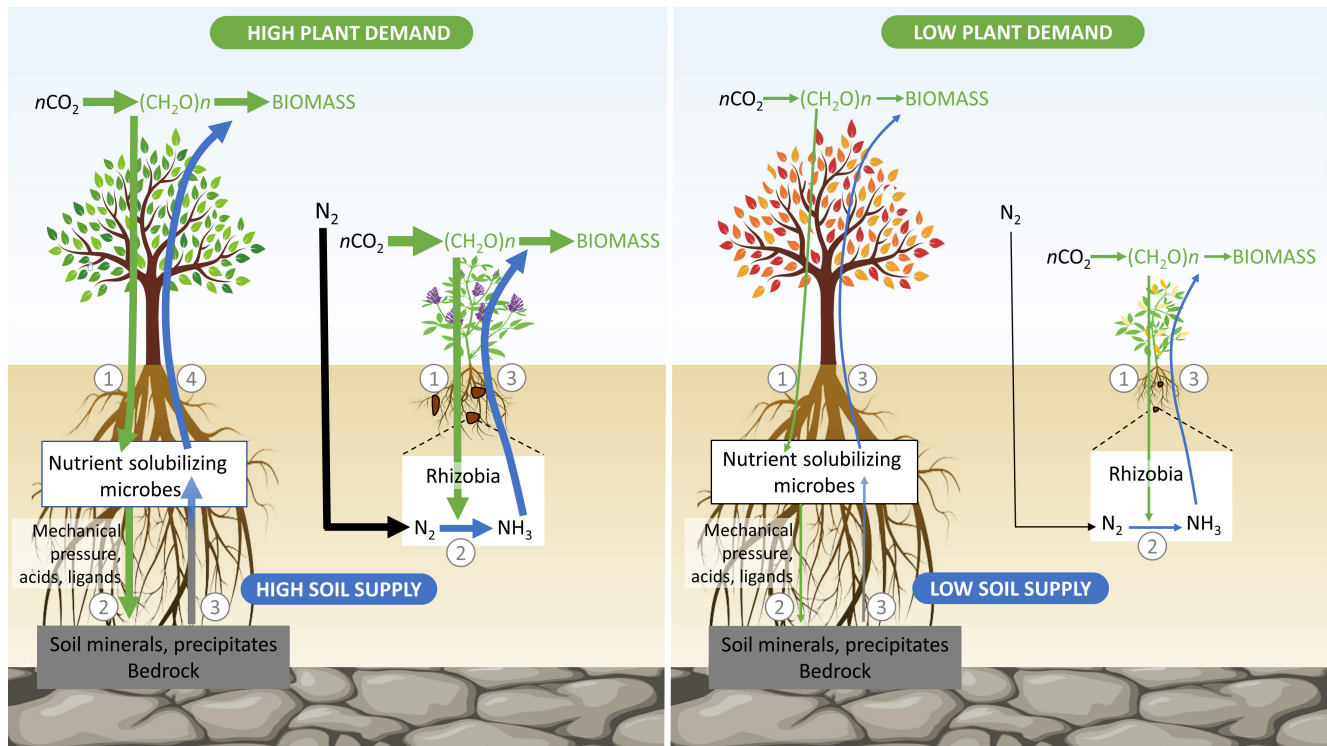


FIGURE 4 Synchrony between plant nutrient demand and soil supply of inorganic nutrient retrieved from the atmosphere, soil minerals, and bedrock (Sync-Inorganic). This example illustrates the cases of (1) legumes whose roots associated with Rhizobia fix atmospheric N in nodules (brown circles in the alfalfa root system in the figure), and (2) plants whose roots associated to some microbes (e.g., mycorrhizal fungi, phosphorus solubilizing bacteria) accelerate rock/mineral weathering and solubilization of occluded nutrients. This example describes the seasonal change in plant demand and soil supply, but the adjustment between plant demand and soil offer can be faster (within minutes for N_2 fixation). Green, blue, and black arrows describe flows of plant material, plant-available nutrients and atmospheric N, respectively.

an increase in N_2 fixation (Lawn & Brun, 1974). Conversely, factors reducing photosynthesis reduce N_2 fixation (Lawn & Brun, 1974). Photosynthesis modulates not only nodule number and growth, but also the activity of nitrogenase (Udvardi & Poole, 2013), leading to a fast (hours) synchrony between plant demand and microbial N_2 fixation. This synchrony system can account for up to 100% of the N taken up by legumes and contributes to over 16% of current global net primary production (Cleveland et al., 2013).

Rock, soil minerals, and precipitates represent a crucial source of phosphorus (P), potassium, calcium, magnesium, and iron for plants (Landeweert et al., 2001). These nutrients are not directly available to plants, and first need to be solubilized (P precipitates) or released from the mineral matrix (rock) through physical and chemical weathering before being absorbed by plants. Roots can directly accelerate this nutrient mobilization through the secretion of protons and ligands solubilizing and desorbing nutrients from the mineral phase (Lambers et al., 2009). Rhizodeposition also supports large communities of root-associated microbes that accelerate weathering of minerals, amplifying the nutrient availability to plants by several orders of magnitude (Lambers et al., 2009; Landeweert et al., 2001; Figure 4). For example, mycorrhizal hyphae exert a mechanical pressure that provokes physical distortion of the mineral lattice structure facilitating subsequent chemical alteration (Finlay et al., 2020). The production of organic acids by phosphate solubilizing bacteria

increases plant P uptake and growth (Chen et al., 2021; Rodríguez & Fraga, 1999). All these mechanisms of nutrient supply are related to the delivery of carbon by plants that trade it with microbes in a bidirectionally controlled nutrient market (Kiers et al., 2011; Selosse & Rousset, 2011). Overall, the rate of plant photosynthesis determines the amount of carbon that can be dealt with microbes carrying out mineral dissolution/weathering, allowing, in the form of a compromise, a synchrony between plant and microbial demand and supply of carbon and nutrients. The contribution of this synchrony system to plant nutrition remains unclear due to the difficulty to separate the different sources (organic versus inorganic) and chemical states of nutrients (e.g., precipitated P, P complexed with metals; P occluded in minerals) used by the symbionts. However, new P inputs from rock weathering are estimated to contribute no more than 3% of current global net primary production (Cleveland et al., 2013).

2.3 | Synchrony on multiple nutrients simultaneously promoted by a common market (Sync-Market)

In the previous sections, we summarized how soil nutrient supply (all nutrients confounded) may adjust to overall plant nutrient demand controlled by the amount of photosynthetic C available for

biosynthesis. However, plants as well as microbes need a variety of nutrients in specific ratios (Elser et al., 1996). These stoichiometric constraints raise the question of a synchrony acting simultaneously on multiple nutrients. The different synchrony systems outlined above appear unable, individually, to bring nutrients in the ratios suitable for plant needs. Although research on the coupling of multiple elements in ecosystems is still in its infancy, a number of empirical results support the existence of a synchrony on multiple nutrients (Nasto et al., 2019; Treseder & Vitousek, 2001). Plants can balance the macro- and micro-nutrients they receive by modulating the energy they allocate to microbial partners controlling acquisition pathways for particular nutrients (Treseder & Vitousek, 2001; Werner et al., 2014). For example, a lack of P triggers a greater allocation of C to mycorrhizal fungi and associated microbes which secrete phosphatases or protons to acquire soil P (Treseder & Vitousek, 2001).

Synchrony on multiple nutrients could also occur through a common market system established through mycorrhizal networks and interlinked food webs (Sync-Market, Figure 5). Mycorrhizal fungi form networks of hyphae that act as common highways for the movement of C and nutrients, redistributing these commodities across space and between plants of either the same or different species (Beiler et al., 2010; Wipf et al., 2019). Although field estimates of these nutrient transfers are lacking (Karst et al., 2023), pot experiments using the applications of isotope-labeled elements suggested substantial nutrient exchanges between neighboring plants through mycorrhizal networks (Hartnett & Wilson, 2002; Wilson et al., 2006). In these studies, interplant P transfer via arbuscular mycorrhizal fungi accounted for on average 17% of the total P taken up by tallgrass prairie grasses. These nutrient transfers suggest

that mutualistic fungi trade nutrients not only with the plants with which they are directly associated, but also with other symbionts that are themselves connected to other plants. In such a mycorrhizal network, the two symbionts (plants and fungi) can interact with many different partners. These multi-partner interactions have been shown to enforce the mycorrhizal mutualism by favoring the more cooperative partners (Kiers et al., 2011). Indeed, plants can detect, discriminate, and reward the best fungal partners with more carbohydrates. In turn, fungal partners enforce cooperation by increasing nutrient transfer only to those roots providing more carbohydrates. We suggest that mycorrhizal network can also connect and promote resource exchanges between partners with different needs or supplies with beneficial effects for the nutrition and growth of the two symbionts (Figure 5). Indeed, the capacity of mycorrhizal fungi to trade the various soil-acquired nutrients against plant-carbon can be enhanced when they are connected to plants with qualitatively different needs (e.g., different N/P/K/S ratios of biomass). On the plant side, the mycorrhizal redistribution of nutrients between plants with different needs and/or benefits from different soil resources better satisfies the demand of plants in multiple different nutrients (Figure 5). Overall, this nutrient redistribution limit local excess of particular soluble nutrients. Therefore, the common market could maximize synchrony at different scales (from plant to ecosystem) and for several elements simultaneously, explaining the positive effects of common mycorrhizal networks observed on plant nutrition and growth (Wipf et al., 2019). However, we must remain cautious about the temporal stability of mycorrhizal networks and their possible impact on nutrient dynamics, as few long-term field studies have been carried out on this subject to date (Karst et al., 2023).

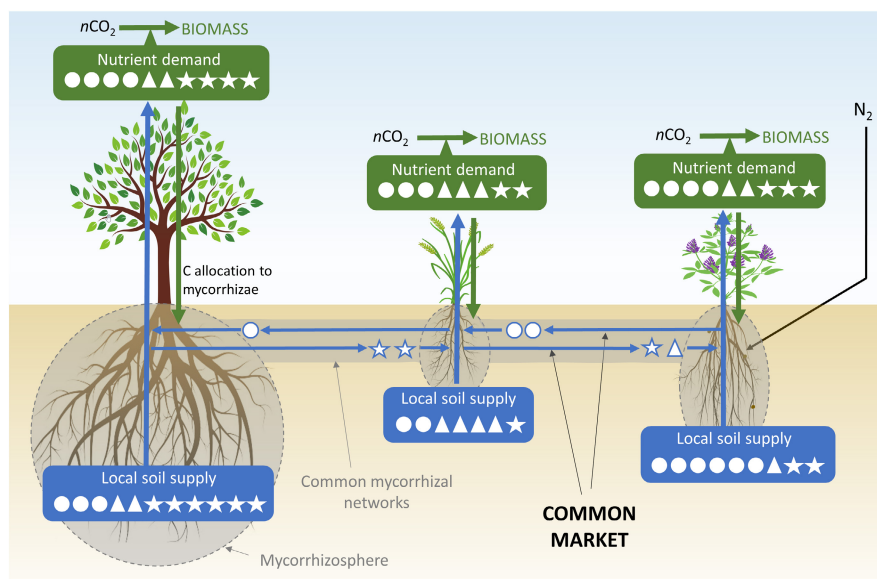


FIGURE 5 Synchrony between plant demand and soil supply on multiple nutrients can be facilitated by a common nutrient market supported by mycorrhizal networks. The symbols (triangle, circle, star) illustrate different nutrients. The local soil supply represents the amount of soluble nutrients delivered by the soil biota (from organic and inorganic nutrient reserves) before the nutrient redistribution between plants through the common market. This local soil supply can vary with local soil characteristics, root depth, and plant nutrient-acquisition strategies. The nutrient redistribution between plants by the mycorrhizal network is better able to satisfy the plant demand in multiple nutrients and limit local excess of soluble nutrients.

3 | INFLUENCE OF ABIOTIC AND BIOTIC FACTORS ON SYNCHRONY

3.1 | Pedoclimatic context and plant functional types

Building on the recent scientific advances, we propose a framework with four systems capable of synchronizing the soil nutrient supply to plant demand at a range of time scales (from hours to seasons). Two systems (Sync-FreeOM, Sync-Inorganic) are based on plant-products such as litter or nodule-supporting tissues of legumes, and microbial symbionts that tightly interact with plant roots such that they can be considered as the extended phenotype of certain plants (Fernandez et al., 2022). For the remaining systems (Sync-MAOM, Sync-Market), synchrony emerges from diffuse interactions between distinct functional types of microbes and plants and therefore can be considered as ecosystemic regulations. These four synchrony systems co-occur in most ecosystems, their relative importance depending on pedoclimatic context, plant functional type, and biodiversity level (Figures 6 and 7).

Sync-Inorganic plays a key role in young soils where organic nutrient reserves are limited and soil inorganic nutrient reserves

dominate (Figure 6). The effectiveness of Sync-Inorganic for plant nutrition in young soils depends on the mineralogy of bedrock and soil minerals that determine the availability of macro- and micro-nutrients for plants. Sync-Inorganic is also determined by the plant communities present and their ability to retrieve nutrients from atmosphere and soil minerals. For example, the importance of Sync-Inorganic increases with the proportion of legumes. The contribution of synchrony systems based on soil organic reserves (Sync-MAOM, Sync-FreeOM) increases with soil age as organic matter accumulates and inorganic reserves are depleted. The change of the dominant synchrony systems over time (Sync-Inorganic vs. Sync-Organic) is supported by the observed changes in root symbionts and plant nutrient-acquisition strategies in response to the dynamics of main form of nutrient reserves with soil age (Albornoz et al., 2016; Lambers et al., 2008; Zemunik et al., 2015). In the longer term, inorganic and organic reserves of certain rock-derived nutrients (e.g., P) may both decline due to continuous nutrient losses from ecosystems. This depletion of total soil nutrient reserves can limit synchrony in highly weathered soils, leading to plant productivity decline (Wardle, 2004).

Sync-MAOM is promoted by resource-acquisitive plant species producing litter with a chemistry conducive to rapid decomposition

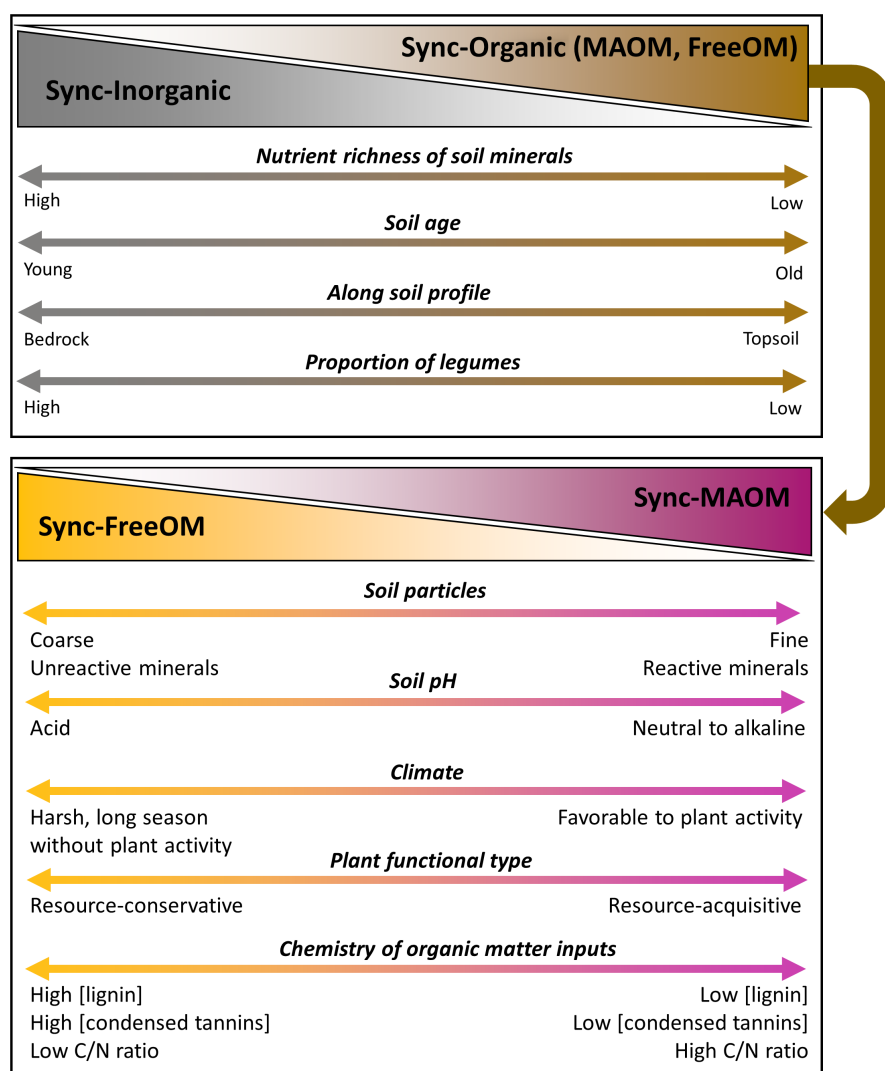
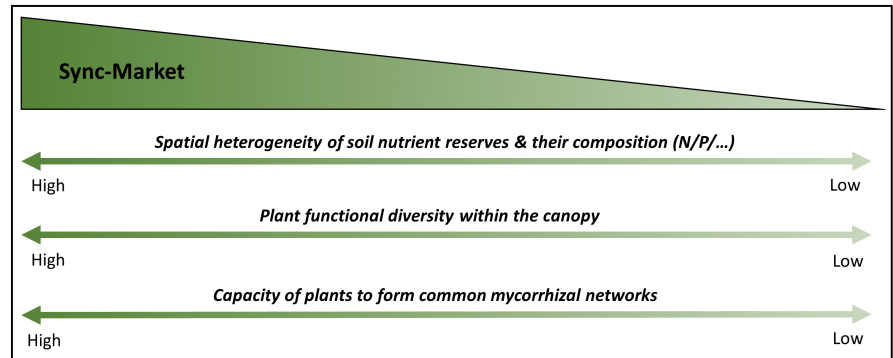


FIGURE 6 Relative importance for ecosystem functioning of the synchrony systems based on nutrients retrieved from atmosphere and soil minerals (Sync-Inorganic) and from soil organic nutrient (Sync-Organic) in relation to pedoclimatic contexts and plant functional type. The Sync-Organic is composed of two distinct synchrony systems mobilizing different types of soil organic matter, namely the mineral-associated organic matter (Sync-MAOM) and the free organic matter (Sync-FreeOM).

FIGURE 7 Expected contribution to ecosystem functioning of the synchrony system based on a common nutrient market (Sync-Market) in relation to pedoclimatic contexts and plant functional diversity.



by microbes that release the organic compounds leading to MAOM formation. This formation depends on interactions with minerals, and the contribution of Sync-MAOM increases as soil particle size decreases and mineral reactivity increases (Kögel-Knabner & Amelung, 2021). Moreover, Sync-MAOM requires a regular plant supply of energy-rich substrates to M- and I-microbes. Thus, Sync-MAOM may dominate where climatic conditions are favorable to plant activity most of the year.

Sync-FreeOM is promoted by resource-conservative species producing litters with a chemistry unfavorable to decomposition. When rich in condensed tannins, this litter complexes the small organic compounds released by microbes building large reserves of FreeOM. This contributes to nutrient conservation even under conditions of low MAOM formation potential and periods of plant inactivity. Thus, Sync-FreeOM is expected to dominate in coarse-textured soils and/or under climates with long season(s) without plant activity (Adamczyk et al., 2019; Clemmensen et al., 2013). The change of the dominant synchrony systems (Sync-MAOM vs. Sync-FreeOM) according to pedoclimatic conditions can be paralleled to the change in humus forms (Mull, Moder, and Mor) and nutrient cycling described along environmental gradients (Chapman et al., 2006; Ponge, 2003).

Sync-Market is induced when different plants connected by common mycorrhizal networks have complementary nutrient needs and/or local soil nutrient supply. Thus, the contribution of Sync-Market is expected to increase with spatial heterogeneity (from nanoscale to soil profile) of soil nutrient reserves (organic and inorganic) and their elemental composition (e.g., N/P/S ratio) (Figure 7). Plant functional diversity (plant with different C/N ratio in biomass, root depth, exudates...) within the canopy promotes Sync-Market by increasing the complementary effects between plants in terms of nutrient needs and local soil nutrient supply. The contribution of Sync-Market to ecosystem functioning is also determined by the capacity of plants and fungi to form common mycorrhizal networks.

3.2 | Biodiversity: A key asset promoting synchrony

Higher plant and microbial diversity improve multiple ecosystem functions such as primary production, nutrient retention, and soil C storage (Hector, 2011; Lange et al., 2015; Scherer-Lorenzen et al., 2003;

Wagg et al., 2014) that are related to synchrony. Recent evidence also indicates that the higher primary production promoted by plant diversity is associated with an improved soil nutrient supply (Maestre et al., 2012; Oelmann et al., 2021). We propose that biodiversity could promote synchrony across scales ranging from individual plants to whole ecosystems, through three non-exhaustive pathways.

3.2.1 | Biodiversity promotes synchrony through the functional complementarity of organisms

Synchrony systems clearly show an ecological division of labor (Hector, 2011) that may emerge from evolutionary processes (Lu & Hedin, 2019; Williams & Lenton, 2007): each function of the system is carried out by specific groups of biota such as organic nutrient reserve formation (I-microbes, conservative plants) and decomposition (M-microbes, ectomycorrhizal, and ericoid fungi), N₂ fixation (Rhizobium, legumes) etc. The maintenance of these functional groups is fundamental for the synchrony generated by each of these systems. Moreover, co-occurrence of plant species with different nutrient-acquisition strategies (e.g., legumes/non-legumes, acquisitive/conservative, P-mobilizing plants) (Gross et al., 2007) is also expected to promote both the existence of—and the interaction between—synchrony systems with complementary roles in ecosystems. Sync-inorganic brings nutrients from atmosphere and bedrock to the ecosystem while Sync-MAOM and Sync-FreeOM accumulate these nutrients in organic reserves, limiting nutrient loss and allowing nutrient recycling when needed by plants and/or microbes. These synchrony systems create major nutrient sources for plants while Sync-Market helps to balance the proportion of different nutrients supplied in relation to the multiple element requirement of plants. The proximity of roots of neighboring plants with different strategies facilitates nutrient transfer from plant to plant for their mutual benefit in terms of nutrition and growth (Homulle et al., 2022; Montesinos-Navarro, 2023). This nutrient transfer takes place at different time scales (hours to years) according to the processes involved, including nutrient exchanges across mycorrhizal networks (Sync-Market), direct transfer of root exudates, and decomposition of plant materials. The exchange of N and P between legumes and P-mobilizing plants is a classic example of plant-plant interactions which improve overall plant-soil synchrony.

3.2.2 | Biodiversity facilitates synchrony by ensuring the temporal and spatial stability of plant–soil interactions

Synchrony requires that the connection between plants and microbes is maintained in space and time. Given that species can occupy different niches, this space-to-time occupation by plants and microbes often depends on species diversity. For example, soil occupation at various soil depths but also across coarse and fine spatial scales requires multiple plant species with contrasted root architecture and traits (Roscher et al., 2012). Succession of plant species with different phenology contributes to maintaining a permanent plant cover in diversified ecosystems (Valencia et al., 2020) and a continuous energy supply to microbes, which is particularly important for Sync-MAOM (Figure 2). Importantly, increased diversity will also promote temporal and spatial stability by promoting functional redundancy among species conferring greater resistance to environmental fluctuation and disturbance overtime (García-Palacios et al., 2018).

3.2.3 | Biodiversity stabilizes resource-exchange mutualisms

We detailed several systems of synchrony based on mutualism between plants and their fungal/bacterial symbionts, and the subsequent resource exchanges (Sync-FreeOM, Sync-Inorganic, Sync-Market). The maintenance of such mutualisms is not obvious from an evolutionary point of view: any partner that invests less in the resource exchange would have an immediate benefit, while the cost (lower partner abundance or activity) would be shared by all, creating a classical tragedy of the commons (Foster & Kokko, 2006; Hardin, 1968). We suggest that diversity on both sides (plants and microbes) facilitates the maintenance of the resource exchange. Indeed, the diversity of partners allows the possibility of partner choice and reward/sanction, known to stabilize this type of mutualistic interaction (Bull et al., 1991; Foster & Kokko, 2006; Kiers & Denison, 2008).

We have highlighted the role of functional groups of plants and microbes in setting up synchrony, but many other biota are likely to be involved. For example, the predation and recycling of microbial biomass by soil micro-fauna (e.g., protozoa) (Irshad et al., 2012; Potapov, 2022) and viruses (Kuzakov & Mason-Jones, 2018) contribute to nutrient mineralization and production of small organic residues building the organic nutrient reserves (MAOM and FreeOM).

3.3 | Plant plasticity and adaptations to unbalanced soil supply

Despite existing mechanisms that facilitate supply–demand synchrony, strong spatial and temporal variations in soil nutrient

availability or plant demand generated by exogenous factors such as animal excretion or extreme climatic events can induce transient periods of asynchrony (excess or deficiency) (Augustine & McNaughton, 2004; Xi et al., 2014). Insufficient soil supply in relation to the demand of a given plant may also arise due to limiting nutrient reserves in soil and to localized plant–plant competition for nutrients (Lekberg et al., 2018). Plants can respond in two ways to unbalanced soil supply:

3.3.1 | Changes in physiology and morphology to enhance acquisition of limiting resources

Plants are able to adapt their physiology and morphology over short-time scales (hours–weeks) in response to nutrient availability (Hermans et al., 2006). Under high nutrient supply, plant allocation of C and nutrients shifts toward greater investment in shoots and photosynthetic proteins enhancing C acquisition (Maier et al., 2008). In contrast, under low nutrient supply, plants promote nutrient acquisition and nutrient supply from microbes by increasing root-to-shoot ratios, up-regulating root membrane transporters, and changing root architecture and exudation (Meier et al., 2020; Nacry et al., 2013).

3.3.2 | Nutrient storage

When supply exceeds plant demand, many plant species adopt a luxury nutrient uptake (Tripler et al., 2002). These excess nutrients are stored in vacuoles in the short term (days), or in large storage organs such as rhizomes for remobilization several months–years later during periods of insufficient soil supply (Millard & Grelet, 2010). Reserves play a central role in the nutrition of perennial plants, with remobilized N from previous year storage often representing more than 50% of N recovered in new shoots (Millard & Grelet, 2010). At the ecosystem scale, plant nutrient storage presents the same advantages as synchrony since it promotes (i) biomass production by alleviating the nutrient limitation of plants and (ii) nutrient retention by preventing accumulation of soluble nutrients in soil.

4 | IMPLICATIONS FOR AGROSYSTEMS IN A GLOBAL CHANGE CONTEXT

4.1 | Fertility: An emerging property of plant–soil interactions

Most definitions of soil fertility refer to the inherent capacity of a soil to sustain plant growth and production by providing nutrients in adequate amounts and in suitable proportions (FAO - Global Soil Partnership, 2023). We argue that recent work on plant–soil synchrony calls for an in-depth revision of this concept because (1)

plants can influence the quantity and proportion of soluble nutrients they receive from soil via at least four systems of synchrony, and (2) soil nutrient supply should be considered in relation to the fluctuating plant demand. Hence, nutrient supply from soil is not an inherent property of soil but an emerging property of plant-soil interactions, even if soil characteristics and climate influence the nature and efficiency of these interactions (Figures 6 and 7). This has a practical consequence: depending on the plant species and microbial taxa present and their ability to influence soil nutrient supply, the same soil can support different levels of biomass production as underlined in several experiments (Chapman et al., 2006; Henneron, Kardol, et al., 2020). It may also explain why soils defined as infertile can support similar levels of biomass production as soils defined as fertile in some cases (Hansson et al., 2020; Legout et al., 2020).

Fluctuating plant nutrient demand is increasingly integrated in fertilization management schemes of farmers (Justes et al., 1997; Myers et al., 1994; Thompson et al., 2017). For example, crop demand is a fundamental input of various approaches such as Jubil and 4R designed to fractionate and adapt fertilizer applications over crop development (Drechsel et al., 2015; Justes et al., 1997). Despite this progress, more than 40% of global food production depends now on the use of synthetic N fertilizers whose efficiency of use varies between 20% and 80%, that is, a large part of applied N is still lost to the environment (Lassaletta et al., 2014; Smil, 2001). These nutrient losses can be explained by limitations inherent to developed approaches (e.g., the anticipated plant nutrient demand is dependent on climate conditions which are not controlled) and by the difficulty of access for many farmers to the knowledge and technologies necessary for these approaches (Thompson et al., 2017). We advocate that identifying plant species capable of stimulating soil nutrient supply via synchrony systems opens avenues toward ecological intensification of plant production, and could strongly modify the way agroecosystems contribute to global changes. As previously pointed out by others (Abalos et al., 2019), better accounting of plant functional diversity and its interactions with root symbionts, heterotrophic and chemoautotrophic soil biota is a necessary step toward further improvement of nutrient cycling in agrosystems.

4.2 | Managing synchrony to ensure both productivity and sustainability

There is a great diversity of management approaches currently being explored to reinforce the sustainability of agriculture (no or reduced tillage, organic farming, crop rotation, conservation agriculture, permaculture...). Nevertheless, finding efficient combinations of agroecosystem features for a given pedoclimatic and socio-economic context remains difficult. The adoption of “sustainable” practices does not always solve asynchrony issues. For instance, the incorporation of legumes as green manure in rotations can lead to N losses as high as synthetic fertilizers (Crews & Peoples, 2005),

though this practice has the advantage of reducing the use of mineral N fertilizers whose production generates greenhouse gases. Moreover, management practices often appear to involve trade-offs or offsets between expected outcomes, such as those between yield and greenhouse gas emissions (Shi et al., 2019), and between soil C storage and emission of N₂O (Gregorich et al., 2005). Focusing on plant-soil synchrony can help address these difficulties by guiding the changes to be made in agrosystems to make them sustainably productive; understanding when and how synchrony is enhanced is needed for management decisions. By analyzing the four synchrony systems, we have identified the types of synchrony systems to be promoted according to the pedoclimatic context (Figures 6 and 7) and suggest combinations of practices that could anchor them in cropping systems (Figure 8).

In young soils (e.g., developing Andosols), where inorganic reserves are high and organic reserves can be low, management options should give greater importance to Sync-Inorganic, for example, by incorporating a high proportion of legumes and plant species mobilizing nutrients from soil minerals through their rhizodeposition and association with mycorrhizae (Figure 8). With organic nutrient accumulation and depletion of inorganic nutrient reserves as soils evolve, agricultural practices should promote Sync-Organic, for example by introducing species with high rhizodeposition of energy-rich C for mineralizing microbes (MAOM-sync; Figure 8). In the longer term, the inorganic and organic reserves of some rock-originated nutrients (e.g., P) can limit synchrony in the topsoil of highly weathered soils (e.g., Ferralsols). In these soils, synchrony can be enhanced by including deep-rooting species capable of mobilizing the nutrients from bedrock and redistribute them to the topsoil (Figure 8; Callesen et al., 2016). Combined with these previous practices, moderate inputs of organic and/or synthetic fertilizers can also be an efficient strategy to reconstitute soil organic nutrient reserves and associated synchrony systems (Sync-MAOM, Sync-FreeOM) in nutrient-depleted soils. Recent studies have shown the possibility of stimulating different nutrient-acquisition pathways (organic-P mineralization, inorganic-P dissolution, N₂ fixation) through the selection of specific plant traits (N₂-fixation efficiency, but also types of exudates) (Sauvadet et al., 2021; Waithaisong et al., 2020). It has also been reported that the level of soil weathering determines the type of diversification and nutrient-acquisition strategies able to enhance ecosystem productivity and sustainability (Erel et al., 2017; Waithaisong et al., 2020). In the study of Waithaisong et al. (2020), legumes increased biomass production (+18%) in Andosols but not in Ferralsols, while soil-P-mobilizing tree species increased biomass production (+39%) and soil C stock (+26%) in Ferralsols but not in Andosols (Waithaisong et al., 2020).

Current industrial grain production systems are mostly based on fast-growing acquisitive plant species (Milla et al., 2015) generating MAOM-type soil organic matter. Given that the Sync-MAOM system requires a regular C input from plants to microbes (Figure 2), practices promoting a permanent plant cover in annual cropping systems could enhance synchrony. Along a gradient of increasing novelty, these practices include lengthening of crop rotations, cover/

Synchrony	Conditions of synchrony	Combination of practices to set up for promoting the targeted synchrony
Sync-MAOM	-Acquisitive plant species -Continuous activity of microbes M & I -Reserve of MAOM in soil	- Use/breed acquisitive species with strong capacity of stimulating microbial mineralization/immobilization, e.g. high C rhizodeposition - The carbon:nutrient ratio of plant species or organic residues must be high enough to induce nutrient immobilization. Ideally, the different plant species have contrasting carbon:nutrient ratios (a, c, l, j, k) - Maintain a continuous cover of active plants fueling microbes in energy-rich C (all pictures but e) - Recycle organic nutrients at local scale (farm-watershed) to preserve soil organic reserve on the long-term (d, e, f) - Inoculate with immobilizing and mineralizing microbes in highly degraded soils
Sync-FreeOM	-Conservative plant species -Mycorrhizal fungi -Reserve of FreeOM in soil	- Use/breed conservative species producing recalcitrant litter with reactive compounds fixing organic nutrients (e, f)* - Amend with recalcitrant organic residues harboring reactive compounds more or less charged in organic nutrients (e) - Recycle organic nutrients at local scale (farm-watershed) to preserve soil organic reserve on the long term (d, e, f)
Sync-Inorganic	-Plant symbiosis with mycorrhizal fungi & N ₂ fixing bacteria -Nutrients stored in bedrock, soil minerals and/or precipitates	- Use/breed species with strong capacity of mobilizing nutrients from rock and soil minerals, e.g. mycorrhized roots exerting strong mechanic pressure on minerals, secreting high amount of organic acids & ligands - Use of plant with deep roots colonizing bedrock (g, h, i) - Use of legumes (a, c, k) - Inoculate with mixed mycorrhizal fungi & N ₂ fixing bacteria in highly degraded soils
Sync-Market	-Plant species with complementary nutritional needs -Common mycorrhizal networks	- Mix plant species with different nutrient acquisition strategies and carbon:nutrient ratios (a, c, l, j, k) - Promote perennial plants (f, g, h, l, k) and/or permanent plant cover (all pictures but e) to fuel mycorrhizae in energy-rich carbon - No or limited use of soil tillage (b) and pesticides to preserve mycorrhizae networks - Inoculate with mixed mycorrhizal fungi in highly degraded soils
Increasing overall synchrony	-Synchrony systems adapted to pedoclimatic context -Complementary synchrony systems -Plant plasticity & reserve	- Analyze the soil profile and climate, defining the proportion of the different synchrony systems to promote accordingly - Mix plant species with different nutrient acquisition strategies (a, c, l, j, k) - Breed crops species for their suitability to association - Promote perennial plants with high reserve and organ plasticity (f, g, h, l, j, k)

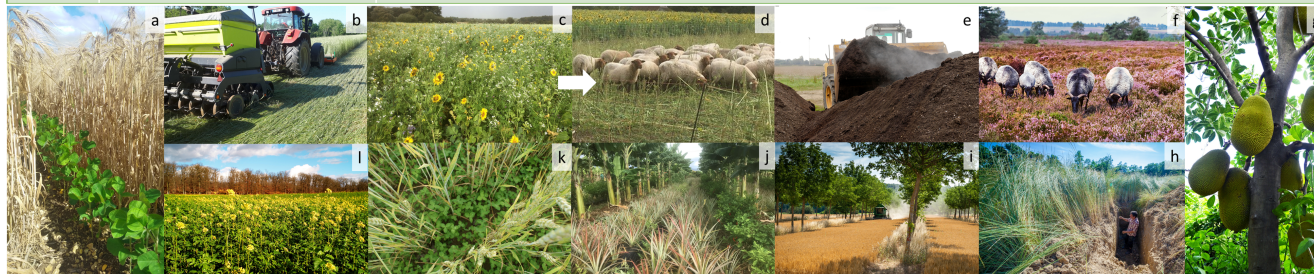


FIGURE 8 Combinations of agricultural practices promoting synchrony between soil nutrient supply and plant nutrient demand through the four synchrony systems synthesized in this framework (Sync-MAOM, Sync-FreeOM, Sync-Inorganic, Sync-Market). Some practices specifically stimulates one system of synchrony while others stimulate several systems of synchrony simultaneously. The types of synchrony system and the combination of practices must be adopted regard to the pedoclimatic context. Photographs illustrate examples of practices promoting synchrony. Some of them have ancestral origins (f, g, j), others have been developed and tested in the last decades (a, b) or are still under development in agricultural research centers and/or farmers' networks. (c, d, h, k). (a) Relay cropping with soybeans sown during barley growth (©ARVALIS/GENDRE Sophie); (b) direct drill on a rolled barley cover (©ISARA/VINCENT-CABOUD Laura); (c) mixture of 12 species of annual crops that (d) was consumed as a standing crop by sheep (©A2C/THOMAS Frédéric); (e) production of compost used as a substrate in market gardening or as an amendment in agriculture. Once stabilized, the compost is composed of recalcitrant plant residues enriched with microbial compounds (©INRAE/MAITRE Christophe); (f) extensive grazing of heathlands (©SHUTTERSTOCK); (g) the “bread-tree” *Artocarpus altilis* (©SHUTTERSTOCK); and (h) the cereal *Thunopyrum intermedium* (©ISARA/DUCHENE Olivier) are two examples of perennial plants that can be used as source of carbohydrates and proteins; (i) agroforestry associating a barley crop with a walnut tree plantation (©INRAE/NICOLAS Bertrand); (j) association of banana, pineapple, and pepper plantations (©A2C/THOMAS Frédéric); (k) wheat cultivation on a living clover cover (©ISARA/DUCHENE Olivier); and (l) cover cropping with mustard (©INRAE/WEBER Jean).

relay cropping, and introduction of perennial grain crops (Figure 8). In agreement with this idea, meta-analyses have shown that cover cropping reduces nitrate leaching by 70% on average (Tonitto et al., 2006) and increase soil organic C by 15.5% (Jian et al., 2020), provided the cover crop is not a pure legume stand. Indeed, plant materials must have a carbon to nutrient ratio high enough to stimulate nutrient immobilization by I-microbes (Figure 2).

In view of the involvement of soil minerals in MAOM formation, the synchrony system that most crop species may generate (Sync-MAOM) is inadequate for coarse-textured soils with low mineral reactivity. This explains why ecosystem conversion to cropping induces faster and higher losses of C and N in sandy than in clay soils (Burke et al., 1989). Ancient management practices such as extensive heathland grazing and pine forestry show that sandy soils can support long-term biomass production while maintaining soil organic matter when conservative plants are

present (Figure 8; Armolaitis et al., 2013; Makineci, 2021; Rosa García et al., 2013). We suggest that the sustainability of many agrosystems or forestry systems established on coarse-textured soils may be improved by introducing conservative species. These conservative species can be grown alone or in association with acquisitive species such as annual crops. For example, cereals such as wheat could be intercropped with conservative legumes such as *Lotus corniculatus* and conservative grasses such as *Festuca ovina*, instead of intercropping with fast-growing species such as *Trifolium repens*. In these associations, the litter of conservative species will compensate for the lack of reactive soil minerals by chemically binding small organic nutrients released by microbes, preventing their leaching (Figure 3). Rhizodeposition from acquisitive crop species will foster mineralization-immobilization fluxes (Figure 2) allowing them to feed on mineral nutrients. The feasibility of such intercropping is supported by the co-existence of

resource-acquisitive and resource-conservative species within many different ecosystems, including in coarse-textured soils (Gross et al., 2017). However, research is needed to quantify the effect of such associations in an agricultural context involving disturbances and species with different traits (Milla et al., 2015). The other benefits of using conservative species could be (1) low competitive pressure for resource use when they are associated with crops and (2) maintenance of a high level of synchrony even when the ecosystem faces long periods of plant inactivity (Sync-FreeOM vs. Sync-MAOM, Figure 6). Therefore, the use of conservative species could be a way to promote agrosystem sustainability in coarse-textured soils and in situations where maintaining an active plant cover throughout the year (condition for Sync-MAOM) is not possible due to climatic, economic, or technical constraints.

By coupling complementary synchrony systems, the association of plant species with different nutrient economies (legumes/non-legumes; acquisitive/conservative; organic-P-mobilizing plants...) could increase the overall level of synchrony in agrosystems. Plant associations can be implemented over time (crop rotation) and space (intercropping) (Figure 8). The complementary effects between crop species can be facilitated by mycorrhizal networks and the resulting common nutrient market (Figure 5; Li et al., 2022), which depends on a combination of practices (Figure 8). Although current plant associations are made with limited knowledge on the nutrient economy of plants, recent meta-analyses confirm the strong positive impact of crop associations on agrosystem productivity and sustainability (Feng et al., 2021; Tang et al., 2021; Xu et al., 2020; Yu et al., 2015). For example, grain yields in annual intercropping systems have been shown to be on average 22% higher than in corresponding monocultures and have greater year-to-year stability (Li et al., 2021; Yu et al., 2015). This over-yielding can be ascribed to a soil nutrient supply better synchronized with plant demand since plant uptake of P and N increased by 24% and 15%–29% under intercropping relative to monocultures (Fan et al., 2019; Tang et al., 2021). Studies have estimated that, for the same yields, current intercropping systems can reduce the fertilizer requirement by 12% for P (Tang et al., 2021) and up to 44% for N (Xu et al., 2020). Another example is the simultaneous insertion of grain legumes and cover crops in long rotations that can reduce N fertilizer requirements by 49%–61% (depending on species) with no detrimental effect on wheat yield and grain quality (Plaza-Bonilla et al., 2017). Finally, soil C sequestration is enhanced from by the mixing of functionally different plant species, as in intercrops (+4%) (Cong et al., 2015) or agroforestry systems (from +26 to +40% depending on soil layers considered) (De Stefano & Jacobson, 2018). Until now, most of the associations tested were limited to two species, but some farmers mix more than 10 species (Figure 8). These crops are harvested as fodder or consumed on site by animals, promoting nutrient recycling and preservation of soil organic nutrient reserves over time.

We have mainly focused our discussion on plant functional diversity as the simplest, and most informed (in terms of impacts), way to increase synchrony in agrosystems. However, our framework points to other key components of synchrony such as soil diversity, plant/

microbial genotypes, and quantity/quality of organic matter inputs. Considering these components suggests other synchrony-promoting practices (Figure 8). Some are already operational such as field inoculation with microbes such as N₂-fixing bacteria, phosphate solubilizing bacteria (Afzal et al., 2010), and mycorrhizal fungi (Rillig et al., 2019; Ryan & Graham, 2018). Other promising practices require further research such as the breeding of new crop varieties/species on their suitability to association or their ability to stimulate soil nutrient fluxes (Barot et al., 2017; Litrico & Violle, 2015). By screening different wheat genotypes, it has suggested that thicker wheat roots release more carbon into soil, which enhanced soil N mineralization and thereby the supply of available N to plants (Kelly et al., 2022). Importantly, managing synchrony will systematically require a systemic approach and a combination of practices as suggested in Figure 8. For example, field inoculation with microbes will be ineffective and short-lived if it is not accompanied by other practices (e.g., reduced tillage, permanent plant cover) that will create conditions favorable to the growth and functioning of those inoculated microorganisms (Rillig et al., 2019). We also stress the importance of managing synchrony throughout the year, not just during crop growth but also during periods of low plant activity, when the risk of nutrient losses is greatest.

Significant amounts of nutrients leave croplands in the form of harvested products and/or losses through leaching and denitrification. For example, a wheat grain harvest exports an average of 120 kg of N and 30 kg of P per hectare (Debaeke et al., 1996). These exports often lead to either a decrease in available nutrients in soils, which penalizes production particularly in developing countries, or the application of synthetic fertilizer to maintain a high level of production such as in intensive cropping systems. It has been reported that approximately 50% of the applied N fertilizer is lost to the environment (Crews & Peoples, 2005; Zhang et al., 2021). Several regions of the world have adopted policies to reduce synthetic fertilizer applications as such applications seriously harm climate and ecosystem health, and deplete limited natural mineral deposits (European Commission, 2020; Stokstad, 2022). Our review suggests that practices promoting synchrony can help to decrease the quantities of synthetic fertilizers applied while maintaining, or even increasing, crop system productivity and longevity. This may result from (1) a reduction of nutrient losses (70% for N) enhancing nutrient use efficiency (Tonitto et al., 2006), (2) a better use (+22%) of water and light resources (Yu et al., 2015) by reducing the nutrient limitation of plant growth and periods of bare soil, and (3) the mobilization of nutrients from natural reserves (atmospheric N₂ and soil minerals), which can represent several hundred kilograms per hectare and per year for N (Carlsson & Huss-Danell, 2003). Managing synchrony may therefore have important implications for the economic and environmental outcomes of modern agriculture. Nevertheless, it is worth mentioning that the reservoirs of rock-derived nutrients have limits, especially in old highly weathered soils. The amount of inorganic phosphorus easily assimilable by soil–plant systems rarely exceeds 1000 kg P per hectare in natural, unfertilized soils (Legout et al., 2020), which could offset the P exports of a

wheat crop for just over 30 years. Moreover, the rates of P release into soils through rock weathering, estimated by biogeochemists at catchment scale, do not exceed 1 kg P per hectare per year, suggesting a limited capacity of soil–plant systems to mobilize nutrients from rocks (Gardner, 1990; Hartmann et al., 2014).

In cases where nutrient outputs largely exceed inputs (e.g., high biomass export without nutrient input) and the capacity of Sync-Inorganic to mobilize nutrients from atmosphere and soil minerals, the resulting decrease in soil nutrient availability is expected to stimulate microbial mineralization over microbial formation of soil organic matter (Sync-MAOM and Sync-FreeOM; Figures 2 and 3) leading to net destruction of this organic reserve (Fontaine et al., 2004; Henneron, Cros, et al., 2020; Perveen et al., 2014). With the help of synchrony systems, primary production can be maintained for decades despite high exports and the absence of nutrient recycling as shown in long-term experiments (Jenkinson et al., 1994). However, the loss of soil organic matter means that agrosystems become a source of CO₂ and that soil nutrient reserves deplete leading undoubtedly to an ecosystem decline over long term (Wardle, 2004). These studies clearly indicate that the long-term sustainability (decades–centuries) of agrosystems relies on a balance between nutrient inputs and outputs at field scale, in particular through practices promoting organic nutrient recycling (Figure 8).

To meet the Paris Agreement target of limiting temperature rises to 1.5°C above pre-industrial levels, agriculture will need to increase biomass supply for fossil fuel substitution and enable negative emissions in the second half of the century through direct greenhouse gas emission cuts and carbon storage in ecosystems (Frank et al., 2019). This is especially challenging because agriculture must also feed a growing human population. Adopting practices that promote synchrony may help achieve this goal. By improving N use efficiency and mobilizing N from the atmosphere, these practices can maintain, or even increase, biomass productions while reducing the use of mineral N fertilizers (Plaza-Bonilla et al., 2017; Tonitto et al., 2006) that generate greenhouse gas during their production and after their application in field due to enhanced soil N₂O emissions. It has been estimated that the synthetic N fertilizer supply chain is responsible for the emissions of 1.13 GtCO₂e in 2018, representing 10.6% of agricultural emissions (Menegat et al., 2022). Therefore, substituting, at least partially, synthetic fertilizer inputs by synchrony systems can be an effective strategy to reduce greenhouse gas emissions of agrosystems. Agricultural practices promoting synchrony can also reduce N₂O emissions by maintaining low concentrations of mineral N in soil. For example, a meta-analysis of mitigation measures for N₂O emissions recently indicated that the incorporation of crop residues that stimulate microbial immobilization (C/N of residues >30) (Sync-MAOM; Figure 2) can significantly decrease N₂O emissions (Abalos et al., 2022). The incorporation of perennial vegetation and their regular C supply to soil microorganisms, essential for all synchrony systems except Sync-FreeOM, would be another example of practices that can reduce mineral N content and N₂O emissions in cropping systems (Figure 8). Indeed, it has been shown that N₂O emissions are reduced between 79%

and 89% under perennial vegetation relative to annual crops (Gross et al., 2022; Tenuta et al., 2019). As described earlier, the greater nutrient retention induced by practices promoting synchrony is often associated with an accumulation of soil organic matter sequestering carbon from the atmosphere (Gross et al., 2022; Jian et al., 2020; Waithaisong et al., 2020). These results imply that managing synchrony can simultaneously reduce N₂O emissions and mitigate the increase in atmospheric CO₂. Fostering synchrony will also help to reduce N and P leaching from agrosystems that is currently leading to a global eutrophication of terrestrial and aquatic ecosystems with significant consequences for biodiversity, human health, and economic activities (Sobota et al., 2015; Yang, Boncoeur, et al., 2018).

In conclusion, some of the management practices we have identified as promoting synchrony have already been tested and shown to be effective in reducing fertilizer use and nutrient losses, as well as associated pollution such as nitrate contamination of drinking water, ecosystem eutrophication, and greenhouse gas emissions (Drinkwater & Snapp, 2022). They can also be effective in improving biomass production and soil C storage under specific conditions. The recent insights synthesized here draw out the conditions of success of these practices in terms of pedoclimatic context and combination with other practices (Figure 8). This synthesis also suggests new management options based on plant traits (e.g., amount and type of rhizodeposition, content of condensed tannins in litter) and microbial traits (including adequate traits of microbial inoculants) that should help improve agrosystem sustainability, even in the most difficult pedoclimatic conditions (e.g., sandy soils, long season without plant activity). Future priorities are to (1) integrate this scientific knowledge into tools used by practitioners for redesigning agrosystems, (2) develop methods/proxies to quantify the level of synchrony, and (3) continue efforts to fill knowledge gaps on the synchrony in various natural ecosystems. In particular, additional research is needed to better understand i) the mechanisms of FreeOM synchrony under conservative herbaceous plants, ii) the quantities and rates at which nutrients can be released or stored by the various synchrony systems, iii) the synergies and trade-offs between synchrony systems, and iv) the resistance and resilience of the different synchrony systems to disturbances (e.g., extreme climate events, plant cutting, and harvest). These advances will allow future cropping systems to better benefit from nature-based solutions (Eggermont et al., 2015) and reinforce their sustainability in a global change context.

AUTHOR CONTRIBUTIONS

Sébastien Fontaine: Conceptualization; funding acquisition; resources; writing – original draft; writing – review and editing. **Luc Abbadie:** Writing – review and editing. **Michaël Aubert:** Writing – review and editing. **Sébastien Barot:** Writing – original draft; writing – review and editing. **Juliette M. G. Bloor:** Writing – original draft; writing – review and editing. **Delphine Derrien:** Writing – original draft; writing – review and editing. **Olivier Duchene:** Resources; writing – original draft; writing – review and editing. **Nicolas Gross:** Writing – original draft; writing – review and editing. **Ludovic Henneron:** Writing – original draft; writing – review and editing. **Xavier Le Roux:** Writing – original

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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