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## **Chapter 10**

### **Unravelling the phosphorus cycling from the functional trait approach of plant-soil interactions**

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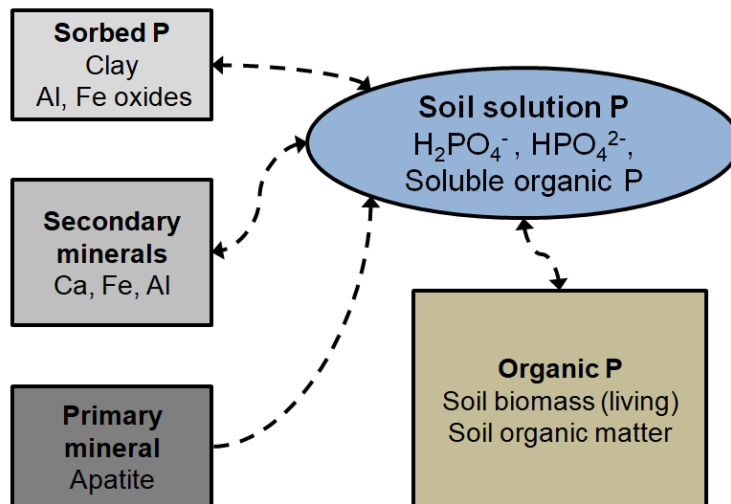
## **Abstract**

Phosphorus (P) is a key limiting element in most of the soils worldwide. This chapter provides a contemporary review on the role of plant traits in the plant-soil microorganisms processes influencing P availability in ecosystems, in order to provide insights into functionally optimal vegetation (or crops) designs enhancing P availability and cycling efficiency. Characterising a wide range of P acquisition traits in vegetation highlighted multiple tradeoffs, notably between P mining traits and P foraging traits, while also underlining the considerable contribution of plant-soil microorganism interactions to P acquisition. The spectrum of diverging P acquisition strategies identified could underpin complementary multispecies vegetation and crops designs. The examination of the role of litter or crop residue traits on P release from residues and its impact on P availability offered precious insights into the soil and microbial dynamics involved and the central role of residue C:P ratio. The effects of vegetation or crops on P availability via P release from residues were however shown to be highly mediated by soil P availability, suggesting different locally adapted vegetation and crops designs. The new understanding gained on the effects of vegetation and crops on P availability via their diverse traits and strategies for P acquisition, the impact of their traits on P release from residue, and its mediation by soil properties could constitute a sound basis for modelling vegetation effects on P availability and develop decisions support systems.

**Keywords** Agroecology, Belowground functional traits, Functional ecology, Phosphorus acquisition, Plant-microorganism interactions, Plant-soil feedback, Plant-soil interactions

## **1. Introduction**

Phosphorus is a limiting nutrient in most of the soil worldwide. Even in primarily nitrogen limited soils often occurring in Western Europe, phosphorus is often the second most limiting element for plant growth (Vance 2001). Phosphorus is essential for life, playing a central role in plant energy production via molecules of adenosine triphosphate (ATP), but also being a key building element for proteins or even deoxyribonucleic acid (DNA). Phosphorus in soil is present in a multitude of different inorganic and organic forms (Fig. 1) which differ in their ability for plants.



**Figure 1 Phosphorus pools in soil**

Only inorganic phosphorus in solution is directly available for plant uptake. Most of soil phosphorus is however present as insoluble precipitated or fixed forms, with only a small fraction of this pool of insoluble phosphorus being labile and in equilibrium with the soil solution (Stutter et al. 2012; Pierzynski et al. 2015). Phosphorus is strongly and quickly adsorbed to soil constituents, especially in soil with high iron and aluminium oxides, clay or organic matter content. Phosphorus may also precipitate with cations (Al, Fe, Ca), forming insoluble, poorly plant available phosphorus forms. Phosphorus is thus very immobile in soil due to reactions with multiple soils constituents. Phosphorus sorption/desorption dynamics and precipitation with soil constituents are influenced by multiple soil properties, especially soil pH.

Phosphorus availability tends to be higher soils with neutral pH. With increasing soil acidity, aluminium and iron become increasing soluble and then precipitate with phosphorus, reducing its solubility. By contrast, in alkaline soil, P may precipitate with calcium and magnesium, which in turn decreases phosphorus availability (Mengel et al. 2001). A significant amount of soil phosphorus can be present in organic forms, 30 to 65 % of total phosphorus (Condon et al. 1990). Organic phosphorus as for inorganic phosphorus can be tightly bound to soil components, making it inaccessible to plants. Organic phosphorus, specifically, needs to undergo mineralization through enzymatic action by plants or microorganisms before it can be utilized. The mineralization of organic phosphorus is also influenced by soil pH. As a result, the distribution of phosphorus pools in the soil is uneven both chemically and spatially due to its limited mobility (Amadou et al. 2021; Bai et al.

2021). The effective management of phosphorus availability, considering its chemical, temporal, and spatial aspects, poses a significant challenge in agroecology. Various organic forms of phosphorus, including phosphomonoesters, phosphodiesteres, nucleic acids, and organic polyphosphates, are present in organic inputs and soil. However, their specific chemical properties and behavior are not well understood, making it difficult to determine their availability to plants. The interplay between plants, soil microbes, and organic phosphorus regulation is crucial, but the mechanisms involved, especially under field conditions, remain unclear. Soil microbes greatly influence the amounts and turnover of organic phosphorus, while plants employ strategies such as increased root growth, specialized roots, high-affinity phosphate transporters, root exudates, and interactions with rhizosphere microbes to enhance phosphorus availability. Nonetheless, the mechanisms by which these strategies enable plants to access organic phosphorus are not fully comprehended (Amadou et al. 2021, 2022; Condrón et al. 2005). The hydrolysis and release of organic phosphorus through enzymatic activity depend on the chemistry of the organic phosphorus compounds, soil properties, and rhizosphere microbes. Organic phosphorus compounds adsorbed to mineral surfaces may not be readily available to plants, potentially limiting plant growth. The solubility and availability of these compounds, particularly in the presence of major soil minerals, are still subject to debate (Amadou et al. 2021). Further research is necessary to understand the temporal changes in organic phosphorus compounds, their interactions with soil minerals, and their influence on the phosphorus cycle within ecosystems (Amadou et al. 2022b). Enhancing our understanding of organic phosphorus will help in the utilization of renewable phosphorus fertilizers and improve phosphorus availability for crops (D'Amico et al. 2020). Overall, the fate of organic phosphorus through the soil-plant system presents uncertainties and challenges that warrant comprehensive investigation.

Due limited phosphorus availability in most contexts, important phosphorus inputs are required to ensure productivity in cultivated systems (Menezes-Blackburn et al. 2018). Most historical agriculture practices relied on saturating soil phosphorus fixing capacity in order to maintain optimum level of available phosphorus concentration (Fox and Kamprath 1970). Fertilization in these systems originates from non renewable, geographically uneven resources of rock phosphate, the source of many concerns for sustainable and equitable use of these resources (Richardson et al. 2011). Over-fertilization to compensate for soil phosphorus fixation led overtime to build up of a stock of poorly available “legacy”

phosphorus pools in soils (Liu et al. 2015; Menezes-Blackburn et al. 2018). Improving phosphorus efficiency requires reducing fertilizer loads, increasing phosphorus recycling and use efficiency but also exploiting the stock of legacy phosphorus in soils (Simpson et al. 2011).

Plants are the central drivers of many mechanisms involved in the biogeochemical cycling of phosphorus in agroecosystems. Via efficient use of the diverse pools of phosphorus in soil, plants can offer to increase phosphorus cycling efficiency in agroecosystems (Lynch 2015; Menezes-Blackburn et al. 2018). Plants influence phosphorus cycling via three main mechanisms: i) Phosphorus acquisition by plants via phosphorus foraging and mobilization; ii) Interactions with soil microorganisms mediating phosphorus availability in the plant soil microbes system; iii) Release of phosphorus contained in plants residues after destruction or harvest.

## **2. Phosphorus uptake by plants**

Only inorganic phosphorus in solution is directly plant available (Schachtman et al. 1998). However due to low phosphorus availability in many soil contexts, plants have developed several strategies to acquire phosphorus from the diverse soil phosphorus pools which remain to be fully explored (Lynch 2011). These strategies can be grouped in two main phosphorus acquisition strategies: phosphorus foraging strategies and phosphorus mining strategies. Phosphorus foraging strategies rely on maximised soil scavenging for phosphorus acquisition, i.e. exploring a large soil volume to capture available phosphorus. This can be achieved through different plant strategies. In order to forage a larger soil volume, plants can invest more in their root biomass (Hermans et al. 2006). When faced with low phosphorus availability plants with higher root/shoot ratio tend to perform better (Nielsen et al. 2001) and acquire more phosphorus (Steingrobe et al. 2001). Enhanced soil foraging capacity can also be achieved through reducing the cost of soil exploration. Fine, short-lived roots can explore larger soil volume at reduced costs allowing plants to maintain high productivity at lower level of available phosphorus (Lynch 2007). Plant phosphorus foraging capacity can also be increased via strategies increasing area of contact per root length. Plants in phosphorus limiting conditions tend to develop more root abundance and longer root hairs (Lynch 2007). As phosphorus is very immobile in soil, root hairs not only increase root area

but also allow access to pools of phosphorus that would not diffuse to roots (Fort et al. 2015). In barley, a linear relationship has been identified between root hair length and phosphorus uptake (Gahoonia and Nielsen 2004). A final plant foraging strategy can be through preferential exploration of more phosphorus rich patches. Surface horizons tend to be more concentrated in phosphorus in agroecosystems which can be exploited by plants increasing their root biomass in these horizons, as observed in peas (Liao et al. 2001). Reliance on a specific phosphorus foraging strategy is in part genetic however environmental factors such as soil type and properties also play a still unclear role in defining plant P foraging strategy (Müller and Schmidt 2004). Root hair length was for example observed to be highly responsive to soil strength and porosity in barley (Haling et al. 2014).

Phosphorus mining strategies rely on mobilizing chemically unavailable phosphorus. In order to mobilize this phosphorus, plants can impact several processes driving phosphorus availability. Phosphorus adsorption/desorption equilibrium can be influenced by exudation of carboxylates which compete with phosphorus for adsorption sites on to mineral surfaces or form complexes with cations such as iron and aluminium which in turn affects mineral dissolution rate (Lambers et al. 2006; Richardson et al. 2011; Wang and Lambers 2020). Phosphorus precipitates can be dissolved via proton release by plants, which is especially relevant for calcium phosphate precipitates. Plants may also stimulate the mineralization of organic phosphorus by secreting enzymes such as phosphatase which leads to the release of plant available inorganic phosphorus and may strongly contribute to total plant uptake (Kroehler and Linkins 1988). Finally, a last phosphorus mining strategy consists in the formation of cluster roots. Cluster roots combine phosphorus foraging strategies and phosphorus mining strategies. As such they tend to express high fine roots, surface area, root hair length and abundance, as well as high root exudations to access pools of hardly available soil phosphorus. As for phosphorus foraging strategies, P mobilization by plants can be affected by multiple environmental factors such as phosphorus availability, pH or soil type (Pearse et al. 2006; Li et al. 2007). However, the relative effects of all these factors need to be fully investigated to gain a better understanding of plant phosphorus acquisition.

### **3. Role of plant – soil microorganisms interactions for phosphorus acquisition**

Soil microorganisms are key drivers of phosphorus cycling in agroecosystems, strongly contributing to several processes affecting phosphorus availability such as organic matter mineralization or phosphorus mobilization (Richardson et al. 2011). Soil microbial

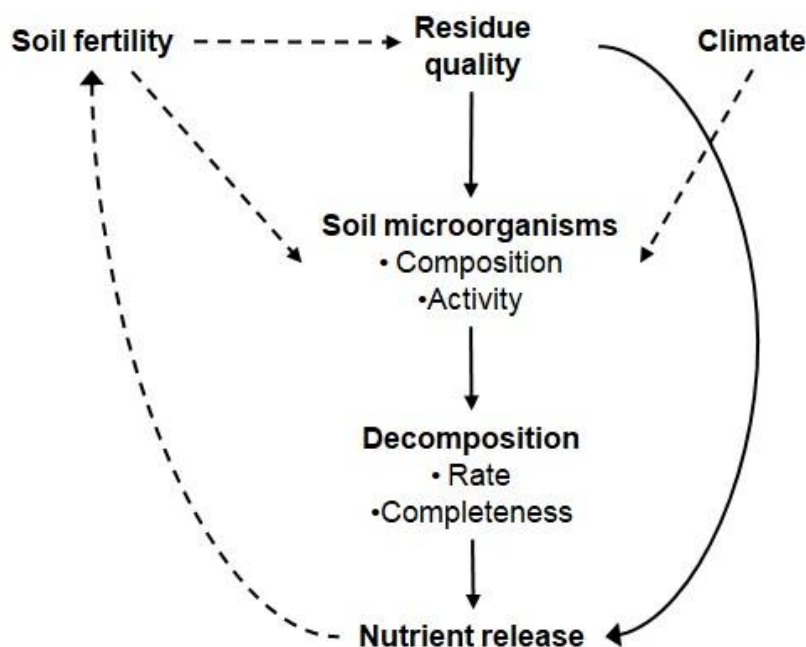
communities in the rhizosphere of plants are not directly under plant control, with soil properties (pH, clay content, organic matter, ...) and native soil microbial communities being important determining factors (Hunter et al. 2014). However, plants may have considerable impact on soil microbial community and functions, especially in their rhizosphere (Hunter et al. 2014). Association or colonization of roots by Arbuscular Mycorrhizal Fungi (AMF) is the best known plant soil-microorganisms interaction for phosphorus acquisition. As much as 80 % of plant species are involved in association with AMF (Schüßler 2002). Through this association, fungi and plants interact with plants providing sugar to the fungi in exchange for water and nutrients (Willis et al. 2013). Association with AMF allows plant to forage phosphorus from an important soil volume, up to 25 cm away from the roots (Smith and Read 2010). Up to 75 % of annual phosphorus uptake by plants can be through association with AMF (van der Heijden et al. 2008). In addition to foraging for available phosphorus, there is recent evidence that AMF can contribute to mobilizing soil phosphorus, either by increasing organic phosphorus mineralization or via their own interactions with bacterial communities (Sato et al. 2015; Zhang et al. 2016, 2018). AMF contribution to plant phosphorus uptake is however strongly impacted by soil phosphorus availability (Grman and Robinson 2013). Maximum benefits from association with AMF are observed in contexts with low available phosphorus concentrations while negative impacts on plant growth have been reported in contexts with high available phosphorus concentrations due to the carbon cost of this association for the plant (Johnson et al. 1997).

Interactions with bacterial communities can also strongly contribute to phosphorus uptake. Many plant exudates including carboxylates are quickly metabolised in soil and play the role of a carbon source for rhizosphere bacteria possibly influencing bacterial functions and communities (Marschner et al. 2002; Paterson et al. 2007; Adeleke et al. 2017). In turn, rhizosphere bacteria subsequently influence phosphorus availability in the rhizosphere. Between 1 and 50 % of rhizosphere bacteria are phosphorus solubilising bacteria (Kalayu 2019), potentially mobilizing phosphorus from poorly available sources and benefiting plant phosphorus uptake. Several genera of rhizobacteria are known to release phosphatase and phytase, contributing to mineralization of organic phosphorus (Krey et al. 2011; Mukhametzhanova et al. 2012; Miao et al. 2013). Precise microbial components associated with phosphorus solubilisation are however not well known and likely to vary depending on environmental conditions and other factors (Hunter et al. 2014). Rhizosphere microbial communities are influenced by soil type and plant age for example (Marschner 2001; Smalla

et al. 2001). In addition, microbial communities can also influence phosphorus uptake by plants through eliciting plant defence pathways (Hammond 2004). Phosphorus deficiency responses in roots are indeed regulated via general stress response pathways as well as phosphorus specific responses (Hammond 2004). Rhizosphere microbial communities via eliciting plant defence pathways may thus increase plant phosphorus uptake (Yao et al. 2011). Overall plant microbial interactions for phosphorus acquisition are highly complex and quickly evolving leading to still not fully understood consequences on phosphorus cycling (Hunter et al. 2014). Exploring these interactions and selecting for beneficial plant characteristics could improve phosphorus uptake capacity (Richardson et al. 2011).

#### 4. Phosphorus release from litter and crop residues

Phosphorus release from crop residues is a complex process involving multiple steps and influenced by many factors such as climate, soil properties, residue quality and microbial communities (Prescott 2005). As for carbon, the release of phosphorus from residues and its effects on phosphorus availability in soil follows a two stage pattern : a rapid initial release of labile phosphorus then followed by a longer phase of slow phosphorus release from recalcitrant organic phosphorus sources in biomass (Umrit and Friesen 1994; Jalali and Ranjbar 2009; Damon et al. 2014) (Fig. 2).



**Figure 2 Diagram of phosphorus release from residue. Adapted from Prescott (2005)**

Fast initial release of phosphorus is generally in the form of inorganic phosphorus (orthophosphate) even though, to a lesser extent, some easily decomposed organic phosphorus forms can also be quickly released. Between 35 to 75 % of the total phosphorus in crop can be present as orthophosphate and is easily leached to soil during residue decomposition (Noack et al. 2012). Phosphorus speciation in residue however can change considerably with vegetative stage (Noack et al. 2012; Damon et al. 2014), resulting in different phosphorus release dynamics. Soil microorganisms play a central role in phosphorus release from residue, not only due to their implication in residue mineralization but also by being more competitive than plants for soil phosphorus uptake. Depending on residue quality, phosphorus can either be quickly mineralized by microorganisms or immobilized in microbial biomass. Residue where quality meets microbial demands are quickly mineralized whereas if microbial demands are not met, important microbial immobilization of phosphorus from soil solution can occur. Phosphorus immobilized in microbial biomass is then released by microbial turnover. Microbial turnover times range from days to months (Spohn and Widdig 2017) depending on many factors, including even soil and climate properties (Oberson and Joner 2005; Achat et al. 2010). Recalcitrant phosphorus contained in residue is slowly mineralized over time during the second phase of residue phosphorus release. A significant proportion of the phosphorus involved in this process can however be only partly degraded and converted to recalcitrant organic phosphorus forms (Oliveira et al. 2017). Phosphorus captured by plants and later released could significantly contribute to phosphorus availability in cropping systems. However, our understanding of phosphorus release dynamics remains limited with wide uncertainty on the key parameters involved (Damon et al. 2014).

Although the main mechanisms influencing the role of plants in phosphorus cycling in agroecosystems have been identified, many unknowns remain on the underlying processes and their relative contribution and agronomical significance across different contexts or species, which can prove to be challenging when attempting to design agroecosystems for improved phosphorus availability (Simpson et al. 2011; Hunter et al. 2014; Menezes-Blackburn et al. 2018). Further investigations are needed to quantify the functions ensured by plants in P cycling and highlight the key plant characteristics involved irrespective of local context or species.

## **5. Trait based approach of phosphorus cycling in agroecosystems**

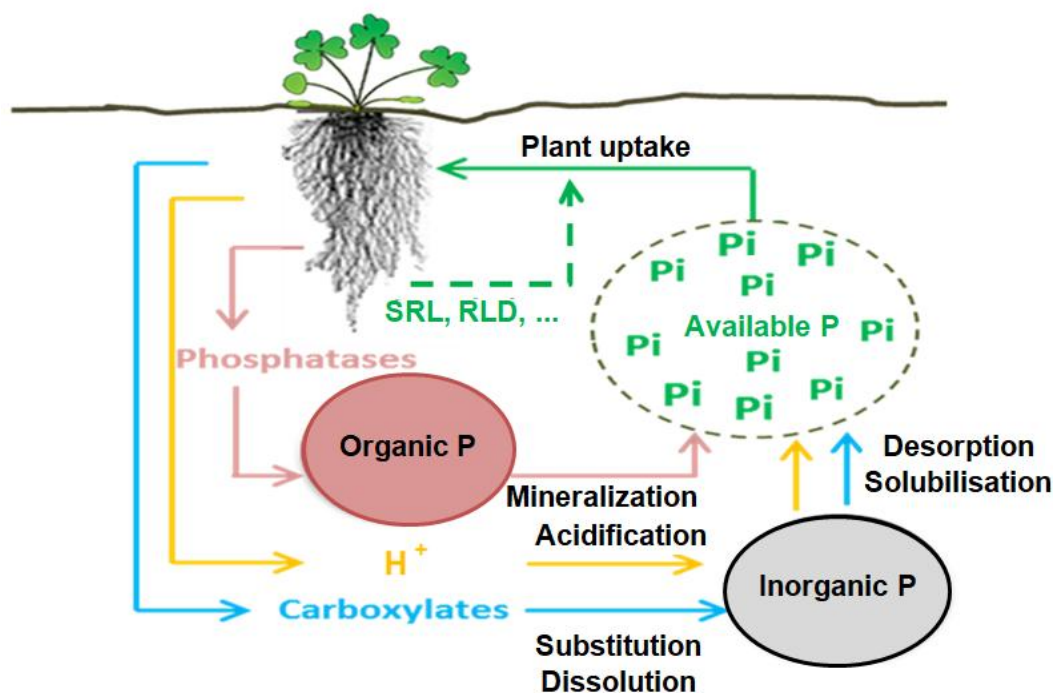
Investigating the role and potential benefits of plants in phosphorus cycling in agroecosystems requires approaches able to highlight and evaluate the influence of plant characteristics on ecosystem processes. Functional ecology offers to examine the response and effects of plant characteristics, namely plant traits, on ecosystem processes (Lavorel and Garnier 2002). Plant traits can be defined as “any morphological, physiological or phonological feature measurable at the individual level, from the cell to the whole organism, without reference to the environment or any level of organisation” (Violle et al. 2007).

Highlighting the plant characteristics or traits involved in plant phosphorus acquisition, directly or via interactions with soil microorganisms, and later release from plant residues and quantifying their effects is key to deepen our knowledge of phosphorus cycling in agroecosystems and design functionally efficient cropping systems and practices (Richardson et al. 2011; Faucon et al. 2017; Schneider et al. 2019).

Plant functional traits influence on phosphorus cycling has received more and more attention recently, with efforts focused on identifying plant traits and strategies leading to improve phosphorus use efficiency in agrecosystems (Richardson et al. 2011; Menezes-Blackburn et al. 2018; Hallama et al. 2019). Gaining a better understanding of the effects of plant functional traits and strategies on soil properties is indeed required in order to achieve desired ecosystem services (Faucon et al. 2017). Highlighting traits or strategies of interest could offer agronomical levers for agroecological intensification.

### ***5.1 Effects of plant functional traits on plant phosphorus acquisition***

Multiple plants morphological, architectural and physiological traits have been highlighted to offer proxy to plant phosphorus acquisition strategies (Fig. 3).



**Figure 3 Role of plant traits in phosphorus acquisition** (adapted from Li et al. (2014))

Plant morphological and architectural traits are the main drivers of plant phosphorus foraging capacity. Plants with high SRL, low root diameter, RDMC and RTD can forage a large soil volume at a relatively lower cost per volume explored (Vance et al. 2003; Schroeder and Janos 2004; Lugli et al. 2020). SRL was for example observed to increase in *Brassica napus* when faced with phosphorus deficiency (Lyu et al. 2016). Preferential foraging of a certain soil volume can be achieved through higher RLD or root branching in this volume (Nanzyo et al. 2002; Postma et al. 2014). Under phosphorus limited condition *Trifolium subteraneum* was observed to adapt by increasing its RLD (Haling et al. 2018).

Plant capacity to mine unavailable phosphorus is driven by multiple physiological traits, mostly involved plant exudation. Root carboxylate exudation, while being challenging to measure in the fields (Oburger and Jones 2018), offers a proxy for strategies influencing phosphorus sorption/desorption dynamics. Malate and citrate are the two most abundant carboxylates released by plants (Neumann and Römheld 1999; Pearse et al. 2006). Their release rate has been observed to increase in phosphorus efficient plants under phosphorus limiting condition (Hoffland et al. 1989; Yan et al. 2004; Shahbaz et al. 2006). Release rates of malate and malonate have also been observed to relate with soil microbial communities in interaction with plant phosphorus acquisition (Honvault et al., 2021a). Plants can influence

soil pH through another physiological trait, that is root proton release which aims at dissolving precipitated phosphorus such as calcium phosphate precipitates. *Fabaceae* are known to strongly influence rhizosphere pH (Maltais-Landry 2015) leading to dissolution of precipitated phosphorus in basic soils (Hinsinger et al. 2011). Plant capacity to access organic phosphorus in soil and to contribute to its mineralization can be measured via traits such as phosphomonoesterase release (PME) (Lambers et al. 2006). Species exhibiting higher PME release or activity in the rhizosphere such as *Brassica napus* have been observed to benefit more from organic fertilizer such as sewage sludge (Nobile et al. 2019).

Morphological and physiological traits in turn tend to be part of tradeoffs due to their carbon cost for the plant (Lynch and Ho 2005; Walk et al. 2006; Ma et al. 2018). A spectrum of phosphorus acquisition strategies centred around trade-offs axis between plant morphological traits denoting high phosphorus foraging capacity and plant physiological traits associated with phosphorus mining and interactions with microorganism has been proposed (Honvault et al., 2021b; Lyu et al. 2016; Wen et al., 2019; Wendling et al., 2016). However, tradeoffs and strategies are plastic to soil phosphorus availability and soil type (Honvault et al., 2021b, Wen et al., 2019) and the effects of tradeoffs and plant functional phosphorus acquisition strategies on phosphorus acquisition and cycling remain to be fully explored (Wen et al., 2019).

## **5.2 Effects of plant traits on soil microbial communities and phosphorus availability**

Relationships between plant traits and soil microbial communities for plant phosphorus acquisition remain uncertain and poorly understood (Hunter et al. 2014). Plant carboxylate exudation rate has been identified to indicate root presence to microbial partners. Many soil-borne microorganisms such as bacteria and AMF follow gradient of exudates including carboxylates to roots (Whipps 2001). Several carboxylates released by roots have been observed to result in specific shifts in rhizosphere microbial communities. Citrate release by plant was shown to induce shifts in microbial and bacterial communities while malate more specifically influenced bacterial communities (Marschner et al. 2002). Malonate and malate were observed to relate with bacterial communities in interaction with plant phosphorus acquisition (Honvault et al., 2021a). In *Arabidopsis thaliana*, malate produced by roots proved to select for the presence of plant growth promoting rhizobacteria (Rudrappa et al. 2008). In turn interactions between plant and microorganisms can also be identified via their feedback on plant traits such as the reduced carboxylate exudation observed in root colonized by AMF

(Ryan et al. 2012; Del-Saz et al. 2017). Plant morphological traits also can play an important role in plant-microorganisms interactions. Roots with lower diameter have for example been observed to be less associated with AMF. Finer roots have also been observed to release less exudates involved in plant-microorganism interactions (Honvault et al., 2021a). Shifts in microbial community structure and activity due to interactions with plant traits in turn influence phosphorus availability for plant uptake. Increasing evidence point toward an important role of plant traits in plant soil microorganisms interactions, however contrasting and unclear effects of plant traits and their consequences for phosphorus cycling and availability remain to be fully explored (Hunter et al. 2014; Sasse et al. 2018). Gaining a better understanding of plant traits effects on microbial communities is a major challenge but also an opportunity to potentially increase phosphorus acquisition efficiency (Richardson et al. 2011; Hunter et al. 2014).

### ***5.3 Effects of litter traits on phosphorus availability***

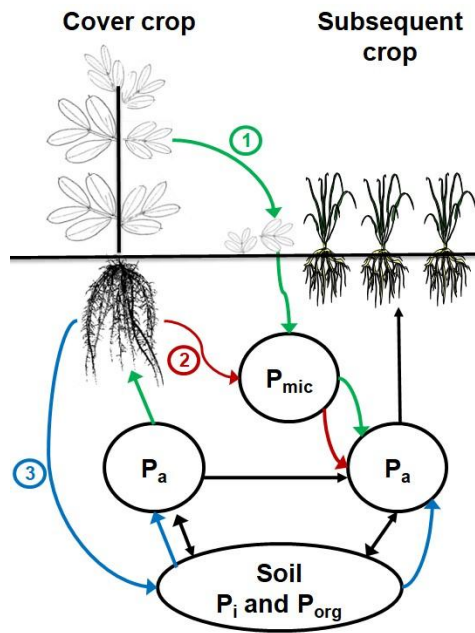
Several litter functional traits drive litter quality for decomposition and phosphorus release. Leaf phosphorus concentration in particular plays a central role in phosphorus release from litter. Concentrations above 3 mg P g<sup>-1</sup> C lead to fast release and mineralization of litter phosphorus (Kwabiah et al. 2003; Iqbal 2009). On the contrary low concentrations below 2 mg phosphorus g<sup>-1</sup> C tend to favour microbial phosphorus immobilization (Kwabiah et al. 2003; Alamgir et al. 2012). Other leaf chemical traits similarly influence the fate of residue during microbial decomposition such as leaf C:N ratio, leaf N:P ratio and leaf C:P ratio. Low attributes of these traits, below 24, 15 and 200 respectively for C:N ratio, N:P ratio and C:P ratio tend to favour fast mineralization and phosphorus release while higher values favour microbial immobilization (Prescott 2005). Leaf structural components such as lignin also strongly impact residue decomposition and nutrient release (Prescott 2010). Morphological and physical leaf traits influence on phosphorus release from litter have received less attention except for SLA (Zukswert and Prescott 2017). These traits could play an important role in phosphorus release due to their implication in defining litter accessibility to decomposers (Zukswert and Prescott 2017). Leaves with high toughness for example decompose and release nutrient slower than leaves with low toughness (Pérez-Harguindeguy et al. 2013). Our understanding of the role of plant traits in phosphorus release from litter remains limited despite many factors being identified (Damon et al. 2014).

## **6. Increasing phosphorus availability and cycling via trait-based agroecological practices**

Incorporating more phosphorus efficient plant in cropping systems could increase phosphorus availability and cycling efficiency (Menezes-Blackburn et al. 2018). Increased phosphorus efficiency can be achieved via genetic modification or breeding (Richardson et al. 2011). However, some agroecological practices such as intercropping or cover cropping also offer the potential to incorporate phosphorus efficient plant in cropping systems.

### ***6.1 Roles and benefits of cover crops in phosphorus cycling***

Cover crops also sometimes named intermediate crops are non harvested crops grown during the off season and providing a range of ecosystems services such as reduced erosion, fixation of atmospheric nitrogen or increased carbons storage (Schipanski et al. 2014; Daryanto et al. 2018). These crops are generally terminated either mechanically, chemically or via freezing before being left to decompose in the field. The effects of cover crops on nitrogen dynamics are well documented. However, despite gaining increased interest for their potential to improve phosphorus availability and cycling efficiency, cover crops effects on phosphorus dynamics have been rarely addressed (Hallama et al. 2019). Cover crops can significantly increase phosphorus availability and phosphorus uptake in subsequent crop through three main mechanisms: i) Phosphorus acquisition by cover crops and later release during decomposition; ii) Shifts in microbial communities and activity leading to improve phosphorus availability in subsequent crops; iii) Lasting mobilization of soil phosphorus pools (Fig. 4).



**Figure 4 Pathway of cover cropping effects on phosphorus availability for subsequent crops** (adapted from (Hallama et al. 2019))

Cover crops can acquire phosphorus pools unavailable to cash crops in rotation (Nuruzzaman et al. 2005; Lambers et al. 2013; Dube et al. 2014). Cover crops species present a variety of phosphorus acquisition traits forming multiples strategies to forage for available soil phosphorus (Wendling et al. 2016) but also mobilize poorly available phosphorus. Through these strategies, between 1 and 30 kg phosphorus  $ha^{-1}$  can be acquired in cover crops and then released during decomposition, contributing to phosphorus uptake by subsequent crops (Damon et al. 2014; Maltais-Landry and Frossard 2015; Wendling et al. 2016). Several cover crop species especially *Fabaceae* can strongly modify rhizosphere properties through their phosphorus mobilization strategies (Maltais-Landry 2015). In turn, rhizosphere modifications by cover crops such as increases in phosphatase activity by around 20 % after cover cropping, can increase phosphorus availability influencing P uptake in subsequent crop (Hallama et al. 2019). Cover crops phosphorus acquisition traits and strategies can thus strongly influence the mechanisms by which they influence phosphorus availability. Living cover crops interact with soil microbial communities potentially leading to positive feedbacks increasing phosphorus availability in the crop-rhizobiome-system (Oberson et al. 2006; Njeru et al. 2014). Shifts in microbial communities and increases in AMF populations under cover cropping can then play the role of inoculums for the subsequent crops indirectly influencing their phosphorus uptake with reports of increases of 50 % in AMF abundance and 25 % microbial phosphorus after cover cropping (Hallama et al. 2019). Despite

significant cover cropping benefits via these processes, several factors limit their use and lead to uncertain influence on phosphorus availability. Water scarcity and short growing season can reduce or negate cover cropping effects. Soil phosphorus availability is especially influential with greater effects overall in systems with lower phosphorus availability and different mechanisms and strategies being of interest in systems with high phosphorus availability (Hallama et al. 2019). Mechanisms involved in phosphorus cycling in cover crops also present complex trade-offs with other cover cropping benefits underlining the need for comprehensive approaches balancing these multiple benefits at the cost of reduced performance in individual functions (Schipanski et al. 2014). Overall cover cropping effect on phosphorus cycling depends on multiple mechanisms and factors offering opportunities for locally functionally optimal designs. However, the multiplicity of mechanisms involved in the effect of cover crops on phosphorus availability, coupled with their high variability and changing relative contributions poses complex challenges that need to be fully investigated and elucidated in order to maximise cover cropping benefits.

## ***6.2 Challenges in designing cover crops for increased phosphorus availability in agroecosystems***

Achieving functionally optimal cover crop designs increasing phosphorus availability and cycling efficiency requires fully understanding the factors involved in the multiple mechanisms contributing to cover cropping impact on phosphorus availability, starting with cover crops phosphorus acquisition strategies. Cover crop phosphorus acquisition strategies indeed play a major role in defining the mechanisms of phosphorus benefits (Hallama et al. 2019). Wendling et al (2016) identified five main phosphorus acquisition strategies in cover crops based on above and belowground functional traits. However, phosphorus mining traits such as carboxylate exudation, phosphomonoesterase release and association with soil microorganisms such as AMF were not measured in this study and require further investigation due to their potentially large role, especially in contexts with low phosphorus availability (Smith and Smith 2011). Although still to be fully explored in cover crops (Wen et al. 2019), recent efforts point toward a spectrum of phosphorus acquisition strategies aligned along central tradeoffs axis between phosphorus mining traits and phosphorus foraging traits (Honvault et al., 2021b; Wen et al., 2019). Evidence also points to similar tradeoffs between plant traits involved in phosphorus mining or foraging and association with microorganisms (Ryan et al. 2012; Chen et al. 2016). Phosphorus mining traits, such as malate and citrate release for instance appear to play a role in mediating plant-

microorganisms interactions for phosphorus acquisition, with tradeoffs with phosphorus foraging traits (Honvault et al., 2021; Marschner et al. 2002). Understanding the diverse phosphorus acquisition strategies in cover crops and the tradeoffs involved is key to maximise cover cropping benefits (Wendling et al. 2016). However the relevance of specific strategies and tradeoffs are strongly influenced by soil characteristics and especially soil phosphorus availability (Hallama et al. 2019; Honvault et al., 2021b; Wen et al., 2019). Maltais-Landry and Frossard (2015) highlighted the low influence of phosphorus mobilization on phosphorus cycling efficiency in systems with high phosphorus availability and highlighted the importance of phosphorus release from cover crop residues in that context. In contrast, low to neutral or even negative effects of cover crop residue decomposition on phosphorus availability have been observed in contexts with medium P availability due to microbial phosphorus immobilization (Hansen et al., 2022). The main factors influencing phosphorus release dynamics from cover crop residues, namely phosphorus concentration and speciation in residue, but also residue C:N and C:P ratio as well as SLA have in turn mostly been identified. However a wide range of values have been reported for these factors (Prescott 2005; Pérez-Harguindeguy et al. 2013; Damon et al. 2014), suggesting limited consensus between studies. Soil initial phosphorus availability appear to be key in determining the contribution of cover crop residues to phosphorus availability and the factors involved in these dynamics (Hansen et al., 2022). Maximising cover crops benefits for phosphorus uptake in the subsequent crops requires fully understanding phosphorus release dynamics in order to adapt cover crops management and design to ensure that phosphorus release dynamics from residue match subsequent crops requirement (Wendling et al. 2016). A few models such as the Agricultural Production Systems Simulation or the CENTURY model propose to address this issue however their data intensive design make them challenging to use at farm level (Parton et al. 1988; Keating et al. 2003; Damon et al. 2014). Moreover, the multiple mechanisms involved in cover cropping effects on phosphorus cycling still remain to be fully integrated in these models and decisions tools, suggesting further investigations of the relative contribution of processes such as rhizosphere chemical modification or interactions soil microorganisms and associated legacy effects (Hallama et al. 2019).

## **Conclusion and perspectives**

A vast array of chemical, physiological, biological and morphological traits indeed contribute to the capacity of plants to access the various pools of P in soils and thus plant influence on P cycling in agroecosystems. These traits are associated in complex tradeoffs due to the carbon cost associated with their expression. Tradeoffs between the proportion of fine roots and biological interactions with root-associated microbiome suggested diverging P acquisition strategies relying either on increased P foraging or P mobilizing capacity for P uptake. Investigating plant-soil microorganisms interactions allowed us to identify a probable additional tradeoff axis. The functional approach taken offers precious insights into the plant traits and strategies involved in this role, providing elements of understanding toward optimal crops associations designs and management for increasing P cycling efficiency in cropping systems. In turn, these new knowledges gained on the influence of plant traits on P cycling in agro and ecosystems offers to improve biogeochemical models.

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