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## Review

# Unravelling the Role of Rhizosphere Microbiome and Root Traits in Organic Phosphorus Mobilization for Sustainable Phosphorus Fertilization. A Review

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**Abstract:** Moving toward more sustainable sources for managing phosphorus (P) nutrition in agroecosystems, organic phosphorus (Po) derived from organic inputs and soil is increasingly considered to complement mineral P fertilizer. However, the dynamics of P added by organic input in soil-plant systems is still poorly understood and there is currently no clear information on how the Po composition of these amendments determines P availability through interactions with the soil microbiome and root traits. Here, we review the main mechanisms of rhizosphere microbiome and root traits governing the dynamics of organic input/soil-derived Po pools in the soil-plant system. We discuss the extent to which the major forms of Po derived from organic input/soil can be used by plants and how this could be improved to provide efficient utilization of organic inputs as potential P sources. We provide new insights into how a better understanding of the interactions between Po forms, root traits, and rhizosphere microbiomes can help better manage P fertilization, and discuss recent advances in the mobilization and recovery of Po from organic inputs. We then develop proposed strategies in agroecology that could be used to improve Po utilization, specifically by better linking plant traits and Po forms, and developing new cropping systems allowing more efficient Po recycling.

**Keywords:** agroecology; biogeochemistry; cover crops; organic inputs; organic phosphorus; plant traits; rhizosphere soil; rhizosphere microbiomes



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## 1. Introduction

Phosphorus is a limiting nutrient for the productivity of agroecosystems [1–3]. This is due to its low availability in soil which results from its low solubility and its strong affinity for mineral surfaces. Phosphorus fertilization is therefore needed to achieve high yields. Most of the P currently used in chemical fertilizers is derived from phosphate rocks [4]. These resources are unevenly distributed at the Earth's surface and, in the European Union (EU), food production is dependent on imported primary P [4,5]. Since the reserves are located in only a few places on Earth, and thus are controlled by a few countries, the EU's P supply is vulnerable to geopolitical issues with possible problems with the accessibility and price of P fertilizers in the mid-term [5]. Additionally, phosphate rock is a strategic resource whose mining can lead to occupations and armed conflicts. Moving towards more sustainable sources for managing P in cropping systems, renewable nutrient-rich organic amendments are increasingly considered to complement P fertilizers produced from phosphate rocks, not only by scientists but also by politicians and stakeholders [6]. The use of organic inputs represents a shift from a linear use of a limited resource towards a circular economy because it promotes the reduction of fossil fuel use and greenhouse gas emissions [7], while contributing to the development of new green markets [8] and jobs by promoting the conversion of waste into value-added products [9–11]. The use of organic inputs prioritises transition to sustainable agriculture, focusing on prevention of environmental impacts, through the adoption of innovative technological systems [8]. The

sustainability benefit of using renewable organic P depends on farming systems associated with low carbon emissions from renewable P traffic, such as livestock farming systems which use effluents or digestates, or other farming systems which use agro-industry coproducts at territory scale, and urban and peri-urban agriculture systems that valorize sludges. Using organic inputs as a sustainable and renewable resource is a necessity to address the socio-economic and scientific issues that have recently been raised concerning sustainable P management approaches.

Organic inputs include a wide diversity of materials, such as raw or treated livestock manure, food industry waste, urban or domestic sludge from water purification operations or wastewater treatment, raw materials, water and sewage sludge, paper, petroleum products, textiles, chemicals, bio-waste (e.g., green waste composts, organic household, or domestic waste), composted or non-composted digestates from mechanization, ashes (e.g., from biomass burning), dredging sediments, and biochars (i.e., materials resulting from the pyrolysis of certain wastes). Agronomic interest in organic inputs is well documented [12]. For instance, in France, 78% and 62% of P and N, respectively, used in agriculture derive from organic inputs [13]. However, unlike conventional P fertilizers, such as triple superphosphate, P is present in organic inputs in various inorganic and organic forms which vary in their availability to plants [14]. Most research on the fate of P applied to soil has focused on the dynamics of inorganic P (Pi). In contrast, the fate of Po forms, that can account for up to 80% of total soil P [15,16], has been neglected to date, and there remains a lack of knowledge about the contribution of these forms to plant nutrition [14]. A study by Kahiluoto et al. [17] showed that Po from organic inputs could be more available than P from chemical fertilizers. However, this availability was affected by rhizosphere microbiome and root traits [18–20]. Therefore, a better understanding of the interactions between Po forms, root traits, and rhizosphere microbiomes, can help to better manage P fertilization.

By definition, Po is any compound that contains an organic moiety in addition to P. The P atoms are covalently bonded to C via a phosphoester linkage (P–O–C), or phosphodiester linkage (C–O–P–O–C), or directly bonded to C (P–C). According to a broader definition, Po also includes phosphate which is associated with organic matter. Through the application of different technologies from sequential extractions to <sup>31</sup>P NMR spectroscopy, Po compounds have been identified and quantified in various organic inputs. This has been a major step in the better understanding of the different forms of Po and their quantities and dynamics. Globally, both organic inputs and soil contain numerous Po forms in varying amounts. Notable Po forms include phosphomonoesters (e.g., inositol phosphates), phosphodiesters, nucleic acids, and organic polyphosphates (e.g., adenosine triphosphate) [21,22]. Among these compounds, specific forms such as inositol hexakisphosphate (IHP) [23–25], glycerophosphate (GLY) [26–28], and glucose-6-phosphate (G6P) [24,29,30], are generally considered major forms. In addition to these species, several other Po forms are potentially active, but are poorly characterized and remain somewhat enigmatic [31]. Each form differs from the others by its P content and molecular size. These biochemical properties, and their associated adsorption, desorption, and hydrolyzation processes, control their fate and thus their availability to plants. The mobilization of each Po form to plants is driven by soil microbes and root traits in the soil–plant continuum [32,33]. Soil microbes living freely in the complex plant–soil system [34] can significantly control the status and turnover of Po and ultimately its availability in the soil [35]. Furthermore, in response to P deficiency, plants have developed numerous strategies that allow them to mobilize Po and assimilate Pi with greater efficiency in soils. These are mediated by morphological, physiological, biochemical, and molecular mechanisms [36,37]. These strategies consist of: (i) increased root growth, (ii) the establishment of specialized organs, (iii) the expression of high-affinity Pi transporters, (iv) the secretion of root exudates and specific enzymes [38,39], and (v) symbiotic association with the rhizosphere microbiome. It is therefore very probable that the potential of recycled P fertilizers to increase plant uptake depends not only on the forms and biochemical properties of the different Po forms,

but also on the mobilization/acquisition process by microbes and strategies (e.g., proton, carboxylate and phosphatase release) used by plants to increase P availability. Thus, to predict the availability of P in cropping systems, it is very important to consider both the characteristics of the Po forms applied to soil and the mechanisms governing their mobilization/acquisition for crop plants.

The purpose of this review is to (1) highlight the main mechanisms involved in the potential mobilization of Po from organic inputs and soil in the soil-plant system, and (2) to develop emerging strategies in agroecology which can be adopted to improve P availability in cropping systems.

## 2. Amount and Characteristics of Po in Soil and Organic Inputs

Phosphorus in soil comes from both pedogenic and anthropogenic sources, the majority of P being introduced as mineral fertilizers [40] or organic residues [41]. In addition to Pi, soil Po are an important P pool [42], especially in soils treated with organic inputs [43]. Studies which quantify Po in organic inputs and soils report different values for the amount of Po in soils, ranging from 20 to 90% of the total P pool in soils and sediments [44–48]. A random-effects meta-analysis performed by Darch et al. [49], based on different studies, showed that the contribution of Pi and Po to total P varied significantly in organic input or soil (Tables 1–4): for organic input, the contribution of Pi was found to be  $5200 \text{ mg} \cdot \text{kg}^{-1}$  compared to nearly  $4000 \text{ mg} \cdot \text{kg}^{-1}$  for the Po pools. This revealed that Po is as important in amount as Pi in soil and organic inputs. The amount of IHP, a major form of Po, reached  $1325 \text{ mg} \cdot \text{kg}^{-1}$  in organic inputs, an order of magnitude higher than in soil ( $269 \text{ mg} \cdot \text{kg}^{-1}$ ). Moreover, the percentage contribution of IHP to total Po varied across the sample types, with soil (40%) > organic inputs (30%). This is consistent with the view that IHP is preferentially stabilized in soil compared with other Po forms due to its relative recalcitrance [23] caused by its strong binding to the soil [50]. Further  $^{31}\text{P}$  NMR studies have shown that the pool of labile monoester-P compounds was the largest pool of Po [2,51,52], and that phosphonates comprised the smallest [53,54]. Most individual studies that have characterized Po in the environment have shown that total Pi and Po vary with the characteristics of the organic inputs, or soil types and properties, with Pi being more important than Po, but occurring at very similar levels in some samples (Tables 1 and 2). In soils, P forms and amounts vary with soil type [55], land use, and fertilizer history [56]. Given these large pools of Po in soil and fertilizer and the range of values (20–90% of total P) generally contained in soils and sediments [45,48], it is critical to consider Po dynamics along with Pi in order to improve P cycles in agroecosystems.

**Table 1.** Total Pi and Po forms in organic inputs. Values in parentheses are percentage of total extractable P.

N°	Organic Input	Extractant	Analysis	Total Pi	Total Po	References
1	Feces (dairy)	NaOH-EDTA	$^{31}\text{P}$ NMR	$4961 \text{ mg} \cdot \text{kg}^{-1}$ (64)	$2650 \text{ mg} \cdot \text{kg}^{-1}$ (36)	[57]
2	Manure (dairy)	NaOH-EDTA	$^{31}\text{P}$ NMR	$4231 \text{ mg} \cdot \text{kg}^{-1}$ (75)	$1396 \text{ mg} \cdot \text{kg}^{-1}$ (26)	[57,58]
3	Dairy manure–dry	NaOH-EDTA	$^{31}\text{P}$ NMR	$4736 \text{ mg} \cdot \text{kg}^{-1}$ (67)	$2342 \text{ mg} \cdot \text{kg}^{-1}$ (30)	[59]
4	Dairy manure–wet	NaOH-EDTA	Enzymatic hydrolysis	$3840 \text{ mg} \cdot \text{kg}^{-1}$ (57)	$2957 \text{ mg} \cdot \text{kg}^{-1}$ (49)	[60]
5	Dung	NaOH-EDTA	$^{31}\text{P}$ NMR	$58 \text{ mg} \cdot \text{kg}^{-1}$ (22)	$399 \text{ mg} \cdot \text{kg}^{-1}$ (40)	[61]
6	Solid manure (dairy)	NaOH-EDTA	$^{31}\text{P}$ NMR	$5731 \text{ mg} \cdot \text{kg}^{-1}$ (67)	$2848 \text{ mg} \cdot \text{kg}^{-1}$ (33)	[62]
7	Lagoon manure (dairy)	NaOH-EDTA	$^{31}\text{P}$ NMR	$19 \text{ mg} \cdot \text{kg}^{-1}$ (66)	$10 \text{ mg} \cdot \text{kg}^{-1}$ (34)	[62]
8	Cattle manure	NaOH-EDTA	$^{31}\text{P}$ NMR	$3120 \text{ mg} \cdot \text{kg}^{-1}$ (74)	$1080 \text{ mg} \cdot \text{kg}^{-1}$ (25)	[63]
9	Dairy manure	Water	$^{31}\text{P}$ NMR	$1870 \text{ mg} \cdot \text{kg}^{-1}$ (85)	$221 \text{ mg} \cdot \text{kg}^{-1}$ (15)	[60]
10	Dairy manure	$\text{NaAcNa}_2\text{S}_2\text{O}_4$	$^{31}\text{P}$ NMR	$3680 \text{ mg} \cdot \text{kg}^{-1}$ (79)	$944 \text{ mg} \cdot \text{kg}^{-1}$ (21)	[60]
11	Dairy manure	NaOH-EDTA	$^{31}\text{P}$ NMR	$3637 \text{ mg} \cdot \text{kg}^{-1}$ (77)	$964 \text{ mg} \cdot \text{kg}^{-1}$ (23)	[60]
12	Animal species (beef and dairy cattle, swine, chicken, turkey, dairy goat, horse, and sheep)	$\text{H}_2\text{O}$ , $\text{NaHCO}_3$ , $\text{NaOH}$	-	-	$500\text{--}8800 \text{ mg} \cdot \text{kg}^{-1}$	[64]
13	Broiler litter	$\text{NaHCO}_3$	$^{31}\text{P}$ NMR	$1300 \text{ mg} \cdot \text{kg}^{-1}$ (12)	$2800 \text{ mg} \cdot \text{kg}^{-1}$ (25)	[65]
14	Dairy manure	$\text{NaHCO}_3$	$^{31}\text{P}$ NMR	$2400 \text{ mg} \cdot \text{kg}^{-1}$ (35)	$890 \text{ mg} \cdot \text{kg}^{-1}$ (13)	[65]
15	Swine manure	$\text{NaHCO}_3$	$^{31}\text{P}$ NMR	$6500 \text{ mg} \cdot \text{kg}^{-1}$ (21)	$1600 \text{ mg} \cdot \text{kg}^{-1}$ (5)	[65]

**Table 2.** Total Pi and Po forms in different soil types (in mg·kg<sup>−1</sup>). Values in parentheses are percentage of total extractable P.

N°	Land Use	Extractant	Analysis	Total Pi	Total Po	References
1	Semi-arid irrigated arable soils (U.S.)	EDTA	<sup>31</sup> PNMR	141 mg·kg <sup>−1</sup> (72)	57 mg·kg <sup>−1</sup> (27)	[55]
2	Semi-arid irrigated arable soils (U.S.)	Bicarbonate	<sup>31</sup> PNMR	31 mg·kg <sup>−1</sup> (76)	7 mg·kg <sup>−1</sup> (26)	[55]
3	Grassland (Australia)	Deionised water	Enzymatic hydrolysis	1.3 mg·kg <sup>−1</sup> (36)	1.5 mg·kg <sup>−1</sup> (48)	[47]
4	Grassland (New Zealand)	NaOH-EDTA	Enzymatic hydrolysis	454 mg·kg <sup>−1</sup> (56)	23 mg·kg <sup>−1</sup> (4)	[66]
5	Clover and arable plots (Australia)	NaOH-EDTA	<sup>31</sup> PNMR	345 mg·kg <sup>−1</sup> (76)	6 mg·kg <sup>−1</sup> (2.5)	[67]
6	Grassland (U.S.)	NaOH-EDTA	<sup>31</sup> PNMR	221 mg·kg <sup>−1</sup> (82)	54 mg·kg <sup>−1</sup> (19)	[62]
7	Grassland (Netherlands)	NaOH-EDTA	<sup>31</sup> PNMR	406 mg·kg <sup>−1</sup> (56)	207 mg·kg <sup>−1</sup> (44)	[68]
8	Grassland (Ireland)	NaOH-EDTA	<sup>31</sup> PNMR	358 mg·kg <sup>−1</sup> (47)	373 mg·kg <sup>−1</sup> (54)	[69]
9	Grassland (New Zealand)	NaOH-EDTA	<sup>31</sup> PNMR	(32)	(68)	[26]
10	Grassland (England and Wales)	NaOH-EDTA	<sup>31</sup> PNMR	275 mg·kg <sup>−1</sup> (40)	480 mg·kg <sup>−1</sup> (70)	[55]
11	Grassland (England and Wales)	NaHCO <sub>3</sub>	<sup>31</sup> PNMR	18 mg·kg <sup>−1</sup> (25)	70 mg·kg <sup>−1</sup> (80)	[70]
12	Grassland (New Zealand)	NaOH-EDTA	<sup>31</sup> PNMR	500 mg·kg <sup>−1</sup> (50)	20 mg·kg <sup>−1</sup> (3)	[71]
13	Forest, grassland and arable (Germany)	NaOH	<sup>31</sup> PNMR	52 mg·kg <sup>−1</sup> (30)	149 mg·kg <sup>−1</sup> (56)	[56]
14	Grassland (England)	NaOH	<sup>31</sup> PNMR	224 mg·kg <sup>−1</sup> (50)	140 mg·kg <sup>−1</sup> (40)	[72]
15	Semi-arid grassland and arable (Canada)	H <sub>2</sub> O and NaOH	<sup>31</sup> PNMR	175 mg·kg <sup>−1</sup> (58)	117 mg·kg <sup>−1</sup> (42)	[73]
16	Grassland (U.S.)	NaOH-EDTA	<sup>31</sup> PNMR	23 mg·kg <sup>−1</sup> (20)	66 mg·kg <sup>−1</sup> (67)	[74]
17	Arable (Canada)	NaOH-EDTA	<sup>31</sup> PNMR	504 mg·kg <sup>−1</sup> (73)	370 mg·kg <sup>−1</sup> (48)	[75]
18	Grassland (New Zealand)	NaOH-EDTA	<sup>31</sup> PNMR	620 mg·kg <sup>−1</sup> (54)	465 mg·kg <sup>−1</sup> (45)	[71]
19	Burkina Faso Arable Lixisol	NaOH-EDTA	<sup>31</sup> PNMR	19 mg·kg <sup>−1</sup> (23)	-	[53]
20	Madagascar Arable Ferralsol	NaOH-EDTA	<sup>31</sup> PNMR	50 mg·kg <sup>−1</sup> (54)	15 mg·kg <sup>−1</sup> (12)	[53]
21	Australia Grassland Alfisol	NaOH-EDTA	<sup>31</sup> PNMR	35 mg·kg <sup>−1</sup> (39)	16 mg·kg <sup>−1</sup> (17)	[53]
22	Germany Arable Luvisol	NaOH-EDTA	<sup>31</sup> PNMR	249 mg·kg <sup>−1</sup> (74)	35 mg·kg <sup>−1</sup> (13)	[53]
23	Switzerland 2 Arable Luvisol	NaOH-EDTA	<sup>31</sup> PNMR	228 mg·kg <sup>−1</sup> (66)	36 mg·kg <sup>−1</sup> (12)	[53]
24	Switzerland 3 Grassland Cambisol	NaOH-EDTA	<sup>31</sup> PNMR	121–396 mg·kg <sup>−1</sup> (36–66)	8–206 mg·kg <sup>−1</sup> (1–17)	[53]
25	Different soils	-	-	-	(>55)	[76]
26	Caribou soil with conventional cultivation history	NaOH	Enzymatic hydrolysis	1162 mg·kg <sup>−1</sup>	330 mg·kg <sup>−1</sup>	[77]
27	Caribou soil with manure application history	NaOH	Enzymatic hydrolysis	966 mg·kg <sup>−1</sup>	249 mg·kg <sup>−1</sup>	[77]
28	Swine manure		Enzymatic hydrolysis	173 mg·kg <sup>−1</sup>	235 mg·kg <sup>−1</sup>	[77]

Table 3. Amount of Pi and Po species in organic input.

Pi Forms			Po Forms						
			Phosphomonoesters		Phosphodiester				
N°	Organic Input	Orthophosphate Pyrophosphate Polyphosphate	IHP	Labile	Phospholipids	DNA/ Polynucleotide	Other	Phosphanate	Unidentified
1	Feces (dairy)	4961 mg·kg <sup>-1</sup>	1325 mg·kg <sup>-1</sup>	624 mg·kg <sup>-1</sup>	423 mg·kg <sup>-1</sup>	154 mg·kg <sup>-1</sup>	113 mg·kg <sup>-1</sup>	73 mg·kg <sup>-1</sup>	-
2	Manure (dairy)	4231 mg·kg <sup>-1</sup>	496 mg·kg <sup>-1</sup>	503 mg·kg <sup>-1</sup>	210 mg·kg <sup>-1</sup>	108 mg·kg <sup>-1</sup>	83 mg·kg <sup>-1</sup>	55 mg·kg <sup>-1</sup>	-
3	Dairy manure dry	4736 mg·kg <sup>-1</sup>	268 mg·kg <sup>-1</sup>	204 mg·kg <sup>-1</sup>	-	24 mg·kg <sup>-1</sup>	-	-	1842 mg·kg <sup>-1</sup>
4	Dairy manure wet	3840 mg·kg <sup>-1</sup>	678 mg·kg <sup>-1</sup>	608 mg·kg <sup>-1</sup>	-	434 mg·kg <sup>-1</sup>	-	-	1237 mg·kg <sup>-1</sup>
5	Dung	5–24 mg·kg <sup>-1</sup>	61–106 mg·kg <sup>-1</sup>	-	40–103 mg·kg <sup>-1</sup>	58–90 mg·kg <sup>-1</sup>	-	0–2 mg·kg <sup>-1</sup>	-
6	Solid manure (dairy)	5731 mg·kg <sup>-1</sup>	1338 mg·kg <sup>-1</sup>	1236 mg·kg <sup>-1</sup>	154 mg·kg <sup>-1</sup>	77 mg·kg <sup>-1</sup>	-	231 mg·kg <sup>-1</sup>	43 mg·kg <sup>-1</sup>
7	Lagoon manure (dairy)	19.1 mg·kg <sup>-1</sup>	3.2 mg·kg <sup>-1</sup>	5.9 mg·kg <sup>-1</sup>	0.3 mg·kg <sup>-1</sup>	0.3 mg·kg <sup>-1</sup>	-	-	-
8	Cattle manure	3120 mg·kg <sup>-1</sup>	500 mg·kg <sup>-1</sup>	140 mg·kg <sup>-1</sup>	220 mg·kg <sup>-1</sup>	220 mg·kg <sup>-1</sup>	-	-	-
9	Dairy manure	1870 mg·kg <sup>-1</sup>	0	136 mg·kg <sup>-1</sup>	-	18 mg·kg <sup>-1</sup>	67 mg·kg <sup>-1</sup>	85 mg·kg <sup>-1</sup>	-
10	Dairy manure	3680 mg·kg <sup>-1</sup>	444 mg·kg <sup>-1</sup>	369 mg·kg <sup>-1</sup>	-	51 mg·kg <sup>-1</sup>	81 mg·kg <sup>-1</sup>	131 mg·kg <sup>-1</sup>	-
11	Dairy manure	3637 mg·kg <sup>-1</sup>	444 mg·kg <sup>-1</sup>	385 mg·kg <sup>-1</sup>	-	45 mg·kg <sup>-1</sup>	90 mg·kg <sup>-1</sup>	-	-

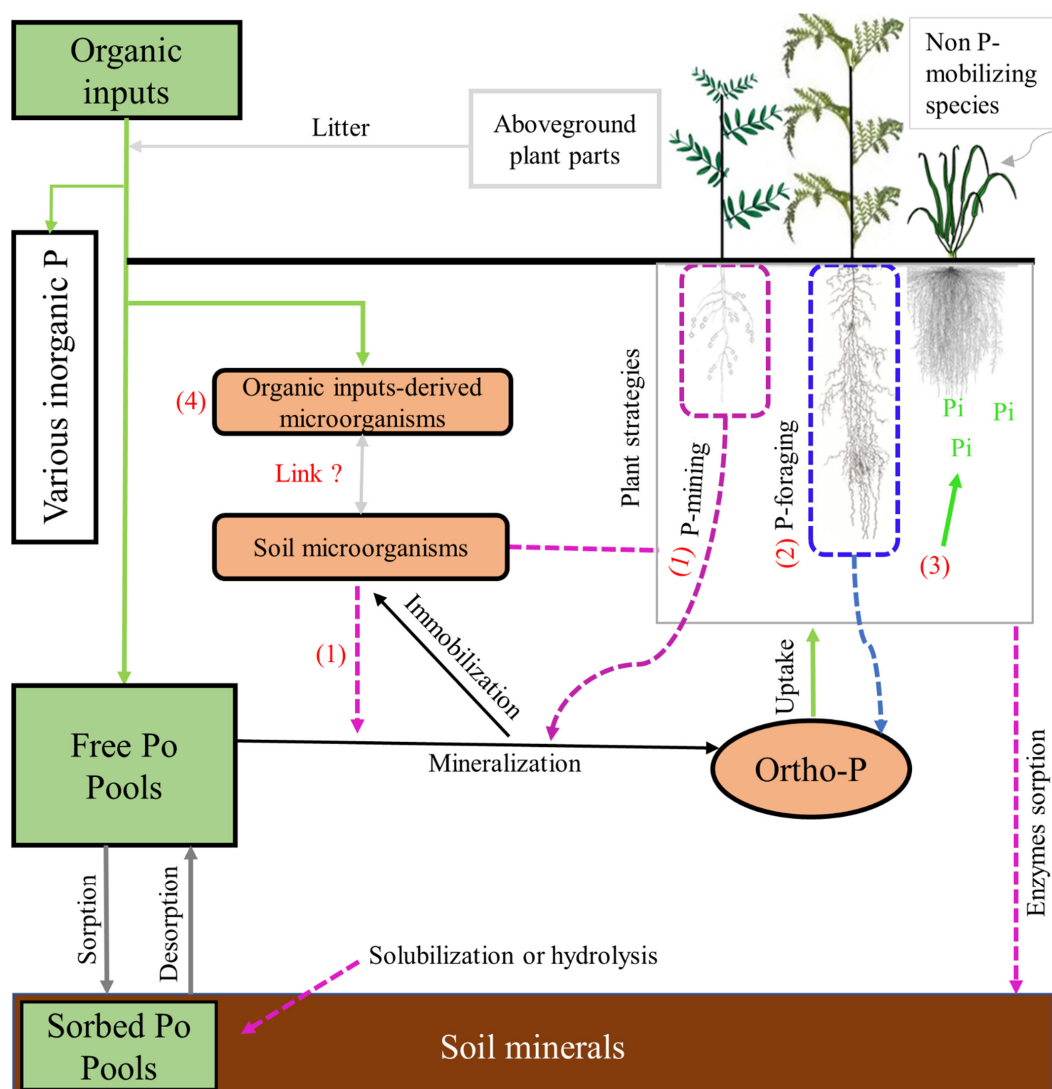
Table 4. Amount of Pi and Po species in soil.

Pi Forms			Po Forms					
			Phosphomonoesters		Phosphodiester		Other P Forms	
Soil Types	Orthophosphate Pyrophosphate Polyphosphate	IHP	Labile	Phospholipids	DNA/ Polynucleotide	Phosphanate	Unidentified	
1	Semi-arid irrigated arable soils (U.S.)	150 mg·kg <sup>-1</sup>	45 mg·kg <sup>-1</sup>	10 mg·kg <sup>-1</sup>	1 mg·kg <sup>-1</sup>	0.3 mg·kg <sup>-1</sup>	1.3 mg·kg <sup>-1</sup>	-
2	Semi-arid irrigated arable soils (U.S.)	31 mg·kg <sup>-1</sup>	1.6 mg·kg <sup>-1</sup>	1.4 mg·kg <sup>-1</sup>	0.1 mg·kg <sup>-1</sup>	0.9 mg·kg <sup>-1</sup>	1 mg·kg <sup>-1</sup>	2.2 mg·kg <sup>-1</sup>
3	Grassland (Australia)	1.3 mg·kg <sup>-1</sup>	0.28 mg·kg <sup>-1</sup>	0.04 mg·kg <sup>-1</sup>	0.2 mg·kg <sup>-1</sup>	0.03 mg·kg <sup>-1</sup>	0.23 mg·kg <sup>-1</sup>	0.8 mg·kg <sup>-1</sup>
4	Grassland (New Zealand)	454 mg·kg <sup>-1</sup>	221 mg·kg <sup>-1</sup>	100 mg·kg <sup>-1</sup>	5 mg·kg <sup>-1</sup>	5 mg·kg <sup>-1</sup>	9.5 mg·kg <sup>-1</sup>	-
5	Clover and arable plots (Australia)	345 mg·kg <sup>-1</sup>	40 mg·kg <sup>-1</sup>	14 mg·kg <sup>-1</sup>	3 mg·kg <sup>-1</sup>	2.5 mg·kg <sup>-1</sup>	-	-
6	Grassland (U.S.)	221 mg·kg <sup>-1</sup>	37 mg·kg <sup>-1</sup>	11 mg·kg <sup>-1</sup>	0.1 mg·kg <sup>-1</sup>	1.8 mg·kg <sup>-1</sup>	0	-
7	Grassland (Netherlands)	406 mg·kg <sup>-1</sup>	150 mg·kg <sup>-1</sup>	56 mg·kg <sup>-1</sup>	0.3 mg·kg <sup>-1</sup>	0.1 mg·kg <sup>-1</sup>	-	-
8	Grassland (Ireland)	353 mg·kg <sup>-1</sup>	239 mg·kg <sup>-1</sup>	100 mg·kg <sup>-1</sup>	-	16.4 mg·kg <sup>-1</sup>	3.2 mg·kg <sup>-1</sup>	-
9	Grassland (New Zealand)	-	-	-	-	-	-	-
10	Grassland (England and Wales)	271 mg·kg <sup>-1</sup>	142 mg·kg <sup>-1</sup>	102 mg·kg <sup>-1</sup>	21 mg·kg <sup>-1</sup>	17 mg·kg <sup>-1</sup>	6.8 mg·kg <sup>-1</sup>	22.6 mg·kg <sup>-1</sup>
11	Grassland (England and Wales)	18 mg·kg <sup>-1</sup>	-	12.4 mg·kg <sup>-1</sup>	0.8 mg·kg <sup>-1</sup>	3.6 mg·kg <sup>-1</sup>	-	39 mg·kg <sup>-1</sup>

Current understanding suggests that Po is as significant in amount as Pi. However, most research on the fate of organic inputs applied to the soil has focused on the dynamics of Pi, while the fate of Po has been neglected, and there remains a lack of knowledge on its contribution to plant nutrition. Thus, there is a need to define standard methods that can help guide Po research and to develop sustainable approaches to improve soil Po cycling. This can be achieved through a multi-pronged combination of sustainable farming systems, genetically improved plants, and beneficial biota (biofertilizers).

### 3. Organic Phosphorus Dynamics in Rhizosphere

Rhizosphere microbiomes and root traits involved in P acquisition are known to affect the dynamics of Po in the rhizosphere and, ultimately, its availability to the plant (Figure 1). Although studies have shown that Po can be significantly depleted within the rhizosphere [78,79], the interaction between rhizosphere microbiomes in the rhizosphere, root traits, and their contribution to Po release to plants, have not so far been fully elucidated [80]. Here we summarize and discuss the role of soil microbial processes, root mechanisms, and their interactions, in the fate of Po forms in the organic-input/soil-plant system.



**Figure 1.** Organic-input/soil-plant-system-related biogeochemical processes that may ultimately modify the dynamics of the Po pool in the rhizosphere: (1) and (2) are the plants P mining and foraging strategies respectively (see Section 3.2 for more details); (3) P-mobilizing crop species improve Po utilization for non-P-mobilizing species, (4) refers to the microorganisms coming from organic input. Indeed, organic inputs involve the addition of carbon sources and often even contain their own microbiota. System modified from [18,81].

### 3.1. Soil Microbial Processes Involved in Po Mobilization

In organic-input-amended-soils and P-depleted environments, there is generally a proliferation of free rhizosphere microbiome and symbiotic associations with mycorrhizal fungi which have the potential to mobilize and mineralize different forms of available and unavailable Po [18,82] (Table 5). Phyla involved in Po mineralization include the dominant phyla *Proteobacteria* followed by *Acidobacteria* and *Actinobacteria* [83,84]. The order *Xanthomonadales* of the *Xanthomonadaceae* family is known to contain several Po mineralizing genes. To obtain P from Po compounds, *Streptomyces* uses an extracellular alkaline phosphatase encoded by the *phoA* gene. Other alkaline phosphatase genes, *phoD* and the *phoC*, were initially described in the *Streptomyces avermitilis* and *Streptomyces coelicolor* genomes, respectively [82]. *Stenotrophomonas* spp. have been shown to be important contributors to Po solubilization. Controlled experiments using plants inoculated with rhizosphere microbiome have provided further evidence for microbially mediated Po bioavailability to plants. Richardson et al. [85] showed that both grasses and legumes exhibited an improved ability to utilize IHP-P when inoculated with bacteria isolates with high phytase activity. *Bacillus* spp. and *Trichoderma* spp. may be able to increase the use of IHP as a P source by plants due to the production of organic anions and phytase [86,87]. Nevertheless, there is little evidence of how these rhizosphere microbiomes may act in the presence of soil minerals that can immobilize both Po and hydrolytic enzymes. Soil minerals such as Fe, Al oxides, and clay minerals are known to considerably reduce the efficiency of applied P. It is assumed that adsorbed Po on Fe and Al oxides is protected from enzymatic hydrolysis leading to its accumulation in soil [21] and its decreased use as a P source by plants. However, García-López et al. [88] showed recently that *Bacillus subtilis* improved the hydrolytic activity of myo-IHP even in the presence of high Fe oxide concentrations. This led to the conclusion that the rhizosphere microbiome could contribute to an increased hydrolyzing capacity in soil with high Po sorption capacity (Table 5). The currently available research is inadequate to explain the extent to which rhizosphere microbiomes are able to access sorbed forms of P. Future work should be conducted by inoculating microorganisms with sorbed P complexes on major soil minerals such as goethite, gibbsite, and major clays, under laboratory conditions and in the field. As most of the legacy P is poorly available to plants, especially the important component corresponding to Po pools [89], understanding the impact of rhizosphere microbiomes in mobilizing this legacy P is crucial to reduce dependence on mined P fertilizers [90]. Moreover, it is important to note that the hydrolysis of adsorbed Po depends to some extent on the release of organic anions or citrate by plant and rhizosphere microbiomes; this promotes the desorption and dissolution of Po making it available for hydrolysis [91].

Different enzymes released by the rhizosphere microbiome that are involved in Po hydrolysis, such as phytases and alkaline and acid phosphatases, act specifically on particular Po substrates [84]. Several studies using soil-specific enzyme additions have been published over the past decades [23,92]. Their results show that Po mineralization can be explained by the specificity of enzymatic activities on Po forms. For example, Scyllo-IHP was found to be most resistant to phytase activity [93], while IHP hydrolysis has been reported for bacterial acid phosphomonoesterases [94]. Other phytases from *Aspergillus* spp. (EC 3.1.3.8) have also been reported to hydrolyze IHP, simple monoesters (G6P, GLY), and phosphoanhydrides, but their ability to hydrolyze diester bonds in nucleic acids [23,95] is contradicted by the results of various studies [96]. Monoesterase enzymes have been found to hydrolyze diester phosphates; however, the release of phosphates from DNA is generally very low. This could be because monoesterases hydrolyze only the 5' and 3' phosphate residues of DNA [97], while the other phosphate groups are not accessible [95]. It has previously been shown that acid and alkaline phosphatase and phytase are not active on nucleotide pyrophosphate that contains nucleotide pyrophosphate bonds, nor on RNA and DNA that contain phosphodiester bonds [98]. In organic inputs, nucleotide pyrophosphatase, which hydrolyzes nucleotide pyrophosphate to nicotinamide mononucleotide and AMP, and a P1 nuclease, which cleaves RNA and DNA to produce 5-phospho-monoesters,

were used to access Po forms. The result showed that both enzymes (nucleotide pyrophosphatase and P1 nuclease) acted only on their own substrates (nucleotide pyrophosphate, or RNA and DNA, respectively). Therefore, it has been suggested that these enzymes could be used to release specific forms of phosphorus when present in the soil [98].

Soil properties may influence the conversion of Po into Pi by the rhizosphere microbiome. Among the soil properties, soil pH is an especially important factor that affects the efficacy and biochemical availability of enzymes that hydrolyze Po forms in the soil. For instance, at a pH of 7.5, *Aspergillus niger* phytases remained in solution, but at a pH of 5.5, they were unavailable [95]. However, the optimal pH varies according to the soil microorganism species and the associated plant. Fungal phytases, such as those of *Aspergillus fumigatus*, require a pH between 4.5 and 6.5, in which 80% of activity takes place [99]. Species such as *Rhizoctonia* sp. and *Fusarium verticillioides* can produce phytases at optimal pH of 4.0 and 5.0, respectively [100], while in bacterial phytases the maximum activity was observed at a pH of 6.0–8.0, as in *Bacillus* sp. [101]. Most of the phytases are acidic and have an optimal pH between 4.5 and 6.0 [102], whereas alkaline phytases in legume seeds [103], lily pollen and cattail pollen, have been reported to have an optimal pH of 8.0 [104]. For example, at pH 7.5, phytases from *Aspergillus niger* remain available in solution, but at pH 5.5 they are not available [95]. It is evident that phosphatases produced by rhizosphere microbiomes are more sensitive to pH. This pH dependence may be even greater than that of plant phosphatases. However, the optimal pH for Po mobilization varies among rhizosphere microbiome species. It is also important to understand how microorganisms could facilitate P mobilization from organic inputs or soil organic matter within a given pH range. We conclude that the determination of the optimal pH for Po mobilization by microbes and root traits requires careful assessment in future research.

In addition to pH, soil temperature has a strong effect on Po availability though studies have shown contradictory results on the influence of temperature on P solubilization by microbes. White et al. [105] found 20–25 °C to be the optimal temperature for maximum microbial solubilization of P while 28 °C was reported by Chauhan et al. [106] and Alori et al. [107]. Others have reported 30 °C as the optimal temperature for solubilization and mineralization of Po [101,108]. Nautiyal et al. [109] reported solubilization and hydrolysis of P at an extreme temperature of 45 °C in desert soil, while Johri et al. [110] reported a low temperature of 10 °C. The optimum temperature for phytate-degrading enzymes ranges from 35 to 77 °C. In general, plant phytases, such as those from cereals, show maximum activity at lower temperatures than microbial phytases [102]. The phytase from *Fusarium verticillioides* showed an optimal temperature of 50 °C and stability up to 60 °C [104]. The optimal temperature for phytase activity towards magnesium phytate (Mg-IHP) has been reported to reach 40 °C without and 50 °C with 5 mM  $\text{Ca}^{2+}$  [111]. Most plant phytases have an optimal temperature of 45–60 °C, as reported by Johnson et al. [112]. The lowest temperature has been reported to be 10 °C [110]. However, it is generally assumed that a higher temperature (>30 °C) has a better effect on Po solubilization and availability as shown by the higher Po solubilization by *Bacillus megaterium* at 36 °C than at 21 °C. As with pH, phosphatases produced by rhizosphere microbiomes are thermostable. Therefore, changes in the interactions between microbes and root traits as a result of temperature variations and how this could affect Po mobilization processes must be considered in the soil-plant system. Furthermore, understanding the optimal activity of microorganisms as a function of soil temperature is an important challenge for improving biofertilizer management practices and their positive effects on Po hydrolysis and P availability. However, despite the challenge of controlling soil temperature, it is nonetheless possible to identify the optimal dates and seasons to apply biofertilizer to maximize its effect. The effectiveness of microbial enzymatic activity is also influenced by different cations and other constituents in the soil solution. Modelling studies have shown that three classes of phytases, histidine acid phosphatases,  $\beta$ -propellant phytases, and purple acid phosphatases, would be unable to hydrolyze  $\text{Al}^{3+}$ ,  $\text{Fe}^{2+}$ ,  $\text{Fe}^{3+}$ ,  $\text{Cu}^{2+}$  salts of IHP, but would be able to hydrolyze  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{Mn}^{2+}$  salts [113,114]. This implies that P mobilization will depend on the nature of the

cation that precipitates Po. Thus, the accessibility of precipitated Po by enzymes and its mobilization for plants will differ considerably depending on the nature and concentration of electrolytes in the soil.

In summary, the hydrolysis of Po and its release by enzymatic activity is generally affected by the biochemical nature of Po and its ability to interact with soil properties and rhizosphere microbiomes. A wide variety of bacteria, fungi, and endophytes can solubilize Po through the production of organic acids [115]. This solubilization is very important because most forms of Po are high molecular weight compounds that are generally resistant to chemical hydrolysis. However, the mechanisms associated with the transformation of Po to Pi are poorly understood, and further work is needed, especially under field conditions. In most studies, the experimental conditions have suppressed interactions between system components. Therefore, these studies generally only indicate what is possible, but they do not necessarily indicate what is likely [116,117]. Indeed, knowledge of Po transformations is a prerequisite for understanding the potential contribution of lesser-known forms of Po in the organic-input-soil-plant system. In any case, it is evident that Po mineralization occurs in the rhizosphere and could contribute significantly to the requirements for plant growth. Factors affecting the rhizosphere microbiome are likely to influence the lability and stability of their enzymes. Some enzymes become stable through interactions with soil minerals and humic substances and retain some enzyme activity [118]. In general, microbial activity is affected by biological (e.g., the amount and type of substrate, concentration of enzyme, etc.) and physicochemical processes (e.g., interactions with soil constituents pH, temperature, etc.). The former cause changes in enzyme production rates and microbial community composition, while the latter cause changes in adsorption/desorption reactions, substrate diffusion, and enzyme degradation rates [119]. Critical factors affecting microbes and their enzyme activities include the amount and type of Po [120], interactions with soil constituents, pH, temperature, and the concentrations of enzyme and product [121]. In addition, because Po adsorbs rapidly and strongly onto soil particles, the binding processes involved also play a crucial role in the activity of rhizosphere microbiomes [122,123]. To date, there are relatively few studies that explore the enzymatic hydrolysis of adsorbed Po. It has been reported that mineral surfaces protect the majority of adsorbed phosphate esters from enzymatic hydrolysis, but whether this is a general finding remains open [38]. Furthermore, the mechanism of this process is largely unknown in the case where the enzyme can access the adsorbed Po forms. The results of Olsson et al. [124] on the hydrolysis of G1P on  $\alpha$ -FeOOH surfaces showed the role of interactions at mineral surfaces with respect to the stabilization of Po molecules in soils [125]. These authors provided a mechanistic explanation of how P can be mobilized via enzymatic activity despite strong interactions with soil minerals. This shed light on previous results showing that microbial stimulation and the resulting enzymatic activity can mobilize adsorbed Po from soil minerals [113]. However, a question is whether the enzyme acts only on the soluble fraction that is reconstituted by desorption of the substrate or whether the hydrolysis reaction occurs at the interface between the aqueous solution and solid particles. We therefore recommend future studies on these issues to better understand the effect of rhizosphere microbiomes on Po dynamics.

Apart from the rhizosphere microbiome, organic-inputs-derived microorganisms also play a major role in the mobilization of Po. Organic inputs imply the addition of carbon sources and often even contain their own microbiota, equivalent to inoculation of microbes, and this is a very important issue that needs more study. Amendment to organic inputs generally increases the diversity of rhizosphere microbiomes and their enzymatic activities in the soil [126]. These positive reactions highlight the role of organic-inputs-derived microorganisms in Po availability and, on the other hand, their high content of organic matter [127] which is the main substrate of most microorganisms [65]. However, complex questions remain about how the addition of organic inputs alters the soil microbial community and especially how this relates to soil Po mineralization. To successfully manage organic inputs, there is a need to develop a consistent procedure to quantitatively

compare the potential of these different microorganisms to release orthophosphate from different sources of Po. As the organic-input/soil-plant continuum consists of various forms of Po with different chemical properties, their solubilization and hydrolysis rates would be strongly related to the diversity of soil microbial communities. Therefore, it is crucial to develop and utilize more advanced approaches to support the roles soil microbes, especially via phosphate-solubilizing microorganism-derived enzymes, play in releasing free Pi from Po forms in the soil [107,128]. In sum, the main microbial processes involved in P dynamics that are synthesized and highlighted in this section, and the factors that influence them, greatly affect soil P mobilization processes. They could, therefore, if well understood, contribute to increasing the P use efficiency of organic wastes and those accumulated in agricultural soils. Furthermore, it is known that plant roots inoculated with commercial microorganisms can express synergistic effects to solubilize Pi in the soil. In contrast, little is known about their effect on Po pools. Therefore, further research is needed to evaluate the application and efficacy of commercial microorganisms on various crops with contrasting root traits and fertilized with different P sources under field conditions.

**Table 5.** Possible root traits and microbial activity involved in Po mobilization (solubilization and mineralization).

Organic Phosphorus Forms	Mode of Action That Root Traits and Microbes Act to Mobilize the Po	Associated Microorganisms	Reference
Glycerophosphate and phytate	Alkaline phosphatase and acid phosphatase; phytase	<i>Bacillus coagulans</i>	[129]
Ca-phytate	pH reduced; phytase	<i>Bacillus altitudinis</i> WR10	[130]
Po pools	Alkaline phosphatase	<i>Aphanothece halophytica</i>	[131]
Na-phytate	pH reduced; phytase	<i>Tetrathibacter</i> sp. PB-03 and <i>Bacillus</i> sp. PB-13	[132]
Phytic acid	Phytase	<i>Bacillus amyloliquefaciens</i> US573	[133]
Total Po pools	Alkaline phosphatase and acid phosphatase	<i>Acromobacter</i> sp. PB-01	[134]
beta-Glycerophosphate	pH reduced; acid phosphatase	<i>Bacillus pumilus</i> strain JPVS11	[135]
5-bromo-4-chloro-3-indolyl phosphate (BCIP)	pH reduced; phosphatase	<i>Agrobacterium</i> sp. and <i>Bacillus</i> sp.	[136]
p-nitrophenyl phosphate (pNPP) and guanosine 5-triphosphate (GTP)	Alkaline phosphatase/phosphodiesterase activity	<i>Pantoea agglomerans</i> strain P5	[137]
Lecithin	pH reduced; organic acid	<i>Microbacterium laevaniformans</i> strain P7 and <i>Pseudomonas putida</i> strain P13	[138,139]
Total Po pools	pH reduced, oxalic acid, citric acid, malic acid, succinic acid and acetic acid; alkaline phosphatase	<i>Cobetia amphilecti</i>	[140]
p-nitrophenyl phosphate	Malic acid, lactic acid and acetic acid; acid phosphatase, pH reduced, oxalic acid, citric	<i>Kushneria</i> sp. YCWA18, <i>Bacillus megaterium</i>	[141]
Fe-Po, and lecithin	pH reduced	<i>Alcaligenes faecalis</i>	[142]
		<i>Serratia</i> sp., <i>Alcaligenes faecalis</i>	
		<i>Ensifer sesbaniae</i> , <i>Gordonia terrae</i> , <i>Bacillus</i> sp., <i>Acinetobacter</i> sp.	

Current cropping models often focus on understanding competition for light and the effects of N or P fertilization, but do not consider interactions with the rhizosphere microbiome and how it affects soil Po forms. Thus, the development of cropping models that consider Po dynamics is needed to determine the efficiency of Po use in multi-species cropping systems and to manage P sustainably in the agroecosystem. Furthermore, it is important to note that current decision support tools do not consider Po sorption, its mineralization kinetics, and the effect of root trait and rhizosphere microbiome interactions on its dynamics. Therefore, in future research aimed at assisting farmers in organic input management, these parameters that govern Po dynamics, should be studied further and integrated into decision support tools. This will not only improve the decision support tools but also make them more focused on Po mobilization in the organic-input/soil-plant system.

Another important factor is the effect of rhizosphere microbial populations on Po mineralization. Some studies have shown that soils taken from the rhizosphere slowed the

sorption of phytate or phytase into the rhizosphere, suggesting that rhizosphere soils alter the adsorption of phytase and thus the release of orthophosphate from soils [114]. This is an important observation because Po dynamics are altered in the rhizosphere, so it is possible that Po from organic inputs is more available around plant roots. Therefore, we strongly suggest that, along with the mobilization process by soil microbes, root mechanisms/traits should be exploited to facilitate soil Po mobilization at the field scale.

The hydrolysis of Po and its release by enzymatic activity is influenced by the biochemical nature of Po and its ability to interact with soil properties and rhizosphere microbiomes. However, current work is insufficient to understand the extent to which rhizosphere microbiomes can access sorbed forms of P from both soil constituents and organic matter. Furthermore, investigations into the potential of microbes to mobilize Po have been conducted on cultivable microbes, yet most root-associated rhizosphere microbiomes are not cultivable. We recommend future investigations to screen rhizosphere bacteria in the presence of different forms of Po and different soil properties, to identify those that are effective in Po mobilization.

### 3.2. Root Mechanisms Involved in the Fate of Po Forms

The contribution of plants to Po availability has been known for many decades. Most plants have developed strategies to increase P acquisition in P-deficient soil or to specifically access different forms of Po and Pi in the soil [143]. These strategies cover a wide range of morphological, architectural, and physiological traits [144]. In general, these traits could be categorized into three types of P acquisition strategies: *foraging*, *mining*, and collective *microbial-root* strategy (Figure 1 and Table 5).

The plant P-*foraging* strategy relates to the acquisition of P in the soil solution through morphological and architectural traits by maximizing soil exploration. Through this strategy, plants can induce a diffusion gradient which in turn favours the desorption process of the different adsorbed Po forms [145,146]. The phosphorus-*foraging* strategy would also improve the efficiency of P uptake by slowing the rate at which Po moves from the free or moderately adsorbed form to the strongly adsorbed form on soil compounds [143]. *Foraging* strategy involves morphological traits such as specific root length, diameter and radius, and architectural traits, including root length density, root biomass, root hairs, and the formation of clustered roots or arbuscular mycorrhizal symbioses that allow plants to increase their *foraging* capacity [147]. These traits alter the C cost of soil exploration by regulating the extent of competition within and between root systems [148,149]. Among morphological traits, root radius is considered important in the efficiency of P use. Plants with finer/thinner roots can explore and contact a greater volume of soil per unit root area. Gahoonia et Nielsen [78] reported that plant species with finer roots may be more effective in mobilizing Po and absorption of Pi from the soil. Very recently, trade-offs between thicker and thinner roots have been observed by Honvault et al. [150]. Thicker roots are reported to have greater carboxylate release and phosphatase activity in the rhizosphere, affecting the desorption and mineralization of Po [150]. In contrast, thinner roots exhibit the morphological traits (*foraging*) that favour the exploration and contact of a larger volume of soil to permit P mobilization process [151,152]. These observations are consistent with other results showing that species with finer fibrous roots express higher levels of morphological traits to access more Po in the soil [147,153,154]. However, since fine roots (i.e., root hairs with small root radius) tend to renew faster than large roots [148], the cost of C to produce fine roots could be higher, since they would also need to be replaced more frequently [149]. In addition to root radius, the formation of root groups, such as proteoid and dauciform root groups, commonly found in plant species belonging to the families *Proteinaceae* and *Fabaceae* [154] and others, is very strongly related to the dynamics of Po in soil. These roots provide a very dense mat of root hairs and also specialize in the efficient synthesis and secretion of citrate and malate (organic anions) and phosphatases, which help solubilize insoluble Po resources and hydrolyze Po for plant uptake [155]. Various effects of root growth and variation in root hair length on Po dynamics and contribution to P uptake have

been reported in several species, including maize, wheat, barley, beans, soybean, and white clover [156,157]. Higher root length density in the upper soil layers was shown to be the most important root trait of wheat for Po mobilisation in response to organic input [158]. Moreover, variation in root growth angle and root hairs may have a significant impact on the total mobilisation of P in the soil [159]. In closely related maize genotypes, the effects of root growth and root hair length variation reportedly led to a 100% increase in total mobilized P and, in other genotypes, to as much as a 600% increase in P mobilization [157]. Such increases occur since root growth maximizes soil exploration and can induce a diffusion gradient and modify soil properties to promote P desorption. Root hairs are smaller in diameter than roots and grow perpendicular to the root axis, forming up to 77% of the root surface [160] of soil/field crops [161,162]. The presence of root hairs can be very important for the effectiveness of Po mobilization through a considerable increase of root area in the soil. It has been reported that root hairs can contribute up to 70% of Po uptake [78,163]. Root hair length and density are highly controlled by P bioavailability. Geometric modeling indicates that root hair responses to P availability interact synergistically to enhance Po and Pi acquisition [164]. Root hairs also aid in the dispersal of root exudates such as organic acids into the rhizosphere, which improves Po bioavailability in many soils [165]. Root morphological traits show a much more significant influence on Po acquisition generally in winter wheat genotypes than biochemical transformation by acid phosphatases [156,166]. These biochemical and morphological changes can vary considerably between and within plant species [18,20]. The potential ability of plants root traits to utilize poorly available Po sources is, however, greatly influenced by genetic makeup.

The plant P *mining* strategy, relates to the acquisition of P in the soil solution through physiological traits involving release of substances into the soil from the roots, including carbohydrates, organic and amino acids, phenolic compounds, proteins, fatty acids, sterols, enzymes, polysaccharides and phospholipids [167,168]. Among these compounds, carboxylic acids, PME activity, phenolic and mucilage compounds, and protons are the main physiological traits involved in P *mining* strategies for Po mobilization [169]. Through this strategy, plants increase the turnover of poorly available Po pools [34,154] by desorption, solubilization, and mineralization processes. Before any hydrolysis process by the enzymes, Po, if not free, must first be desorbed or dissociated from soil minerals or organic matter. The secretion of organic acids by P-mobilizing species improves the availability of Po forms by promoting their desorption from soil constituents to the soil solution, in which they are subsequently mineralized by phosphatases [170]. Organic acids are generally predicted to be strongly linked to Po mobilization in the soil-plant system [171]. Plant roots have the ability to produce organic acids, particularly short-chain organic acids, such as lactate, acetate, oxalate, succinate, fumarate, malate, citrate, isocitrate, and aconitate, which can mobilize both Po and Pi [172]. Among the organic acids, malic and citric acids are the most widespread and abundantly detected in root exudates [173]. Given the highest affinities between Po forms and soil components, chelation between organic acids in root exudates and soil constituents is the main mechanism for Po solubilization by organic acids in soil [174]. Citrate has been shown to chelate Fe and Al oxyhydroxide and Mn and Ca carbonates, which can actively displace adsorbed Po into free forms [175]. Low molecular weight organic acids generally carry one or more negative charges. By complexolysis, negatively charged organic acids can release Po from insoluble forms of Po. These reactions lead to the solubilization of insoluble forms of Po such as Ca-Po, Na-Po etc. [176]. The impact of direct chelation in the solubilization of Po by citrate exudation has, for instance, been demonstrated in rice [177]. In general, citrate and oxalate have a higher potential for mobilization of Po compared to other organic anions [165,171]. After Po is desorbed from soil minerals by organic acids, phosphatases and phytases released by roots can contribute to its efficient use by plants [178,179]. Chickpea, which appears to produce both phosphomonoesterases and diesterases, is thought to improve P nutrition, probably through *mining* and mineralization of Po forms in soil [180,181]. Various studies have demonstrated that plants have a limited ability to access P in the form of IHP (the main

form of Po) due to its low availability in soil solution and low levels of extracellular phosphatase or phytase [31,95]. It has also been shown that wheat and many other species are able to utilize P from G6P, GLY, and phosphodiester (DNA and RNA), due to their *mining* capacity, but are limited to acquiring P directly from myo-IHP, although it is abundant in many soils [92]. This suggests that the biological importance of the different forms of Po will be driven by their turnover rates. Therefore, it was considered that plants with optimal *mining* strategies for phytase release could potentially be used to improve the efficiency of inositol phosphate mobilization. The challenges are to understand the functioning of root-derived phytase activities on Po forms, and the chemical nature, soil properties, and root traits of crop species, to increase Po desorption and hydrolysis.

The collective *microbial-root* strategy refers to the investment of resources by plants to interact with the microbial community to access Po in soil. Many plants have developed a symbiotic association with vesicular arbuscular mycorrhizal fungi (AMF) that grow out from the root into the surrounding soil, extending the capacity of the root to mineralize Po and take up Pi in soil solution [182]. The association of roots with arbuscular mycorrhizae is thought to be much more related to the mobilization of total P than root hairs and root length activity [183]. The symbiotic association of plant roots with mycorrhizae is reported to extend further from the roots than root hairs, and is also active in areas where P forms are adsorbed onto soil components [184,185]. A significant contribution of AMF to the uptake of P by plants has been reported, particularly in soils with high Po binding capacity. It is also accepted that AMF store Po in their vacuoles, which can be hydrolyzed and transported as Pi in the host plant [186]. In addition, AMF also hydrolyze Po by releasing acid phosphatase in the soil. However, the relative contribution of root-derived extracellular phosphatases in the use of Po is still unclear, as the number and activity of bacteria and fungi are higher in the rhizosphere than in the soil in general [34].

Overall, the roles of *P mining*, *foraging* and collective *microbial-root* strategies are understood and their indirect, and sometimes direct, effects on Po dynamics/mobilization have been demonstrated [164,166]. The processes differ according to the nature of Po forms (e.g., phosphate, mono, or diester), the structure and function of soil microbial communities, and the physicochemical properties of the soil and climate. For instance, the availability of IHP, G6P, GLY, and phosphodiester (DNA and RNA), as a direct effect of *P mining*, *foraging* and collective *microbial-root* strategies, remains unclear. Although the release of organic acids can make G6P, GLY, and phosphodiester (DNA and RNA) available to plants, it is less efficient at solubilizing IHP [187], probably due to it binding strongly to soil. Interactions between plant traits in the mobilization of P have been studied but remain poorly understood and unconfirmed. To this end, when developing new crop varieties or cultivars, selection should be based on crops with high Po use efficiency to promote greater P availability. Thus, in future crop breeding programs, traits involved in Po use efficiency should be identified and recorded. Specifically, efficient cultivars with genes and traits that produce strong phosphatase/phytase activities should be identified for better mobilization of the major Po form (Myo-IHP). There may also be trade-offs between physiological and morphological traits [150,154]. These trade-offs have been examined very recently in different crop families and species [150]. Trade-offs between thicker and thinner roots were observed [150], with thicker roots showing greater carboxylate release or phosphatase activity in the rhizosphere. Trade-offs and coordination between traits were strongly influenced by soil type. However, their effect on the availability of Po forms still needs to be elucidated [153]. Thus, we suggest that these strategies can be exploited using combinations of species with contrasting strategies, or by using a single species to better understand their actual effects on Po forms in agroecosystems.

Both plant functional traits and organic input characteristics strongly interact to modulate Po dynamics. However, it is still unclear to what extent these contribute to the mobilization of sparingly available Po forms. Research efforts should focus on understanding the relationships between plant functional traits, Po nature, and organic input properties in order to characterize the dynamics of Po, model its fate in the soil-plant

system, and better understand its consequences for P availability. Further, crop models to estimate total soil Po reserves and, at minimum, its specific forms (IHP, G6P, GLY, etc.), in a multi-species cropping system can be developed based on plant traits (i.e., shoot and root morphological and chemical characteristics), including inter- and intraspecific trait variability and soil properties. This trait-based approach to modeling P mobilization can be developed and would be potentially useful in different climates.

#### 4. Approaches/Strategies to Improve Po-Use Efficiency

##### 4.1. Understand and Manage Plant Traits, Root-Associated Microorganism and Po Pool Interactions to Characterize P Dynamics and P Availability

In agroecosystems amended with organic inputs, it is essential to grow crops able to mobilize and release Po from both soil constituents and organic input. Several direct and innovative approaches have been identified to improve the mobilization of Po forms by plants (Table 6). These include the identification and selection of crop species/genotypes based on their functional traits [14]. This approach uses morphological, architectural [188,189], and physiological traits [157,188,190], and microorganism characteristics, or a combination of both, to access sparingly available Po forms (Figure 1). Several plant species are presumed to be relatively efficient in Po utilization without assistance from the rhizosphere microbiome. Some barley species with long root hairs (up to 1.0 mm) could easily access and mobilize twice as much Po as zita species (*Prunus laurocerasus*) in low P soil [191]. More importantly, allocating C to root hair growth would represent a minor metabolic cost to achieve greater P use efficiency [146,191]. Numerous plant species belonging to the family *Fabaceae* have been classified as efficient Po solubilizers [192]. For instance, legumes (72%) are more efficient than grain or oil crops (22%) in terms of extracellular acid phosphatase activity [193,194]. Compared with non-nodulated legumes, N<sub>2</sub>-fixing species possess a high level of functional plasticity to assist plants in facilitating Po mobilization [20]. Since N<sub>2</sub> fixation is highly expensive in terms of Pi and energy expenditure, it is likely that this group of plants can promote Po bioavailability. A wide range of biochemical, physiological, and molecular mechanisms can give nodulating plants a superior dynamic capacity to utilize soil Po more effectively. Simultaneously, most legumes have a high potential capacity to establish double symbiosis with AMF and rhizobia [19]. This tripartite symbiosis can provide an additional potential advantage that might assist in Po mobilization. Unfortunately, it is still unclear to what extent these symbiotic associations contribute to the mobilization of sparingly available Po forms. Other approaches aim at stimulating rhizosphere microbiomes that would improve plant Po acquisition and thus meet the overall goal of reducing the amount of chemical fertilizer from non-renewable mineral rocks [195,196]. It is therefore necessary to focus on these innovative approaches to optimise the management of organic input in the agricultural system.

Briefly, a better understanding of the impact of Po mobilization and acquisition strategies by plants, which are related to the multiple morphological and physiological traits and the interactions between them, is key in the management of Po availability. Compared to Pi, the impact of these strategies in soil amended with various Po forms has received much less attention. Crop species traits might be used to increase Po mobilization, helping thereby to rethink P fertilization, sustain production, and recycle more Po in organic amended soil, but this requires elucidation of the relationship among the various Po forms in organic inputs and root traits. In addition, understanding the trade-offs and effects of combining traits would allow us to unravel the complexity of the P form acquisition strategies and provide new knowledge for designing cultivated crop communities (i.e., multi-species crops), such as cover crops or intercrops, to improve P acquisition and availability [153,197].

**Table 6.** Case studies used to promote and improve Po-use efficiency in the soil-plant system.

Case Studies	Observation/Concept	Po Forms	Test Plant	Reference
Sewage sludge application in an agroecosystem (long-term (>20 years) cropland field in northern France	Sludge is as effective as TSP to improve soil P availability. Sludge promotes soil enzymatic activities (phosphatases) for Po hydrolysis	Po forms, Apatite-P, Nonapatite-P	Oilseed rape–winter wheat–winter barley rotation	[198]
Measured of ten morphological and physiological traits involved in P acquisition across species in two contrasting soils with moderate P limitation.	There is Tradeoffs between thicker and thinner roots. Thicker roots exhibiting greater carboxylate release or phosphatase activity in the rhizosheath	Total P	Thirteen species of diverse phylogenetic lineages	[150]
Placement of phytase in the vicinity of roots using mesoporous silica nanoparticle materials.	Phytases are stable and resistant to soil degradation	Phytate/IHP	<i>Medicago truncatula</i>	[199]
Intercropping of P-mobilizing and non-P-mobilizing crop species	P-mobilizing crop species (legume) improve Po utilization for non-P-mobilizing species (non-legume)	Phytate	Wheat/chickpea	[170]
Contribution of phytate to plant nutrition is affected by Fe oxides and phosphohydrolases releasing microorganisms in the growing medium.	Phytase activity and organic anions concentration increased with increased Fe oxides in the media. Phytate supplied was recovered as inorganic P at the highest Fe oxide concentration. Inoculants of <i>B. subtilis</i> promoted an enhanced hydrolytic activity at the highest Fe oxide concentration.	Phytate/myo-IHP	Cucumber plants	[86]
Application of phytase to the root medium of plants	Phytase increases Po hydrolysis	myo-IHP (phytin)	Maize	[200]
Inoculation of plants with soil isolates/microorganisms that possess efficient phytase activity	Mineralization of complex organic substrates by phytases	myo-IHP	Pasture legume (subterranean clover, white clover, alfalfa) and pasture grass (wallaby grass, <i>Phalaris</i> ) species	[201]
P-acquisition strategies of three main crops are affected by the application of sewage sludges, compared with a mineral P fertilizer.	Wheat and barley had a greater root carboxylate release. Canola had higher root released acid phosphatase activity which promoted the mineralization of sludge-derived Po	Po forms, Apatite-P, Nonapatite-P	wheat, barley and canola	[166]
Inoculation of plants with arbuscular mycorrhizal fungi	Mycorrhizal colonization contributes to Po cycling and plant Pi acquisition	Phytate, RNA, lecithin	Red clover	[146]
Application of bacterial grazer (nematodes) together with mycorrhiza and P-solubilizing bacteria	Interaction of bacterial grazers with mycorrhiza and phosphobacteria promotes P org solubilization	Phytate	Maritime pine	[202]
Biochar addition to agricultural soils	Biochar enhances Pi-solubilizing bacteria	Po and Pi forms	Ryegrass	[203]
Genetic transformation of plants to overexpress extracellular phytases in root cells	Transgenic lines display better Pi nutrition owing to the efficient release of extracellular root phytases	Phytate	<i>Arabidopsis</i> Subterranean clover Potato Tobacco	[116,201,204]

The strategies of P-acquisition by plants and the impact of root-associated microorganisms in P mobilization are quite well understood and are currently the focus of much research. However, it is still unclear to what extent they may interact with organic input to mobilize sparingly available Po forms. Several plant species belonging to the family

*Fabaceae* are presumed to be relatively efficient in Po utilization without assistance from soil microorganisms. Therefore, future research should test these species under controlled conditions or at the field scale to identify specific plants that are strongly involved in the mobilization of specific forms of Po.

#### 4.2. Development of New Cropping Systems to Recycle P from Po Pools

##### 4.2.1. Cover Crops and Po Availability

Cover crops offer the opportunity to improve Po recycling in agroecosystems by reducing P losses through runoff attenuation and improving P availability through P hydrolysis (Table 6), P release from crop residues, and decreased P sorption [150,178]. As such, in soils amended with organic input with high levels of Po and/or superphosphate, several cover crop species have been effective in utilizing more of the Po and Pi pool, not only by promoting different root traits for soil exploration, but also by developing mechanisms to release various Po species from organic input and soil [85,205]. The use of ryegrass as a cover crop and P fertilizer applications resulted in a decrease in soil IHP stock [206]. In addition, several cover crop species are thought to be able to significantly contribute to the desorption and redistribution of sorbed forms of P from the upper soil layer to the subsoil [207]. Species such as common vetch (*Vicia sativa*) and radish (*Raphanus sativus*) are generally identified as effective for these desorption and redistribution mechanisms [208]. For example, in a high P-fixing soil, the dynamics of various forms of P from different organic inputs were studied in the presence of five cover crop species: vetch, white lupin, forage radish, ryegrass, and black oat, for 5 years in a no-till system. These species were able to mobilize labile and less labile Po and increase the proportion of Pi in the soil solution. Considering the literature on cover crop species, white lupine is widely suggested to be the most efficient for extracting Po and Pi forms and could be considered a P-mobilizing species, although this may depend on the characteristic of the organic input applied [209,210]. Furthermore, though there is little information available in the literature, it is also pointed out that cover crops could specifically increase the dissolution of resistant Po associated with fulvic acid and highly resistant Po associated with humic acid [211,212]. Of the forms of soil Po, IHP can account for more than 70% of soil stocks because of its strong binding to soil minerals. For its more efficient mobilization, Gerke [187], suggests that future research considering P acquisition from IHP should focus on its mobilization from the surface of soil components by root exudates of cover crop species, primarily di- and tricarboxylic acids, which can increase IHP solubility. In sum, cover crops can be an innovative technique to improve the mobilization of Po pools from the organic-input/soil-plant system. However, their effects are mixed and depend on the concentration of P available in the soil and thus on the added P fertilizer [213]. The need is to examine the role of cover crops on desorption, mineralization of Po forms, and consequences for P availability, with a view to model their potential effect on P availability in soils amended with organic inputs. Studies on the impact of cover crops on Po availability are generally conducted over a short evaluation period. Thus, as observed by Calegari et al. [210], long-term studies are needed, as Po mobilization from applied organic inputs may depend on the cover crop species and their ability to desorb and redistribute fixed P. Most studies on the impact of cover crops on P dynamics are descriptive studies in which plant traits and Po forms are generally not characterized. Therefore, we suggest that future studies are needed to quantify species traits that may influence key forms of Po. This is to manage the relationship between cover crops and Po and more broadly between cover crops and organic input.

The wide variability in the potential contributions of Po pools in cover crop systems, and their possible interactions with Pi from crop residues for subsequent crop nutrition, suggest a strong need to integrate soil Po dynamics into crop models in order to select cover crop traits that provide optimal utilization of Po from organic fertilization in cropping systems.

Cover crops have a wide range of P acquisition traits, and thus potentially different P acquisition strategies for exploiting different P pools. An outstanding question is whether

P forms and soil type influence the expression of trade-offs and Po acquisition strategies in cover crops. To answer this question, future research should measure the morphological, architectural, and physiological traits of different cover crop species from various phylogenetic lineages in different contrasting agricultural soil types. This may help to characterize the relationships among traits involved in P acquisition to explore tradeoffs and the main P-acquisition strategies and their mediation by soil type.

#### 4.2.2. Management of Po Inputs in Crop Rotations

The ability of crop species to mobilize Po of organic inputs and soil constitutes an opportunity to define Po management at the crop rotation scale (Table 6). Many *Brassicaceae* crop species (e.g., canola, cabbage, radish) that produce more acid phosphatase than wheat, oats, maize, beans, and chickpeas in response to P deficiency [166,214], can benefit from fertilization with organic inputs. *Brassicaceae* with different P acquisition strategies mineralize Po and improve P availability that would be beneficial to the next crop [147,215] (Figure 1). The large differences in the efficiency of the P uptake strategy of canola, cabbage, and radish on the one hand, and wheat, oats, and barley, on the other hand, can provide a tool to optimize the combination of the rotation crop and the organic input to be applied. In practice, since organic inputs slowly increase the soil P content available to plants after incorporation into the soil [198], *Brassicaceae* crop species should be the first choice in the crop rotation to improve the P content of crops from poorly available forms of Po. For crop species such as wheat and barley that have high specific root length and relatively high carboxylate release, they could be more effective in releasing different forms of P adsorbed and/or precipitated on soil constituents, such as IHP which is very strongly adsorbed on soil. From an agronomic perspective, the most efficient system would be to apply organic input to the *Brassicaceae* species, while the following cereals will benefit from the residual Po. However, this will require more investigation in the future. Another interesting effect of rotational crops for organic input management is the ability of legumes to affect soil P levels. Indeed, legumes significantly decrease soil  $P_i/P_o$  ratio values [33]. Thus, linking the efficiency of legumes to mobilize Po to the type of organic input is an essential step to know and optimize the combination of the crop species in relation to the P fertilizer type, thus allowing for more sustainable P fertilization.

It is now known that the application of organic input in rotations affects soil Po reserves and their dynamics over time [33,198,216]. In general, as Glæsner et al. [217] point out, organic inputs, due to their Po content, have an impact on labile P in crop rotation systems which remains highly available to plants in the soil after long-term application. However, most of the studies do not generally consider how other forms of soil P (already available soil P) are affected in the rotation. In addition, the ability of rotational crops to mobilize Po from organic inputs remains poorly understood. Indeed, recent work suggests that P availability in rotations may change over time due to changes in the dynamics of soil-bound Po pools, which in turn are mediated by the type of crop in rotation (i.e., mobilization/acquisition strategies), concentrations, and forms of Po in organic input. Further studies are needed to determine the relative contribution of rotational crops with contrasting Po acquisition strategies on increasing labile P using isotope-labeling techniques. As an innovative perspective to better manage short- or long-term Po inputs in agrosystems, fertilization management models need to evolve at the rotational scale by integrating plant traits, organic waste forms of Po, and soil properties to model microbial activities and their effects on available P.

### 5. Future Prospects

Given the importance of Po mobilization processes by roots and the rhizosphere microbiome, several suggestions and avenues of research can be identified, as well as promising approaches and innovative techniques that could improve the cycling of Po in the soil for use by plants. This includes a multi-pronged combination of beneficial biota, agronomic management practices, and genetically improved plants:

An important first direction for future research would be to focus on developing new cropping systems to recycle P from Po pools. To this end, understanding the impacts of cropping strategies, whether in rotation or intercropping systems, on mobilized Po could be promising for managing P availability for agroecological development. With this knowledge, crop species/genotypes (with specific morphological and physiological traits) which can enhance Po use efficiency could easily be identified and selected to improve plant P acquisition and thus reduce the amount of P fertilizer needed to maximize production. For this purpose, we suggest that future research studies could test plants with different P mobilization/acquisition traits in monospecific treatment or in multispecies treatment with different sources of Po. This would allow not only evaluation of the overall P uptake between these different treatments (multi-species and monospecific), but also better determination of their higher P use efficiency. Inclusion of multi-species or single-species, with different P-uptake strategies or P-uptake efficiency, as cover crops, or in crop rotation, can help to develop new cropping systems to recycle more Po and reduce the use of mineral P fertilizer. Other practices include better use of organic input as an alternative source of P by its better management in crop rotations, or of biofertilizers (microbial inoculants). The combination of these different practices deserves to be further explored and developed.

Since P availability depends on the interactions between Po and crop traits, the timing of application, and the influence of both Po and the type of organic input and plants on microbial communities, it is necessary to start from the characterization of Po species in organic inputs and then study their relationship with soil properties and plant traits to really understand the P cycle and manage P availability. Furthermore, the direct contribution of Po to plant nutrition also needs to be well understood by quantifying the availability of readily available forms of Po to plants and by better understanding the dynamics of those adsorbed on soil minerals (e.g., the sol-Po bonding complex). This knowledge will be useful to predict P availability as a function of the form that is applied and to better model P behavior as a function of soil properties and organic input characteristics.

At present, it is not known how the application of organic input can have an impact on the structure of the rhizosphere/microbiome/root-traits interaction on Po mobilization in the rhizosphere. Furthermore, the pathways and thresholds of transformation of Po species in soils amended with organic inputs, and especially their interaction or competition with existing Po pools in soils, in relation to mobilization processes by rhizosphere microbiomes and root traits, remain largely unknown. Therefore, it is important for future research to highlight the role of Po forms from organic inputs in the changes of existing soil P forms over time by characterizing the effect of rhizosphere microbiomes and root traits involved in their dynamics and how they relate to soil properties. The identification of these factors is a crucial step in fostering the utilization of soil Po by crop plants. Simultaneously, elucidating the plant uptake system to acquire Po can provide a strong complement to these efforts. Apart from adding different Po species to the soil, the decomposition of organic inputs can activate exogenous microorganisms and organic acids that can influence Po dynamics (e.g., mobilization process), but these aspects are very poorly considered in the literature.

N-P interactions play a major role in the C and P cycles, creating co-limiting or synergistic effects depending on their concentrations, and, accordingly, organic fertilization is jointly managed in the cropping system. Since organic inputs differ in terms of N concentration and organic carbon composition (e.g., cellulose, hemicellulose, lignin) which in turn impact microbiome/root trait interactions (e.g., protons, reduced pH, organic acids, phosphatases), one hypothesis is that different forms of Po would have different response times to changes in nutrient status (e.g., C and N levels) in agricultural ecosystems. Thus, to confirm or refute the hypothesis, future research is needed to evaluate the actual effect of these compounds on Po mobilization in the organic-input/soil-plant system.

Most research on the potential of microbes to mobilize Po has been conducted on culturable microbes. Because most rhizosphere microbiomes associated with plant roots are not culturable, further research on these microbes in the plant rhizosphere is needed,

which will improve knowledge of the microbial community and microbe/plant-root-traits interactions in Po mobilization. Furthermore, since the ability of rhizosphere microbiomes to mobilize Po varies with the forms of Po and their chemical properties, in order to better take advantage of these soil organisms or even select and introduce them, it is recommended that screening of these bacteria in the presence of different forms of Po and different soil properties be investigated, since in most studies, these bacteria have been screened under conditions where neither the forms of Po nor the soil properties are highlighted.

It is known that plant roots associated with the rhizosphere microbiome can express synergistic effects to increase Pi uptake by mobilizing more Po in the soil. Therefore, further research is needed to evaluate the actual effectiveness of beneficial rhizosphere microbiome associations in various crops with contrasting root traits and fertilized with different P sources under field conditions, as well as how the mechanisms by which they mobilize Po are hampered by competition with endemic microorganisms and soil properties (e.g., P sorption capacity, soil P status, pH, etc.).

Sustainable agricultural systems are expected to enhance the diversity of functional microorganisms in the soil, especially those actively involved in P mobilization from organic inputs or soil organic matter. However, given the lack of data about the link between sustainable agricultural systems and Po mobilization, it is important for future research to characterize both the direct and indirect effects of such systems on Po mobilization in the organic-input/soil-plant continuum.

## 6. Conclusions

Organic inputs and soil can be used as a primary or supplementary source for plant P nutrition. This is because Po is as important in amount as Pi in soil and organic inputs. However, the present review highlights that Po present in organic inputs and soil is in various chemical forms which differ in their ability to be mobilized and their availability to plants. These forms of Po tend to be scarcely available in agroecosystems because of their strong affinity for soil mineral surfaces. Rhizosphere microbiomes have the potential to mobilize and mineralize different forms of available and unavailable Po. Various controlled experiments using plants inoculated with the rhizosphere microbiome provide evidence for this. Rhizosphere microbiomes solubilize Po through the production of organic acids and then mineralize it via enzymes. However, the mechanisms associated with this mineralization are poorly understood, and in most studies, the experimental conditions suppress interactions between the components of the system. Furthermore, there is little evidence on how these rhizosphere microbiomes can act in the presence of soil minerals that can immobilize both Po and hydrolytic enzymes. Future work should be conducted by inoculating microorganisms with sorbed Po complexes on key soil minerals under laboratory conditions and in the field. Root traits may alter rhizosphere characteristics to enhance reactions of Po dissolution, desorption, chelation, and mineralization. These traits are related to root *P foraging strategy* and may include alterations in root structure such as plasticity in low P stress responses and the spatial arrangement of roots to induce a diffusion gradient that will in turn promote the process of Po desorption and thus P availability. The expansion of fine roots and the growth of longer, denser, root hairs promote Po acquisition by roots via increased root surface area. Physiological characteristics related to *P mining strategy* may alter pH and/or release carboxylates and phosphatases to increase the turnover of sorbed Po pools. These rhizosphere microbiome and root trait processes continuously interact to modulate the stock of Po in agricultural soils. An alternative approach to P limitation would be to use crop species/genotypes with specific traits, inoculated naturally by rhizosphere microbiomes with suitable Po forms and soil properties, at crop and rotation scales, to increase Po mobilization from organic inputs. Thus, under conditions of P-deficiency or soils amended with organic inputs, understanding of root traits and soil microbes will be effective in increasing plant growth especially by mobilizing highly binding Po forms. The present work reinforces the need to develop future research

to understand the trade-offs between root traits, their relationship to microbes, and their direct effect on Po mobilization and P availability. These mechanisms/processes could be integrated into models and decision support tools for estimating soil P availability and managing P fertility from organic waste.

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