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Review

Arbuscular mycorrhizal Fungi as Inspiration for Sustainable Technology

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Abstract: This review illuminates established knowledge of root–arbuscular mycorrhizal fungi (AMF)–plant mutualism to study the uptake of phosphorus (P) as a critical element for plant nutrition. We focus on P cycling, underscoring the role of AMF in enhancing P acquisition and plant resilience in the rhizosphere. The role(s) of plant roots, root exudates, and biomolecules in relevant soil processes is emphasized in this manuscript. Enhancing P uptake efficiency through AMF interaction presents a promising avenue for sustainable agriculture, with future research opportunities focusing on understanding underlying mechanisms and developing innovative technologies as a need to transition from the use of AMF as a biofertilizer or as an inoculation alternative for seeds to being an inspiration for the development of technology adapted to different crops. This is important to promote responsible agricultural practices and improve crop yields. We provide definitions of key terms and concepts for one of the best-known natural sustainable phosphorus systems. This manuscript illuminates and aims to inspire technology development to overcome the challenge of plant nutrition under P scarcity conditions.

Keywords: arbuscular mycorrhizal; fungi; phosphorus; technology; sensors

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1. Background

Plants, being primarily sessile organisms, utilize their roots for communication and nutrient transport to ensure survival [1]. Under nutrient scarcity or environmental stress, plants must form associations with rhizosphere microorganisms to ensure nutrient and water supply. These mutualistic associations enhance plant root traits and defense mechanisms. One example of such a keystone interaction is mutualism between plants and arbuscular mycorrhizal fungi.

1.1. Arbuscular mycorrhizal Fungi

Arbuscular mycorrhizal fungi (AMF) colonize the root cortex of numerous crop species (Figure 1). This is one of the strategies plants use to uptake phosphorus (P) from soil. Given the central role in P uptake, AMF is critically important to many agricultural systems, especially for soils with limited bio-accessible P [2]. AMF forms associations with 70–90% of terrestrial land plants [3] (excluding cabbage, lupin, and other plants in the Brassicaceae family). The fungi develop extraradical mycelium to uptake crucial nutrients from the soil, including organic phosphorus (Po). AMF–plant interactions are mutually beneficial (referred to as mutualism). Fungi supply nutrients and protection against environmental stress, while plants provide essential carbon to the fungi in return [4]. Some nutrients, particularly P, are not bioavailable to plants [5], limiting crop production [6].

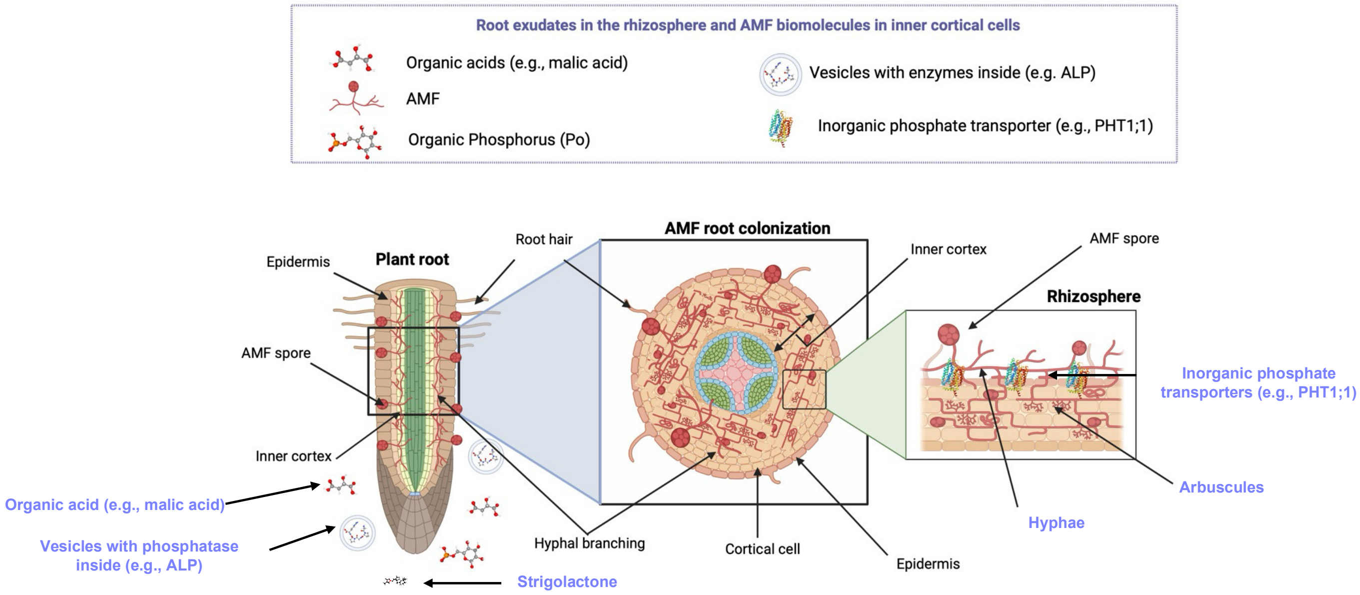

Figure 1. AMF root colonization is a mutualistic relationship for phosphate uptake by plants. The ectomycorrhizae shown on the left side of the diagram depict fungal hyphae [7] extending into the plant root during AMF colonization. The exploded view (middle, right) shows endomycorrhizae, where AMF hyphae extend into the root cortex. The diagrams expand on the work by [5] and highlight seven key structures in purple color. These key structures include: (i) AMF, (ii) root exudates (PubChem ID: 15102684; [8]), (iii) D-glucose-6-phosphate (as an example of organic phosphorus) (PubChem ID: 5958, [9]), (iv) inorganic phosphorus transporters (PiPT; PBD Entry: 8FVZ, [10]), and (v) hyphae. Malic acid was used as an example of an organic acid in soil (PubChem ID: 525). Figure created in Biorender.com.

The exchange of inorganic phosphorus (Pi), photosynthates, and other beneficial carbon plays a crucial role in AMF–root associations. Figure 1 summarizes plant–AMF–soil interactions, highlighting seven key structures related to P uptake. The processes take place in an area surrounding roots known as the ectorhizosphere. This review illuminates each of these seven structures and highlights recent research on P uptake by plants. A systems-level view of these interactions enables a nuanced understanding of factors influencing plant P uptake, including soil conditions and plant adaptive strategies.

1.2. Phosphorus Is a Key Element

Phosphorus (P) is a crucial element for many biological processes and is a core component of several critical bio-macromolecules, including deoxyribonucleic acid (DNA), adenosine triphosphate (ATP), and phospholipid cell membranes, among others [11]. Plant roots acquire P in the form of dissolved inorganic phosphorus (DIP), also referred to as orthophosphate (ortho-P) [12]. In most soils, ortho-P is present at extremely low concentrations. For this reason, plant association with soil microorganisms such as AMF is an evolved strategy for overcoming P-deficiency conditions [13]. Symbiotic AMF facilitates ortho-P uptake to plants through specialized structures, such as arbuscles or mycorrhizal hyphae branches, as shown in Figure 2.

Extraradical hyphae create extensive networks, often extending beyond the plant root–soil volume. Thus, the sequestration of nutrients extends to a spatial region that is not accessible by the plant roots alone. In addition to hyphae, micro- and nano-scale structures such as vesicles store nutrients (including P) [14]. Vesicle-stored nutrients serve as chemical pools in the rhizosphere network. The root–AMF network ensures sustained nutrient/carbon supply to each partner. This mutualism enhances ortho-P absorption, P mobilization in the soil, and overall nutrient use efficiency [15].

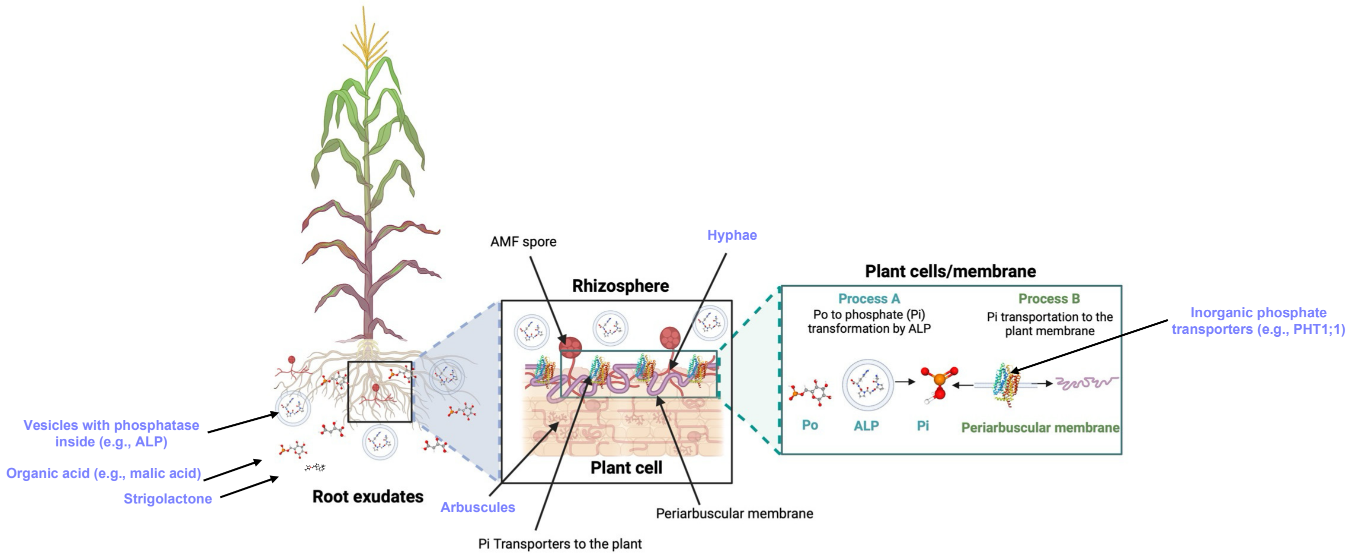

Figure 2. The root–AMF network involves AMF–exudate interactions for P uptake and transport to the plant. The diagram expands on the work by [16,17] and highlights seven key structures in purple color: (i) root exudates (PubChem ID: 15102684; [8]), (ii) D-glucose-6-phosphate as representative Po (PubChem ID: 5958, [9]), (iii) inorganic phosphorus (Pi) (PubChem ID: 1003, [18]), (iv) inorganic phosphorus transporters to the plant membrane (PiPT (PBD Entry: 8FVZ, [10]), (v) Enzymes (PubChem ID: 18985873, [19]) transformation of Po to Pi in the plant cells, (vi) arbuscules, (vii) hyphae, and (viii) vesicles. Figure created in Biorender.com.

Here, we review AMF–plant interactions for (indirect) ortho-P uptake by plants. We summarize seven key structures that are involved in P cycling within soils and highlight the major mechanisms of uptake. We also provide a summary table with key references to the seven key biomolecules involved in the process. Definitions of key terms and concepts are provided in the Supplementary Material. We close by discussing challenges and opportunities for research in AMF–plant interactions related to sustainable agriculture technology development.

2. Mechanisms of P Uptake by AMF–Plant Systems

In soil, P exists in many forms but is often categorized into three major classes: (1) soluble Pi, also referred to as DIP or ortho-P, (2) insoluble phosphorus (inorganic), and (3) Po. In many soils, soluble Pi exists primarily as the dihydrogen phosphate anion ($H_2PO_4^-$) and/or the monohydrogen phosphate anion (HPO_4^{-2}). These two ortho-P forms are commonly referred to as primary and secondary orthophosphates, respectively, with plants preferring the primary form [1]. The rhizosphere is a specialized zone in soil that regulates P dynamics. AMF within the rhizosphere transfers nutrients such as P with plants via mycelium and arbuscules. Each of the seven structures highlighted in Figures 1 and 2 is summarized below.

2.1. AMF

AMF begins its life as a spore (Figure 3) and upon maturation employs various mechanisms to uptake Po and convert to Pi for plant absorption (in exchange for beneficial chemicals). The spore germinates upon perceiving chemical signals from the plant under P deficiency, establishing symbiosis with the plant [20]. AMF enhances P uptake by the extension of mycelium through the soil. The mycelium network increases the surface area for P cycling in the rhizosphere. AMF hyphae effectively allow roots to search and transform soil P into an available form for the host plant. Uptake of Po is followed by translocation along the hyphae from external to internal mycelia, and finally to cortical root cells [11]. The external hyphae of AMF travel beyond the P depletion zone, scavenging a large soil volume and supplying ortho-P to plants in return for carbohydrates from the host plant [11].

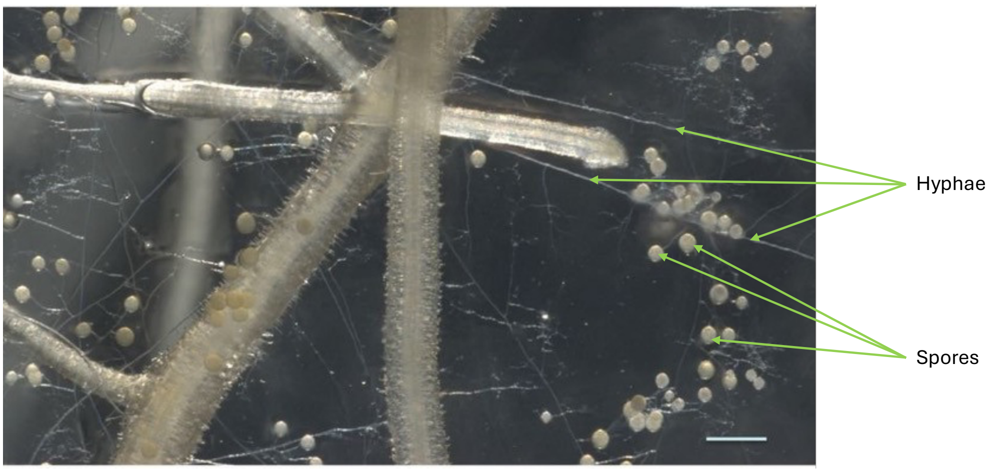

Figure 3. AMF hyphae and spores along the surface of carrot roots (*Daucus carota*) (Scale bar: 750 µm). Photo sourced from Tisserant et al. (2013) [21].

2.2. Root Exudates

Under low P conditions, plants release exudates that include phytohormones such as strigolactones (SL) (Figure 4). SL is a group of chemical compounds derived from the carotenoid biosynthesis pathway [22]. SL are signaling molecules involved in root development and response to abiotic stress conditions [22]. These phytohormones play a key role in signaling the initiation of AMF–plant symbiosis in the rhizosphere [23]. High local concentrations of SL result in the extension of fungal hyphal structures, initiating association and ultimately leading to the formation of arbuscules inside root cortex cells.

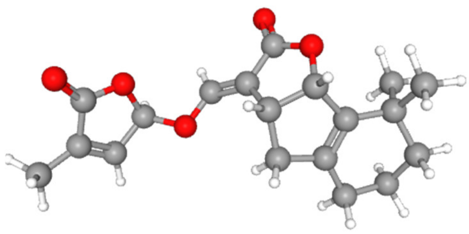

Figure 4. Ball-and-stick model for one example of a strigolactone: 5-deoxystrigol. PubChem ID: 15102684; [8]).

2.3. Organic Phosphorus

Organic phosphorus (Po) is a type of P associated with organic matter or any compound that contains an organic moiety in addition to P [24,25] and includes biologically important compounds such as nucleic acids, phospholipids, inositol phosphates, sugar phosphates, condensed phosphorus [26], monoesters, diesters, and phosphonates [27]. Figure 5 shows a ball-and-stick model for D-glucose-6-phosphate as a representative example of one of the common forms of Po in soil. Po is highly variable in soils, accounting for 20% to 80% of total P, depending on soil type and local practices [2]. Po requires specific catalytic enzymes to make it biologically available to plants as ortho-P [25].

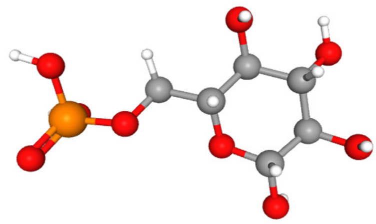

Figure 5. Ball-and-stick model for an example of organic phosphorus common to soil systems (D-glucose-6-phosphate) (PubChem ID: 5958, [9]).

2.4. Inorganic Phosphorus

In non-weathered soils, total P speciation is dominated by sparingly soluble apatite and soluble calcium phosphates. Inorganic P (Pi) is found in both primary minerals (from weathered parent material) and secondary minerals (precipitation of P with Al, Ca, and/or Fe). The soluble phase of Pi (ortho-P) is the primary form that plants uptake for fitness and nutrition [2,27–29]. However, ortho-P may take on four different forms (based on pH), with the dihydrogen form (metal-HPO_4^{-}) being preferred by plants. As shown in Figure 6, speciation curves indicate that the relevant pH for this form in water is between 2.2 and 7.3. The monohydrogen form (metal-$H_2PO_4^{2-}$) is bioavailable to plants (pH 7.3 to 12.4) but has lower metabolic efficiency.

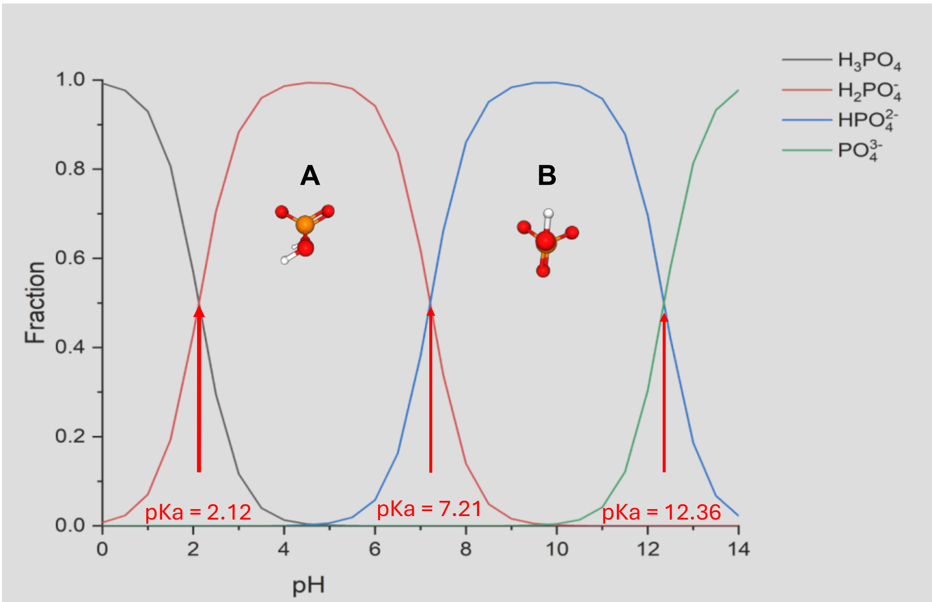

Figure 6. Speciation diagram of orthophosphate ions at different pH. The ball-and-stick model represents (A) Dihydrogen phosphate (PubChem ID: 1003, [18]) and (B) Hydrogen phosphate (PubChem ID: 3681305, [30]).

2.5. Pi Transporters

P transport from AMF to plant roots is mediated by phosphate transport activity and its expression in the extra-radical mycelium. Specific transporters, such as the protein encoded by the phosphate transporter gene (e.g., GiPT from *Glomus intraradices*), play a potentially crucial role in phosphate movement during AMF symbiosis. Plants may rely on phosphate transport via fungal mutualism in certain soil conditions; thus, the AMF influences survival based on P cycling [4]. Figure 7 presents a 3D AlphaFold model and a simple depiction of a phosphate transporter from the PiT family. The diagram also shows relevant processes of Pi transport in the plant membrane (referred to as process B in reference to Figure 2).

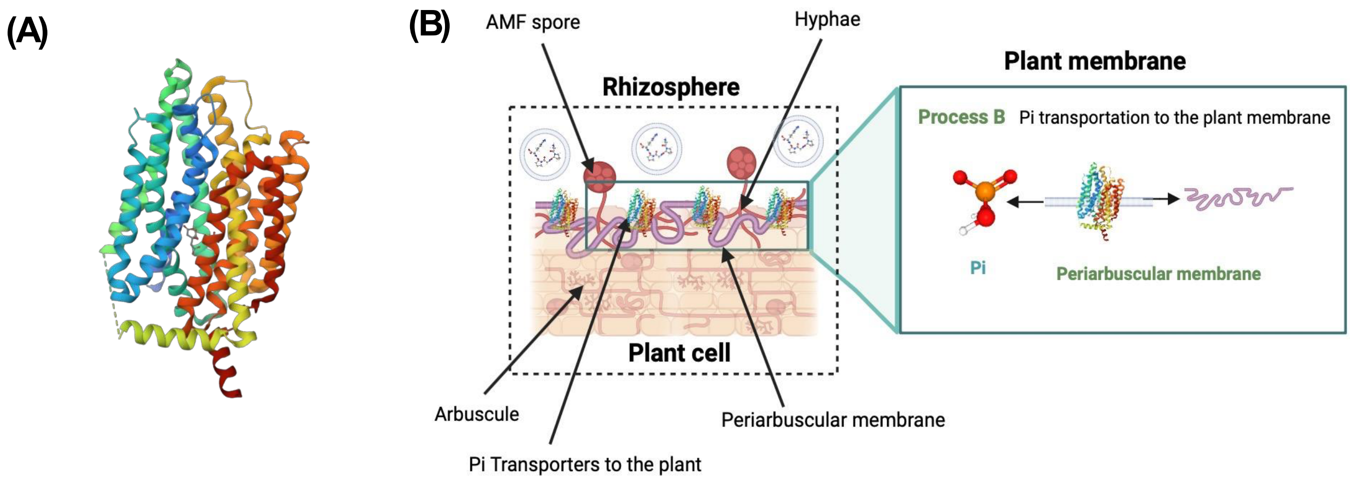

Figure 7. (**A**) A 3D AlphaFold structure of inorganic phosphate PiPT Y150A (PBD Entry: 8FVZ, [10]). (**B**) A simple diagram of PiPT location including (i) inorganic phosphorus (Pi) (PubChem ID: 1003, [18]), (ii) Enzymes (PubChem ID: 18985873, [19]). Created in Biorender.com.

2.6. Enzymes

Phosphatases are proteins that have an affinity for P (Figure 8). Phosphatases are hydrolases that catalyze the hydrolysis of phospho–ester bonds in Po substrates, releasing ortho-P as a reaction by-product. Phosphatases are categorized into many types based on the number of bonds hydrolyzed to release the ortho-P and the optimum pH for the activity [31]. As pH-dependent proteins, these biomacromolecules vary in their function and form based on the pH of the soil and local microbiome. Alkaline phosphatase (ALP) is present in alkaline soils, whereas acid phosphatase (AP) is present in acidic soils [32]. Enzymes such as ALP play a role in solubilizing forms of P which are otherwise unavailable to plants [11]. AMF phosphatases mediate the adsorption process, mineralizing organic P sources [1]. In addition, these proteins intervene in breaking down fine branches of arbuscules, releasing Po.

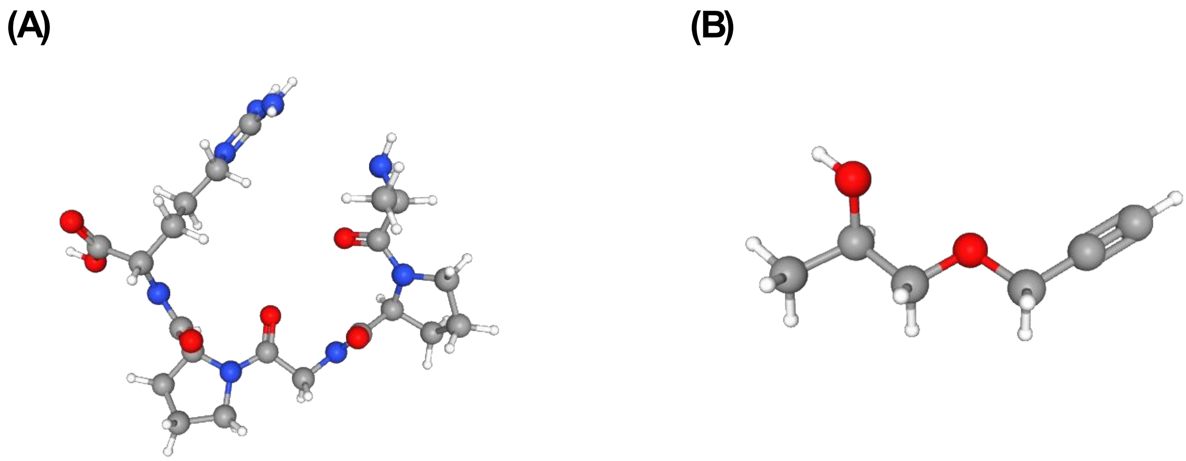

Figure 8. (**A**) Ball-and-stick model of alkaline phosphatase (PubChem ID: 18985873, [19]). (**B**) Ball-and-stick model of acid phosphatase. (PubChem ID: 12951370, [33]).

2.7. Arbuscules

Arbuscules are specialized structures generated within plant root cells by AMF and are essential for nutrient exchange. Arbuscules within root cells have a large surface area and are principal sites for P exchange between fungus and plant [34]. Figure 9 presents a simple diagram of AMF arbuscules in the plant cortical cells (inspired from [35,36]).

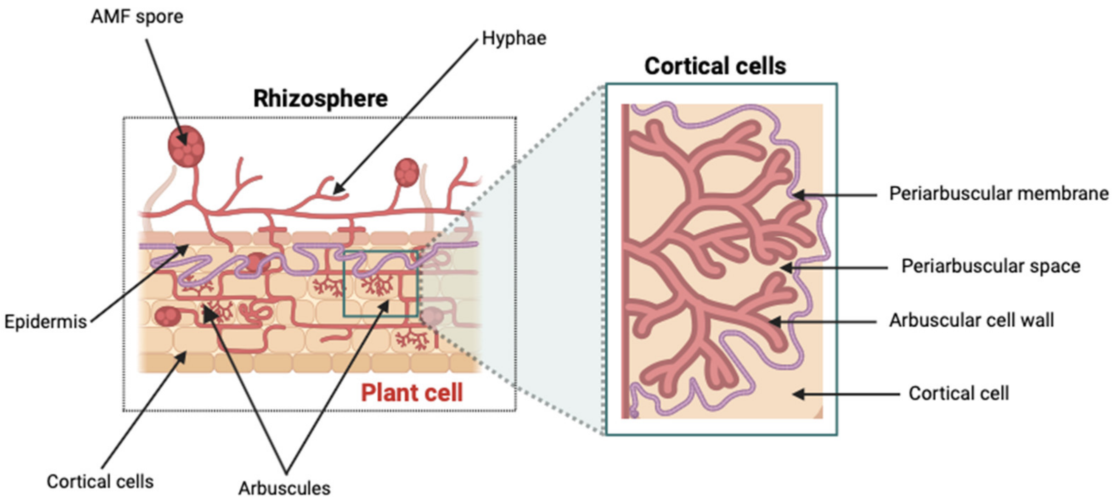

Figure 9. A simplified diagram of AMF arbuscules. Image inspired by adapted from [35,36]. Created in Biorender.com.

2.8. Hyphae

Hyphae are thread-like structures extending into the soil. Mycorrhizal association enhances P absorption by optimizing uptake and utilization, in turn acting as an extended absorption surface. This increases the capacity to acquire P from a larger soil volume than plant roots alone (Figure 10). This bio component in the AMF–plant mutualism contributes to nutrient uptake, initiating P cycling in AMF–plant mutualism [6].

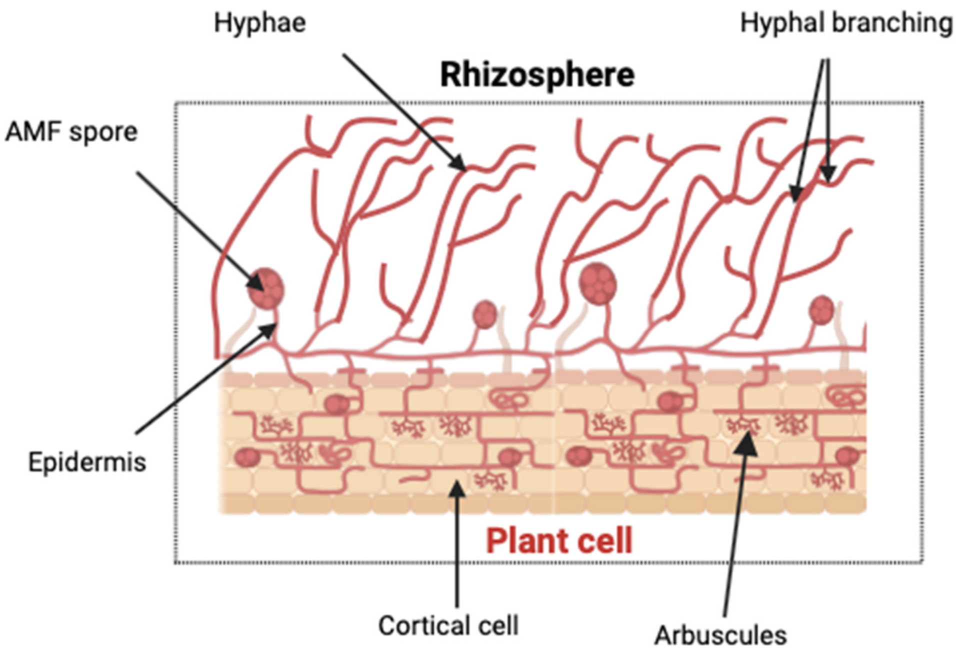

Figure 10. A simple diagram of the hyphae of AMF. Inspired by [37]. Created in Biorender.com.

2.9. Vesicles

Vesicles are storage structures formed by AMF within plant cells (Figure 11). Vesicles contain nutrient reserves that act as a sustained supply for fungi and plants. AMF actively mobilizes P in the soil by releasing vesicles containing enzymes to break down Po into a more plant-available form (Pi). This is especially advantageous in P-deficient soils, making legacy P more accessible to plants [38].

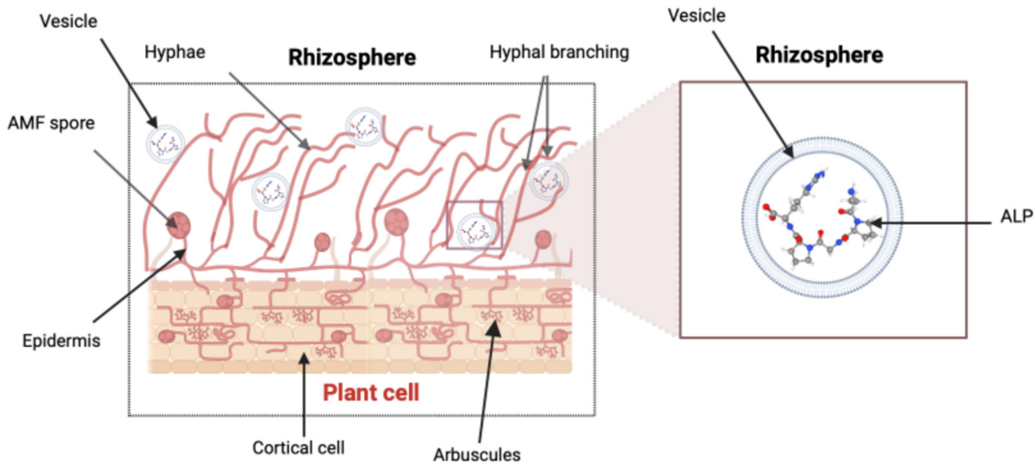

Figure 11. A simple diagram of vesicles from AMF. Inspired by [37]. Enzymes from PubChem (PubChem ID: 18985873, [19]). Created in Biorender.com.

2.10. Summary: Benefits of AMF in Soil

AMF provides numerous benefits for plants, including enhanced nutrient acquisition (P but also N, Cu, Fe, Zn, and other nutrients), disease suppression, plant stress resistance (e.g., drought tolerance, heavy metal resistance), carbon sequestration (stimulation of nitrogen fixation by legumes (green manure)), and growth promotion (e.g., suppression of soil pathogens). Mycorrhizal mutualism increases crop output without the need for P fertilizer, which is a key to sustainable agricultural and environmental practices. This benefit is possible because plant tissue P is proportional to root-accessible P, where the concentration of P in root tissues/mycorrhizal hyphae (i.e., the ectorhizosphere) is approximately 1000 times higher than the adjacent soil [1].

The seven key structures reviewed here interact together to supply the plant with Pi. Table 1 summarizes the major biocomponents of AMF–plant systems and discusses their working principles. These seven key biomolecules have key roles in P cycling, from the generation of signaling molecules such as SL to form associations with AMF, to the increased root surface area for P uptake due to the formation of hyphae, colonization of roots at the root cortical cells by arbuscules, Po transformation to Pi by AMF enzymes, vesicles, and organic acids, and finally Pi transport to plant cells by transmembrane Pi transporters. Beyond P uptake, AMF mitigates adverse effects of common agrochemical inputs such as chemical fertilizers, pesticides, and fungicides.

Table 1. Seven key biomolecules and their role/processes in AMF–plant for P uptake.

Biomolecule	Role in Soil Processes	Role in AMF	Plant Root Processes	References
Phosphatases	Hydrolyze organic P (Po) to release inorganic phosphate (Pi, Ortho-P) as reaction products for plant absorption.	Secreted by fungi (e.g., AMF) to transform (mineralization of) Po into Pi.	Root-associated phosphatases hydrolyze Po in the rhizosphere, making it available for the plant.	[2,11–13]
Phosphate transporters	Pi is released from the arbuscular into the peri arbuscular membrane by the PHT1 transporter.	PHT (e.g., PHT1) family transport mycorrhiza-specific nutrients, inducible through AMF symbiosis with plant hosts, from the soil to the shoot and mycorrhizal symbiotic interface.	Phosphate transporters, such as the PHT1 family, are present in plant roots' root epidermis and are expressed for the uptake of phosphate.	[39–41]

Table 1. *Cont.*

Biomolecule	Role in Soil Processes	Role in AMF	Plant Root Processes	References
Organic acids	The process involves the solubilization of P from mineral surfaces through ligand ex-change or the ligand-promoted dissolution of Fe oxides.	AMF microbiota promotes plant growth by the production of organic acids.	Plant root responses to P starvation result in the exudation of organic acids like citric and malic acid in the rhizosphere.	[6,38,42]
Strigolactone	Plant hormones that play a crucial role in promoting plant AMF associations during the release of P starvation in the rhizosphere.	Hypha branching and root colonization of symbiotic AMF are stimulated by these substances, which also encourage the production and release of SLs by plants, attracting beneficial microbes.	Transported from roots to shoots, these substances control shoot branching (primary root growth, lateral and adventitious root formation, and root hair development) and promote plant growth.	[23,43–46]
Arbuscules	Enhance nutrient uptake by forming associations in the rhizosphere	Major site or resource exchange within the soil regulates the colonization process between AMF plants.	Formed arbuscules within the inner root cortical cells of the host plant allowing plant–AMF nutrient exchange	[7,17,47]
Hyphae	Threadlike structures that extend into the soil matrix, increasing the surface area available for Pi uptake.	Serves as a conduct for P uptake and C exchange to AMF in return. Hyphal branches form the association with plant roots.	Increase surface area for nutrient exploration, enhancing the Pi acquisition in places where plant roots alone do not have access to it.	[7,41,48]
Vesicle	Serve as storage reservoirs for phosphatases, lipids, and carbohydrates.	Store and transport Pi acquired by AMF from soil to the plant host.	Enhance Pi transfer from AMF to the plant root cells within vesicle structures. Allows access to Pi more efficiently.	[7,49,50]

PHT1—phosphate transporter. AMF—arbuscular mycorrhizal fungi. SLs—strigolactones. Pi-transporter—phosphate transporter. Pi—inorganic P. Po—organic P.

3. Future Research Opportunities

In this section, we discuss how AMF–plant interactions shown in Figures 1–11 and Table 1 can be expanded for future research opportunities to address the challenges of P sustainability in two critical areas of technology development, such as (i) P sensing/monitoring, (ii) P recovery technologies, or (iii) Enhancing plant P uptake. AMF has been studied by inoculation in seeds to analyze their behavior-enhancing P uptake by plants before and after inoculation. This section aims to explore the potential of understanding the working principles of AMF through its seven key structures to develop technologies for P monitoring, recovery, and uptake in agricultural systems.

3.1. *Monitoring P within Natural Systems*

Biosensors (as an alternative to metabolomics analysis techniques) can be used to manipulate the biosynthesis pathways of plant metabolites (e.g., organic acids, P transporters, and other compounds involved in P acquisition pathways) implicated in phosphorus uptake. Biosensors can be designed to detect and measure specialized metabolites in plants (e.g., protein, nucleic acid, and transcript factor-based biosensors) [51]. Molecular biosensors are focused on the specialized metabolites in plants and the development of synthetic biology techniques (e.g., identifying functional genes associated with P uptake and metabolism in plants) to detection of changes in the concentration or activity of target metabolites involved in phosphorus uptake.

The design, build, test, and standardization of the sensor can be an area or opportunity for sensor development. An area of exploration is the identification of the binding domains of the metabolites, allowing the creation of standard parts for metabolite biosensors. In that sense, synthetic biological principles can prove biosensors with highly selective, and sensitive, tools for real-time monitoring of metabolite dynamics in plant tissues or rhizosphere environments [51].

Quantifying environmental P is essential for sustainable P management, such as precise fertilizer use or other water/soil quality monitoring. Current analytical methods for quantification of P are classified into five categories: chemical, biological, molecular, staining, and sensor/biosensor techniques [52]. Laboratory methods based on spectrophotometry, chromatography, or other methods are well established for high-throughput precise analysis [53]. However, the cost of sample analysis and relatively low turnaround time limit the spatio-temporal resolution of studies. For this reason, portable methods are critically important in most studies of P. Chemical techniques (colorimetry/spectrophotometry) are the current standard method adopted by the U.S. Environmental Protection Agency (US-EPA) and many other organizations. This chemical technique is based on a colorimetric response resulting from the interaction between exogenous molybdate and soluble phosphorus (as well as other exogenous chemicals). The reaction is used both in the lab and in the field for monitoring P (specifically, soluble molybdate-reactive P). In addition, portable chemosensor technologies aim to provide alternative methods for in-field measurement of inorganic and/or organic phosphorus. For example, electrochemical biosensors for environmental P quantification have attracted attention due to their unique features, such as reagent-free quantification, affordability, and portability [54]. Quantification of P is critically important to understanding/managing the dynamic nature of plant–AMF mutualism and often requires numerous devices to collectively achieve a specific monitoring goal. Although currently no devices have been developed, the AMF–plant mutualistic system is an excellent source of inspiration for biomaterial/biosensor researchers.

3.2. P Recovery

Excessive runoff of P from agricultural systems into surrounding water bodies can lead to eutrophication and harmful algae blooms. To address this, P recovery technologies are under development by many research groups, industries, and non-profit groups (among others). Some nature-inspired P recovery technologies include biosorbents based on P-binding proteins (PBP) and/or P-selective-binding protein (PstS), and other wastewater treatment systems based on whole cell systems [55]. AMF in association with wheat has been proven to play a key role in the recycling of P from sewage sludge [56]. The association of AMF with plants can decrease the need for P fertilizer application and in turn decrease P loss from agricultural systems [57]. This demonstrates the potential of AMF–plant systems to promote P circularity, contributing to sustainable management. Another potential application involves the development of biotechnologies based on phosphatase and/or phosphate transporters from the AMF–plant systems. By using phosphatase as a molecular sorbent, highly specific recovery of ortho-P from wastewater streams may be possible. Another opportunity is the use of phosphate transporters (e.g., PHT1), which have a binding motif with a high affinity towards primary/secondary ortho-P [58]. With advanced molecular biology techniques, the specific binding motif of PHT1, or a recombinant phosphatase, could be produced in an expression system, such as bacteria or yeasts. Molecular techniques may allow the development of truncated recombinant proteins that are sustainable for use as a receptor/sorbent.

3.3. Enhancing P Uptake

Encouraging mycorrhizal symbiosis helps to improve early P uptake, potentially increasing crop output without the need for P fertilizer. This is possible because plant tissue P grows in proportion to the amount of P accessible to plants, and the concentration of P in root tissue or mycorrhizal hyphae is around 1000 times higher than that just in soil solution [1]. The seven key structures mentioned in this review interact all together to supply the plant with Pi. Biomolecules have key roles in all the processes, starting with the generation of signaling molecules such as SLs to form associations with AMF, the increased root surface area to P uptake by the hyphae, the colonization at the root cortical cells by the arbuscules, Po transformation to Pi by the enzymes, organic acids, and finally the Pi transportation to the plant cells by the Pi transporters.

4. Conclusions

This manuscript illuminates established knowledge of root–AMF mutualism in the rhizosphere. Understanding the AMF–plant association is critical for development of sustainable agricultural practices. Technologies such as biofertilizers and seed inoculants employ AMF successfully and inspire new technologies such as biomolecular sensors or new bioremediation strategies based on isolated biomaterials. A systems-level view of plant-AMF interactions is important for development of sustainable P practices, as mimicry of the mutualistic association between AMF and plant roots requires development of multi-component biosystems that operate in dynamic environments.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/encyclopedia4030077/s1.

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