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From Legacy Phosphorus to Resource via Immobilization and Activation for Enhanced Fertilizer Efficiency

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Abstract: Phosphorus (P) is an essential macronutrient central to nucleic acid synthesis, photosynthesis, and energy metabolism. Although agricultural soils contain substantial total P reserves, only a minute fraction is plant-available, leaving more than 40% of global croplands P-deficient. Fertilizer supplementation is therefore indispensable; however, most applied phosphate is rapidly immobilized through precipitation with Ca, Al, or Fe minerals or by strong sorption to soil matrices, resulting in crop recovery efficiencies typically below 25%. This inefficiency has generated extensive residual and legacy P pools that can buffer crop demand yet also contribute to eutrophication when mobilized into surface waters. This review explores the dynamics of these hidden soil P reserves and evaluates emerging strategies to transform them into renewable agronomic resources. Engineering approaches including biochar amendments and bioelectrochemical systems such as soil, sediment, and plant microbial fuel cells, can restrict dissolved P losses, induce redox-mediated immobilization, and support controlled P recycling. Complementary biological pathways mediated by phosphate-solubilizing microorganisms and rhizospheric enzyme systems reactivate immobilized or organic P, thereby improving plant nutrient acquisition and fertilizer-use efficiency. Framed within a phosphorus cascade perspective, this synthesis highlights how integrating soil chemistry, microbial ecology, and environmental engineering can enhance P utilization, sustain crop productivity, and mitigate nutrient driven water pollution.

Keywords: Biochar amendment, Nutrient recycling, Phosphate-solubilizing microorganisms, Rhizosphere nutrient dynamics, Soil phosphorus transformation

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Introduction

Climate change and population growth are intensifying global pressures on agriculture to secure sufficient food supplies [1,2]. By 2050, the world population is projected to exceed 9.7 billion, requiring substantial improvements in crop productivity under increasingly variable environmental conditions [3,4]. Declining soil fertility, driven by intensive land use, further constrains yields and heightens the risk of food insecurity [5,6]. Addressing these challenges depends on enhancing agricultural productivity while improving the efficiency of P fertilizer management.

P is an essential macronutrient that underpins nucleic acid synthesis, photosynthesis, and energy transfer via adenosine triphosphate [7,8]. Plants acquire P primarily as orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) from the soil solution, yet concentrations are typically very low (0.05 to 0.30 μg P mL^{-1}). Although soils contain substantial total P reserves, less than 1% exists in dissolved, plant-available forms [9,10]. Fertilizer inputs are therefore indispensable, but phosphate anions are highly reactive and rapidly immobilized through precipitation and sorption with calcium, aluminum, and iron compounds, leaving only 10-25% available to crops in the year of application [11]. As a result, more than 40% of the world's arable soils remain P-deficient [12,13], with similar limitations reported in grassland and managed systems (e.g., smart-farm) [9].

Low crop recovery combined with long-term fertilizer surpluses has driven the accumulation of residual P in soils [14,15]. This accumulated pool, termed "legacy P" [16], represents the net balance between inputs (i.e., fertilizers, manures, atmospheric deposition, and weathering) and outputs (i.e., crop harvest, leaching, runoff, and drainage) [14,17,18]. Regional nutrient budgets highlight the scale: between 1965 and 2007, arable land in Oceania and Western Europe received cumulative inputs of 560 and 1115 kg P ha^{-1}, respectively, while crop uptake accounted for only 100 and 350 kg P ha^{-1} [10,19]. Consequently, soils retain large stores of P bound to minerals and organic matter [20]. While these reserves may buffer crop demand during fertilizer scarcity, excessively high legacy P levels can also disrupt soil nutrient balance by reducing the availability of essential micronutrients such as iron and zinc, thereby constraining plant nutrition, disturbing metabolic processes, and ultimately lowering crop yields [21-25].

The Korean context exemplifies this dual challenge. Nutrient balance assessments identify Korea as one of the OECD countries with the highest positive P surpluses, reflecting decades of intensive livestock manure application despite a ~20% decline in cultivable land between 1990 and 2017 [26]. During this period, Korea and Japan reported the second- and first-highest average P surpluses, 46 and 57 kg ha^{-1}, respectively, among 34 OECD countries. Historical analyses likewise place Korea among the top two nations in nutrient surpluses across both OECD and Asian contexts [13, 27]. These patterns underscore the agronomic and environmental consequences of persistent P accumulation, constraining crop performance through nutrient imbalances while simultaneously increasing the risk of diffuse losses and downstream eutrophication.

Legacy P is tightly linked to the soil–water continuum [28]. Under rainfall and hydrological transport processes, surplus P is mobilized through runoff, leaching, and subsurface flow, ultimately contributing to eutrophication in rivers and lakes [29-33]. P enrichment stimulates harmful algal blooms that degrade water quality, reduce biodiversity, and impair ecosystem services such as fisheries and recreation [34,35]. These blooms also threaten drinking water supplies, as cyanobacteria release toxins, taste- and odor-causing compounds, and precursors of disinfection by-products, while simultaneously increasing turbidity and pH [36-38]. Conventional drinking water treatment plants often struggle to remove cyanobacteria effectively, and pre-oxidation may exacerbate risks by inducing cell lysis, toxin release, and by-product formation [39,40]. Thus, legacy P is both a constraint on soil fertility and a major driver of water quality deterioration with direct implications for ecosystem integrity, human health, and water resource management.

Taken together, legacy P stocks in soil represent both an opportunity and a challenge. If mobilized efficiently, they could reduce reliance on external fertilizer inputs and sustain crop production [41]. Estimates suggest that accumulated soil P could support maximum global yields for nearly a century if it were plant-available [42,43]. Realizing this potential, however, requires targeted strategies that enhance bioavailability through chemical, biological, and technological interventions. Such approaches increasingly depend on interdisciplinary advances that integrate soil science, microbiology, and environmental engineering, with emerging tools offering novel avenues for P management [44-48].

This review synthesizes current understanding of residual and legacy P cycling in agricultural soils and evaluates strategies for activating these pools. Particular emphasis is placed on soil amendments and environmental microorganisms, which are central to P mobilization and retention [41,49-51]. Among soil amendments, biochar, a carbon-rich, stable, nutrient-bearing material, has attracted considerable interest for its ability to alter nutrient dynamics and improve P availability [52,53]. Notably, engineering-scale biochar systems have also shown promise in reducing dissolved P losses from tile-drained fields while allowing captured P to be recycled back into soils, thereby contributing to both soil fertility and environmental protection [52]. In parallel, bio-

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Agric. Environ. Sci. 2025, 44, 422-442

electrochemical technologies such as soil, sediment, and plant microbial fuel cells are being explored for their capacity to stimulate redox-mediated transformations and trap P at soil–water interfaces [46,54-57]. Complementing these technological strategies, phosphate-solubilizing bacteria (PSB) represent key microbial groups that secrete organic acids and enzymes to mobilize otherwise recalcitrant P pools, thereby enhancing plant uptake [10,55,58-60]. Collectively, microbiological and scalable technological approaches provide synergistic pathways to reframe residual and legacy P as a resource rather than a liability, thereby advancing the sustainability of agroecosystems.

Results and Discussion

P Cycling in the Soil

P cycling at the global scale is frequently described as an "open" or "sedimentary" system, in contrast to the comparatively rapid and atmosphere-linked cycles of carbon, nitrogen, and sulfur [61,62]. In contrast to these elements, P lacks a major gaseous phase, and its redistribution occurs predominantly through soils, waters, and living organisms. Microorganisms play central roles in this process, acting as both sources and sinks of P via transformations that span a wide redox spectrum, from reduced phosphine (–III) to oxidized phosphate (+V) [44,63]. Despite its ecological importance, the biochemical and genetic mechanisms that govern many of these microbial transformations remain poorly resolved.

Soils represent the largest terrestrial reservoir of P and serve as the critical interface linking global P pools with plant and microbial demand (Fig. 1). Within soils, phosphorus is broadly classified into three categories: (i) soil solution P (<10 μmol L^{-1}), directly available for plant uptake; (ii) inorganic P (Pi), often associated with calcium, iron, or aluminum compounds; and (iii) organic P (Po), contained in microbial biomass, residues, and humic substances [64,65]. The availability of P is determined less by total content than by solubility and speciation, both of which are strongly regulated by soil chemistry, mineralogy, and biological activity. More than 80% of fertilizer-derived phosphate can become unavailable within days of application, primarily through precipitation with Ca^{2+} in calcareous soils or with Al^{3+} and Fe^{3+} in acidic soils, as well as through sorption to mineral oxides or microbial immobilization [66,67]. Beyond these internal soil processes, phosphorus dynamics extend along the soil–water continuum: surplus P in surface layers is mobilized via runoff, erosion, or leaching, fueling eutrophication, harmful algal blooms, and the release of algal organic matter that ultimately complicates drinking water treatment by increasing cyanotoxins and precursors of disinfection by-products (DBPs).

Organic P in Soil

Organic P typically constitutes 30–50% of total soil P, though this proportion can vary widely with land use and soil type [68]. Major Po forms include orthophosphate monoesters (e.g., inositol phosphates), diesters, phosphonates, and organic polyphosphates [69]. Inositol hexa-phosphate is particularly abundant due to its strong sorption to mineral surfaces, which prevents hydrolysis and renders it relatively recalcitrant [70]. By contrast, phosphomonoesters and diesters are more labile and can be mineralized rapidly under favorable conditions. Anthropogenic activities also contribute novel Po compounds, such as phosphonate-based pesticides and detergent additives, thereby diversifying soil Po pools [71]. The microbial community acts as both a sink and a source of Po, immobilizing P into biomass and releasing it through enzyme-mediated mineralization, especially via phosphatases [72,73]. Differences in mineralization kinetics across compounds create a wide spectrum of turnover rates that regulate plant availability and long-term cycling [74].

Inorganic P in Soil

Inorganic P, often accounting for 60–80% of total P in agricultural soils, is dominated by mineral-associated forms [14,75]. Primary minerals such as apatites [$Ca_5(PO_4)_3OH/F$] are slowly weathered sources of Pi, whereas secondary minerals include Al-

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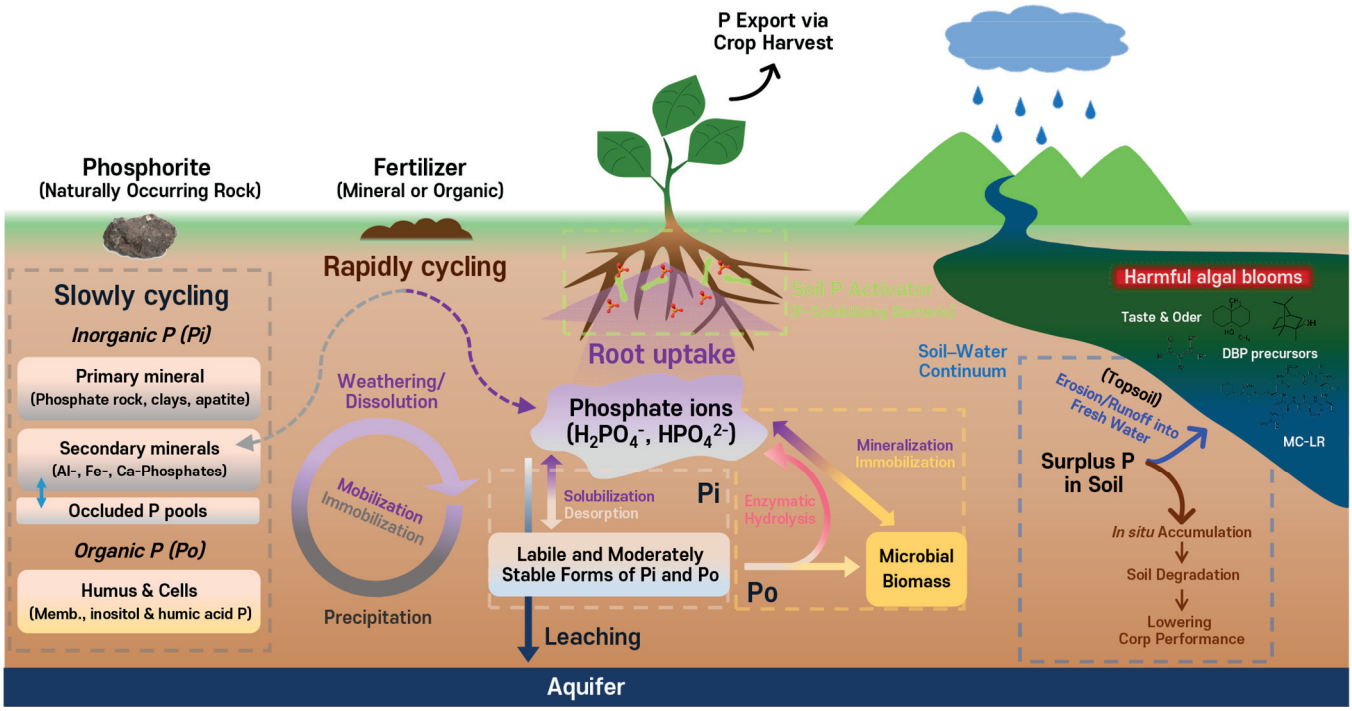

Figure 1. Conceptual schematic of soil P cycling, showing transformations within soil–plant systems and P transport to freshwater, where it drives eutrophication and harmful algal blooms.

and Fe-phosphates (e.g., variscite, strengite) and sparingly soluble Ca–P compounds [76-78]. Soil pH exerts a strong control on speciation: $H_2PO_4^-$ dominates under acidic conditions, HPO_4^{2-} under neutral to mildly alkaline conditions, and PO_4^{3-} under high pH [79]. The relative distribution of Pi pools along a continuum of lability reflects interactions among dissolution–precipitation, adsorption–desorption, and mineral occlusion. While labile Pi fractions can exchange rapidly with the soil solution and support plant uptake, semi-labile and non-labile pools become locked within mineral matrices, effectively sequestering P over agronomic timescales [80-82].

Coupled Biotic and Abiotic Transformations

Soil P dynamics are governed by a complex interplay of biotic and abiotic reactions, some occurring within seconds and others over decades [83,84]. Abiotic processes include adsorption to Fe- and Al-oxides, precipitation with Ca^{2+}, and dissolution equilibria, all of which are sensitive to pH and redox status [85]. Biotic processes include microbial immobilization, enzymatic mineralization of organic P, and rhizosphere-driven mobilization through exudation of phosphatases and organic acids [84]. Together, these processes regulate the equilibrium concentration of phosphate in soil solution, which remains extremely low relative to crop demand. The microbial biomass in particular acts as both a transient reservoir and a mediator of transformations, stabilizing P in the short term while driving long-term cycling through mineralization–immobilization feedbacks [86-88].

Consequences of P Dynamics Along the Soil–Water Continuum

The accumulation of P in topsoil represents not only a constraint for crop nutrition but also a critical source of downstream water quality degradation. Surface soils (i.e., topsoil; 0–15 cm) typically contain 50–3000 mg P kg^{-1}, and when surplus P from fertilizers and manures exceeds crop uptake, the risk of mobilization via erosion and runoff rises sharply [15,89-92]. P exported from fields through dissolved pathways or as enriched particulates is a primary driver of nutrient loading in rivers and lakes, where it accelerates eutrophication [93-95].

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Agric. Environ. Sci. 2025, 44, 422-442

P enrichment promotes harmful algal blooms (HABs), dominated by cyanobacteria, diatoms, or green algae, that profoundly alter aquatic chemistry and ecosystem functioning [96]. These blooms elevate pH, turbidity, and organic carbon, and they release algal organic matter (AOM) in both extracellular (EOM) and intracellular (IOM) forms [97]. EOM is continuously secreted during active growth, whereas IOM is released during senescence or through cell lysis induced by oxidation, coagulation, or other treatment processes [98]. AOM is chemically complex, containing polysaccharides, proteins, nucleic acids, and lipids, with polysaccharides often comprising up to 80% of the dissolved organic carbon pool. This composition renders AOM a major precursor of DBPs during drinking water chlorination or chloramination [99,100].

DBPs formed from AOM include both carbonaceous species (C-DBPs), such as trihalomethanes (THMs) and haloacetic acids (HAAs), and nitrogenous DBPs (N-DBPs), such as haloacetonitriles (HANs) and haloacetamides (HAcAms) [101,102]. While THMs and HAAs often account for the majority of DBP mass, N-DBPs are increasingly concerning due to their higher genotoxicity and cytotoxicity, despite their lower concentrations [103-106]. Adding to these risks, cyanobacteria frequently produce microcystin-LR (MC-LR), a hepatotoxin of global concern [107]. MC-LR is highly stable, resistant to conventional oxidation, and can persist through standard advanced oxidation processes (AOPs), requiring high oxidant doses and precise control to achieve reliable degradation [108-111].

Thus, P transport from soil to freshwater ecosystems initiates a cascade of consequences that extend beyond ecological degradation to human health risks in drinking water supplies. By driving algal blooms, soil-derived P indirectly intensifies DBP formation and cyanotoxin persistence during disinfection, linking agricultural nutrient surpluses with regulatory and treatment challenges. Recognizing this soil–water treatment continuum is critical for developing P management strategies that safeguard both agricultural productivity and potable water quality.

P Immobilization Strategies in Agricultural Soils

Phosphorus immobilization is increasingly used to curb labile P losses from intensively managed soils and to mitigate downstream eutrophication. A wide spectrum of phosphorus-immobilizing materials (PIMs) has been explored, including natural clays, industrial by-products (e.g., red mud, steel slag), chemical amendments (e.g., aluminum and calcium salts), and carbonaceous materials derived from biomass [112-115]. These amendments are generally low-cost and widely available, often providing dual benefits: reducing P leaching while improving soil physicochemical conditions to enhance crop P uptake and utilization efficiency. Their efficacy, however, varies markedly with soil texture, pH, application rate, and amendment composition [116,117].

Among PIMs, two complementary approaches are particularly promising. Biochar, produced by pyrolysis of agricultural residues, functions as both a P-retaining medium and a soil conditioner, aligning nutrient management with circular-economy principles. Bioelectrochemical systems, notably soil, sediment, and plant microbial fuel cells (MFCs), represent an emerging technology that modulates P availability through microbially driven redox reactions at the soil–water interface. Together these strategies integrate material engineering and microbial ecology, offering scalable options for in situ control of P mobility and long-term agroecosystem sustainability.

Biochar: Properties and Mechanisms in Soil

Definition and production

Biochar is a carbon-rich, porous material produced via thermochemical conversion of biomass under oxygen-limited conditions. Feedstocks range from crop residues and forestry by-products to animal manures and sewage sludge, providing a versatile reuse pathway for agricultural and municipal wastes [118]. Pyrolysis temperature and residence time largely govern its yield and functionality. Low-temperature ("slow") pyrolysis (300–650°C) typically produces biochar with higher volatile-C and nutrient content, whereas high-temperature (>650°C) conditions enhance carbon stability, aromaticity, and mineral ash content [119]. This variability allows tailoring of biochar properties for specific agronomic or environmental applications, including nutrient retention and pollutant immobilization [120-122].

https://doi.org/10.5338/KJEA.2025.44.41
Agric. Environ. Sci. 2025, 44, 422-442

Physicochemical properties

Biochar's performance in soil is largely dictated by its porosity, surface area, and surface functionality. The coexistence of nano-, meso-, and macropores provides large sorptive surfaces for ions and microbial colonization. High-temperature biochars generally exhibit greater surface area and mineral content (Ca, Mg, Fe, Al) than low-temperature counterparts, favoring phosphate sorption through electrostatic and ligand-exchange interactions [123]. Conversely, low-temperature biochars retain more labile organic matter and surface functional groups, which enhance cation exchange capacity (CEC) and organic complexation potential. Feedstock composition further modulates these characteristics: wood-based biochars possess highly porous, stable carbon matrices, while manure-derived biochars are nutrient-rich and often alkaline, contributing additional phosphorus during application [124].

Biochar–microbe interactions and P dynamics

Beyond its direct sorptive capacity, biochar serves as a biologically active habitat that mediates phosphorus cycling through its interactions with soil microorganisms. The porous matrix offers refugia and attachment sites for microbial communities, including phosphorus-solubilizing bacteria (PSB) and mycorrhizal fungi, thereby supporting sustained microbial activity even under stress conditions. Biochar's redox-active surfaces can shuttle electrons or adsorb root exudates, indirectly influencing microbial respiration and nutrient turnover. PSB associated with biochar surfaces (e.g., *Bacillus*, *Pseudomonas*, *Rhizobium*) release organic acids and phosphatases that convert immobilized P into plant-available forms while maintaining overall P retention by preventing leaching. Meanwhile, biochar–microbe aggregates promote micro-scale gradients of oxygen and pH, enabling simultaneous P immobilization near mineral surfaces and biological mineralization within protected niches. This dual function stabilizes P in soil while sustaining bioavailability to plants. Biochar also influences the microbial community composition and enzyme activity by moderating soil acidity, moisture, and redox potential. Increased microbial biomass and alkaline phosphatase activity are frequently reported following biochar addition, reflecting stimulated P turnover. Thus, biochar functions as both a biophysical scaffold and biogeochemical moderator, bridging abiotic P immobilization and biotic P recycling, which is crucial for closing the soil–plant phosphorus loop in sustainable agroecosystems.

Effects on soil properties

Biochar incorporation induces multifaceted changes in soil physicochemical and biological properties that directly regulate phosphorus (P) mobility and availability. Its high surface area and reactive functional groups facilitate sorption and physical entrapment, thereby reducing P leaching and promoting soil aggregation. The intrinsic alkalinity of many biochars increases soil pH, which can mitigate Fe/Al-driven phosphate fixation in acidic soils, while shifts in micronutrient solubility may occur in more alkaline systems. Improvements in aeration, moisture retention, and habitat heterogeneity further stimulate microbial metabolism and enzyme-mediated P mineralization, underscoring that biochar–soil interactions are highly context-dependent [125].

Recent meta-analyses provide quantitative evidence supporting these mechanisms. A global synthesis of 124 studies reported that biochar increased available P and microbial biomass P by 45% and 48%, respectively, across diverse soil and biochar types, while concurrently reducing NO_3^-–N and NH_4^+–N concentrations unless combined with organic fertilizers. Biochar characteristics, particularly feedstock, pyrolysis temperature, and C:N ratio, were identified as major regulators of soil P responses, with low-temperature or manure-derived biochars showing the strongest enhancement of P availability [126,127]. Complementarily, a 2024 meta-analysis demonstrated that straw- and wood-derived biochars improved plant biomass (up to 20–30%) and grain yield while strengthening lodging tolerance, especially in soils with high organic matter content and fine texture conditions that promote P cycling and nutrient efficiency [128]. Furthermore, a 2023 global meta-analysis revealed that biochar generally increases bacterial richness and diversity, accompanied by shifts in major phyla such as decreased Acidobacteria (−14.6%) and increased Gemmatimonadetes (+19.8%). These microbial community changes were strongly associated with biochar load, C:N ratio, pyrolysis temperature, and soil pH, suggesting that biochar-driven enhancements in microbial diversity and functional potential may further reinforce P mineralization and soil fertility [129].

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Agric. Environ. Sci. 2025, 44, 422-442

Current mechanistic understanding combined with emerging meta-analytic evidence highlights that biochar exerts synergistic physicochemical and biological effects on soils, improving P availability, nutrient efficiency, crop performance, and microbial functioning. These findings emphasize the importance of selecting biochar types and application conditions optimized for specific soil environments.

Mechanisms of P immobilization

The immobilization of P by biochar occurs through several concurrent mechanisms (Fig. 2) [130-132]. (i) Electrostatic attraction and anion exchange between phosphate species ($H_2PO_4^-$, HPO_4^{2-}) and protonated or cationic surface sites; (ii) Ligand exchange on Fe, Al, or Ca oxide phases; (iii) Physical entrapment within micropores; (iv) Biochar–microbe coupling that enhances phosphate sorption via biofilm development and microbial EPS binding; and (v) pH-mediated precipitation or solubility control.

Through these combined abiotic–biotic mechanisms, biochar minimizes P losses to leaching and runoff while sustaining biologically available P pools. Engineered or microbially inoculated biochars further enhance these functions, positioning biochar as a key multifunctional amendment for circular nutrient management [133].

Microbial fuel cells: mechanistic routes for P immobilization in situ

Definition and system principle

Microbial fuel cells (MFCs) represent a class of bioelectrochemical systems that exploit the metabolic activity of electroactive microorganisms to convert the chemical energy stored in organic matter directly into electricity while driving redox transformations in environmental matrices [134]. Among their many configurations, soil and sediment MFCs (SMFCs) have emerged as promising in situ platforms for the remediation of organic and inorganic contaminants [135,136]. These systems generally consist of a buried

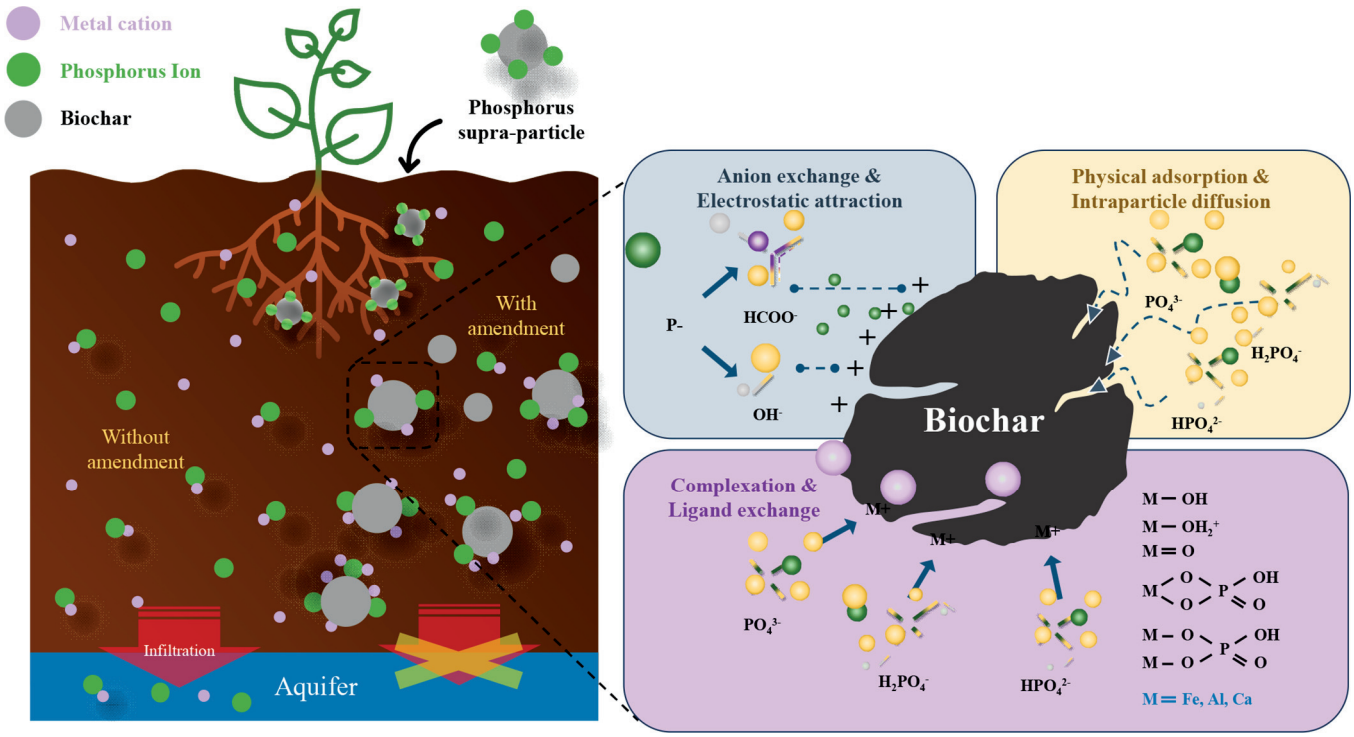

Figure 2. Conceptual schematic illustrating phosphorus (P) immobilization mechanisms in soil following biochar or supraparticle fertilizer amendment. The amendment enhances P retention through anion exchange, electrostatic attraction, physical adsorption, intraparticle diffusion, and complexation or ligand exchange with metal oxides (Fe, Al, Ca). These processes collectively limit P mobility, reducing leaching and infiltration into the aquifer, thereby mitigating risks of groundwater contamination and preserving water quality

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Agric. Environ. Sci. 2025, 44, 422-442

anode located in the reduced soil or sediment layer and a cathode positioned near the oxic interface (e.g., soil surface or overlying water), typically connected through an external circuit and operating without a physical membrane [46]. During microbial respiration under anaerobic conditions, electroactive bacteria oxidize organic substrates, liberating electrons that are transferred to the anode as an insoluble electron acceptor [137]. The electrons then migrate through the external circuit to the cathode, where they reduce terminal electron acceptors such as dissolved oxygen [138]. This process establishes a self-sustained redox gradient across the soil profile and induces proton flux through the porewater, thereby influencing geochemical equilibria relevant to nutrient and metal cycling.

When implemented within agricultural soils or rhizospheric environments, MFCs can modulate the redox potential and pH distribution in the vicinity of roots or electrodes, generating favorable conditions for the immobilization of P species (e.g., Pi & Po) [57]. Despite limited experimental evidence, these autogenic electrochemical gradients have been shown to suppress P leaching toward groundwater by promoting adsorption, precipitation, and bio-mineralization near the cathodic zone (Fig. 3a). Accordingly, MFCs provide a mechanistically rich and environmentally sustainable framework for in situ phosphorus capture rather than acting solely as bio-power devices [54].

Extracellular Electron-Transfer (EET) Mechanisms

The functional efficiency of MFCs hinges on the ability of microorganisms to exchange electrons with insoluble electron acceptors or donors, a process termed extracellular electron transfer (EET) [139,140]. Two fundamental pathways are recognized: direct electron transfer (DET) and indirect (mediated) electron transfer (IET or MET). These EET modes dictate how electrons generated from microbial metabolism reach the anode or are relayed to other mineral phases (Fig. 3b & c).

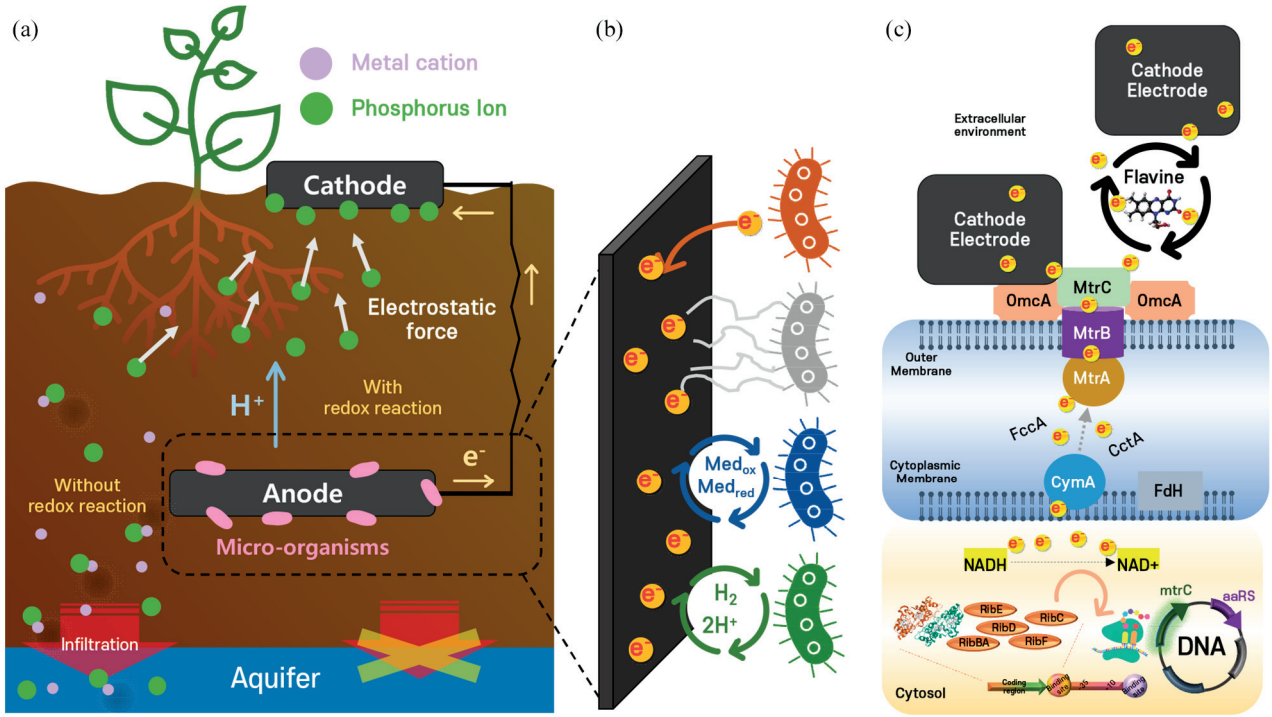

Fig. 3. Conceptual model of soil microbial fuel cell (SMFC) mediated phosphorus immobilization in soil. (a) In situ soil or plant MFC configuration showing suppression of phosphorus leaching toward groundwater, where redox-driven electron flow promotes phosphate migration and accumulation near the cathode zone; (b) Core electron-transfer routes in MFCs: direct cell–electrode contact, nanowire conduction, mediator-assisted transfer, and hydrogen-mediated indirect transfer; (c) Electron-transport pathway in Shewanella oneidensis MR-1 from NADH oxidation through cytoplasmic and outer-membrane cytochromes enabling extracellular electron discharge to the cathode.

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Agric. Environ. Sci. 2025, 44, 422-442

(i) Direct Electron Transfer

DET is mediated through electrically conductive cellular components such as outer-membrane c-type cytochromes and conductive pili ("nanowires"). Electroactive genera including Shewanella and Geobacter utilize multicomponent cytochrome complexes, including the Mtr (metal-reducing) system in Shewanella oneidensis MR-1, comprising CymA, MtrA, MtrB, MtrC, and OmcA, to bridge the quinone/quinol pool within the cytoplasmic membrane to the outer membrane and, ultimately, to extracellular solid electron acceptors [141,142].

These cytochromes and e-pili facilitate electron discharge from the cell to the anode surface or to Fe- and Mn-bearing minerals, overcoming the insulating barrier of the cell envelope [143]. In Geobacter sulfurreducens, type IV pili composed of PilA subunits form nanowires with metallic-like conductivity, which support biofilm formation and long-range electron transport over micrometer distances. Atomic-force microscopy and cryo-electron studies have confirmed that these structures exhibit high current densities capable of reducing Fe(III) and Mn(IV) oxides reactions directly relevant to phosphate immobilization via Fe–P or Mn–P co-precipitation.

(ii) Indirect (Mediated) Electron Transfer

In IET, redox-active soluble compounds serve as electron shuttles between microbial cells and external acceptors. These mediators may be endogenous (biosynthesized by microbes) or exogenous (artificially added). Endogenous mediators include flavins such as riboflavin and flavin mononucleotide (FMN), which possess conjugated cyclic structures and high redox potentials that enhance electron mobility. For instance, *S. oneidensis* secretes flavins that reversibly couple to the Mtr system to facilitate metal reduction and electrode respiration [144]. Exogenous mediators, including neutral red, methylene blue, anthraquinone-2,6-disulfonate (AQDS), or thionin, can further augment electron transfer, especially for weakly electroactive strains. For example, thionin addition enabled Saccharomyces cerevisiae to achieve significant anodic current production by enhancing electron shuttling across cell membranes. The incorporation of such mediators increases the rate and distance of electron flow, thereby intensifying redox cycling processes in soil MFCs that indirectly regulate the Fe/Mn speciation and phosphate binding capacity [145].

Mechanistic scenarios for in situ P capture

SMFCs harness extracellular electron transfer (EET) to couple microbial oxidation of organics at the anode with reduction reactions at a spatially separated cathode (Fig. 3a). When deployed directly in soils or sediments and/or configured around plant rhizospheres, this bioelectrochemical architecture establishes persistent redox and pH gradients that can be engineered to immobilize P in situ rather than allowing it to leach to groundwater or surface waters [54]. Although empirical demonstrations of P immobilization under autogenic MFC-driven electrochemical conditions remain limited, the underlying geochemical drivers are well established. The operation of soil or plant MFCs generates several interacting physicochemical and biological pathways that together constitute a cascade of P immobilization processes. The principal mechanisms include:

(i) Cathodic micro-oxidation zone: Oxygen reduction at an air-exposed cathode sustains an oxidizing microenvironment at the soil–water or sediment–water interface. This favors formation and renewal of Fe(III)/Mn(IV) oxyhydroxides with high affinity for orthophosphate and drives Fe–P co-precipitation. In rooted systems, cathodic fields can synergize with radial oxygen loss from roots, intensifying Fe plaque on root surfaces and enhancing phosphate binding (Fig. 3a). (ii) Local alkalinization and mineral precipitation: Cathodic oxygen reduction consumes protons and raises pH in the cathode's diffusion layer. Elevated pH promotes precipitation of Ca/Mg phosphates and, in ammonium-rich matrices, struvite ($NH_4MgPO_4 \cdot 6H_2O$) within centimeters of the electrode [146]. This geochemical "alkaline halo" provides a controllable sink for dissolved reactive P. (iii) Electromigration and electrostatic partitioning: Current flow and localized charge distributions bias anion transport toward the cathode and cation transport toward the anode. While bulk solute movement in soils is diffusion/advection-dominated, sustained low-density currents (μA–mA) can enrich phosphate in the cathodic zone where sorption and precipitation immobilize it. (iv) Redox control of Fe–P cycling: Anodes buried in reduced horizons can act as alternative electron acceptors, tempering dissimilatory Fe(III) reduction and thereby

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Agric. Environ. Sci. 2025, 44, 422-442

limiting P release from Fe–P solids. Where Fe reduction is needed for other contaminant processes, hybrid designs can pair a reactive cathode "cap" that rapidly re-oxidizes Fe2+ and re-sorbs phosphate, closing a bio-redox loop [147]. (v) Biofilm-mediated retention: Electrode-associated biofilms present high-surface-area matrices rich in extracellular polymeric substances (EPS), functional groups, and in situ-formed metal oxides that bind phosphate. Such biofilms can be stabilized in place or periodically harvested as a P-enriched material.

Having established routes to immobilize and spatially retain P, we next consider biological re-activation pathways that return immobilized or legacy P to the plant, principally via phosphate-solubilizing microorganisms

Soil P Activation via Phosphate-solubilizing bacteria

Phosphate-solubilizing microorganisms (PSMs) constitute a diverse functional guild capable of transforming sparingly soluble inorganic and organic phosphorus into plant-available orthophosphate (Pi) [49]. Within this group, phosphate-solubilizing bacteria (PSB) play a central role owing to their high metabolic versatility, rapid growth, and close association with plant roots. Dominant bacterial taxa include *Bacillus*, *Pseudomonas*, *Burkholderia*, *Acinetobacter*, *Rhizobium*, and *Paenibacillus*, whereas fungi such as *Aspergillus*, *Penicillium* and *Actinomycetes* including *Streptomyces* contribute complementary functions through extensive hyphal networks and intense organic-acid exudation [148-150]. Beyond mobilizing phosphorus, PSB frequently produce auxins, cytokinins, gibberellins, siderophores, antibiotics, and deaminase, thereby enhancing root development and plant stress tolerance [151]. Fig. 4 illustrates the representative biochemical mechanisms, including acidification, chelation, siderophore secretion, extracellular polymeric substance (EPS) production, and enzymatic mineralization, that collectively govern soil P activation. The following subsections describe these pathways in detail and their regulatory controls.

Acidification and Chelation via Organic Acids and Proton Release

A principal mechanism of PSB-mediated P solubilization is bio-acidification of the microenvironment. Many Gram-negative

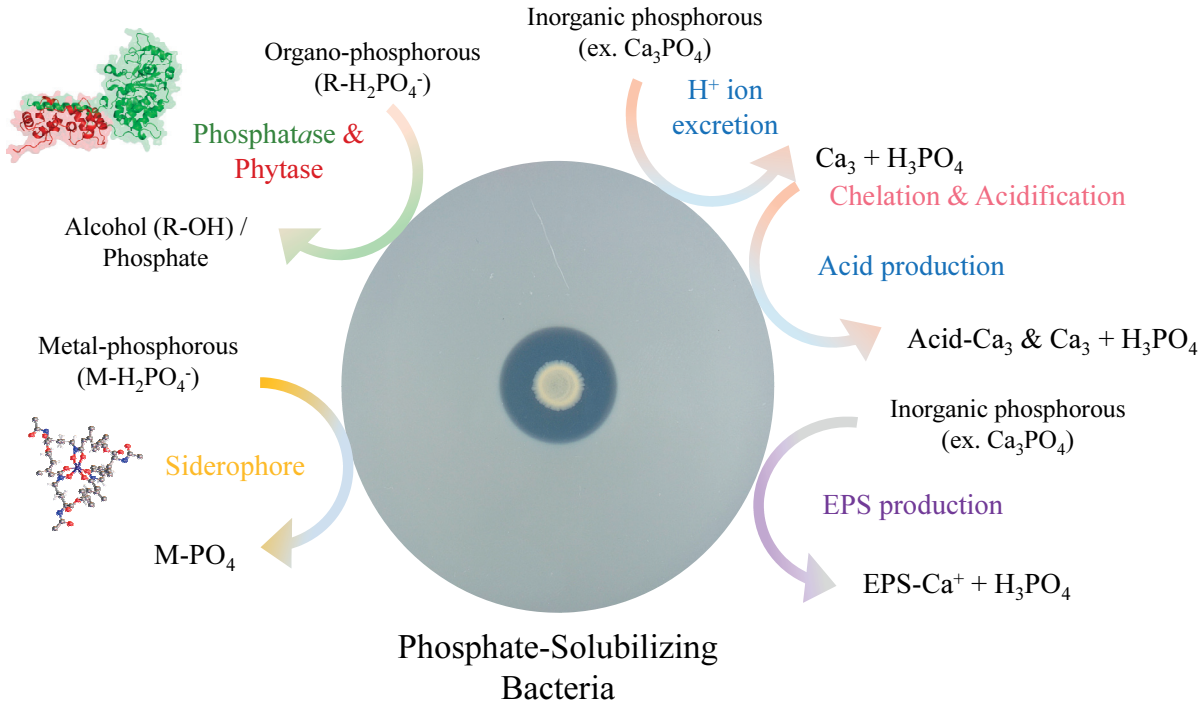

Fig. 4. Mechanistic schematic of inorganic and organic phosphate solubilization by environmental microorganisms. Representative in vitro halo (clear zone) illustrates phosphate-solubilizing activity of an isolated environmental microorganism (Representative halo assay image captured by the author; used with permission).

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Agric. Environ. Sci. 2025, 44, 422-442

PSB oxidize glucose through the pyrroloquinoline-quinone (PQQ)–dependent glucose dehydrogenase (GDH) system, producing gluconic and 2-ketogluconic acids, both potent chelators of Ca^{2+}, Fe^{3+}, and Al^{3+} ions [152]. Additional organic acids such as citric, oxalic, malic, succinic, lactic, fumaric, and tartaric further enhance dissolution by (i) donating H^+ that lowers local pH, (ii) complexing metal cations bound to phosphate, and (iii) competing with phosphate for mineral surface sites.

Respiratory CO_2 hydration and nitrification of NH_4^+ also contribute protons, sustaining an acidic halo around cells and roots. These combined processes convert mineral phosphates such as tricalcium phosphate and hydroxyapatite into soluble orthophosphate without large bulk-soil pH shifts [153]. Carbon source type, C:N ratio, and soil buffering capacity are key determinants of acidification intensity.

Siderophore-Mediated Mobilization of Fe-Associated P

Under Fe-limiting or oxidizing conditions, PSB secrete siderophores that chelate Fe^{3+} with high affinity. By withdrawing Fe from Fe(III) oxyhydroxides and Fe-phosphate complexes, siderophores indirectly liberate adsorbed phosphate, increasing Pi concentrations in the soil solution [154]. This mechanism is particularly relevant in acidic or periodically reduced soils where Fe–P associations dominate P retention. Siderophore production mitigates Fe deficiency in plants, coupling micronutrient acquisition with P mobilization. Regulation depends strongly on Fe availability, pH, and competing organic ligands such as humic substances.

EPS and Biofilm Microenvironments

PSB frequently form biofilms that exude extracellular polymeric substances (EPS) enriched in carboxyl, hydroxyl, and phosphoryl groups. These polymers bind divalent and trivalent cations, weaken phosphate–metal linkages, and create hydrated microenvironments that retain soluble P and enzymes [155]. Co-occurrence of EPS and organic acids markedly enhances phosphate release compared with either mechanism alone, indicating synergistic chemical and structural effects. EPS also improves soil aggregation and root colonization, extending the spatial reach of P solubilization beyond the immediate cell surface.

Inorganic-Acid and Redox-Driven Dissolution

Although less potent than low-molecular-weight organic acids at equivalent pH, microbially derived inorganic acids such as H_2SO_4 (from *Thiobacillus*) and HNO_3 (from *Nitrosomonas*) can dissolve Ca- and Fe-phosphates. In anoxic zones, biogenic H_2S reacts with ferric phosphate to form ferrous sulfate and releases phosphate ions [65]. These redox-dependent reactions demonstrate that P mobilization in soils is not exclusively acid-based but also governed by electron-transfer processes and sulfur/nitrogen cycling [156].

Enzymatic Mineralization of Organic P

Up to 50 % of total soil P exists in organic forms such as phytate, nucleic acids, phospholipids, and organo-phosphonates that require enzymatic hydrolysis before plant uptake [157]. PSB secrete diverse enzymes, including: Phosphatases (acid and alkaline) that hydrolyze phosphate mono- and di-esters [158]. Their expression is Pi-regulated via the Pho regulon, and the principal families (PhoA, PhoD, PhoX) differ in metal cofactors and optimal pH ranges [159]. Phytases, which dephosphorylate myo-inositol hexakisphosphate (phytate), releasing orthophosphate and lower inositol phosphates [160]. C–P bond-cleaving enzymes (phosphonatases and C–P lyases) that mineralize organophosphonates. Acid phosphatases dominate in acidic soils, whereas alkaline forms prevail in neutral to alkaline environments. Temperature, substrate availability, and adsorption to mineral surfaces further influence activity [161]. Together, these enzymes govern the mineralizationn branch of the P cycle, complementing inorganic dissolution mechanisms.

Rhizospheric Integration and Plant–Microbe Coupling

The functional expression of PSB is maximized within the rhizosphere, a narrow soil zone strongly influenced by plant root exudates and microbial activity (Fig. 5). Here, PSB act as biogeochemical intermediaries that bridge insoluble soil phosphorus

https://doi.org/10.5338/KJEA.2025.44.41
Agric. Environ. Sci. 2025, 44, 422-442

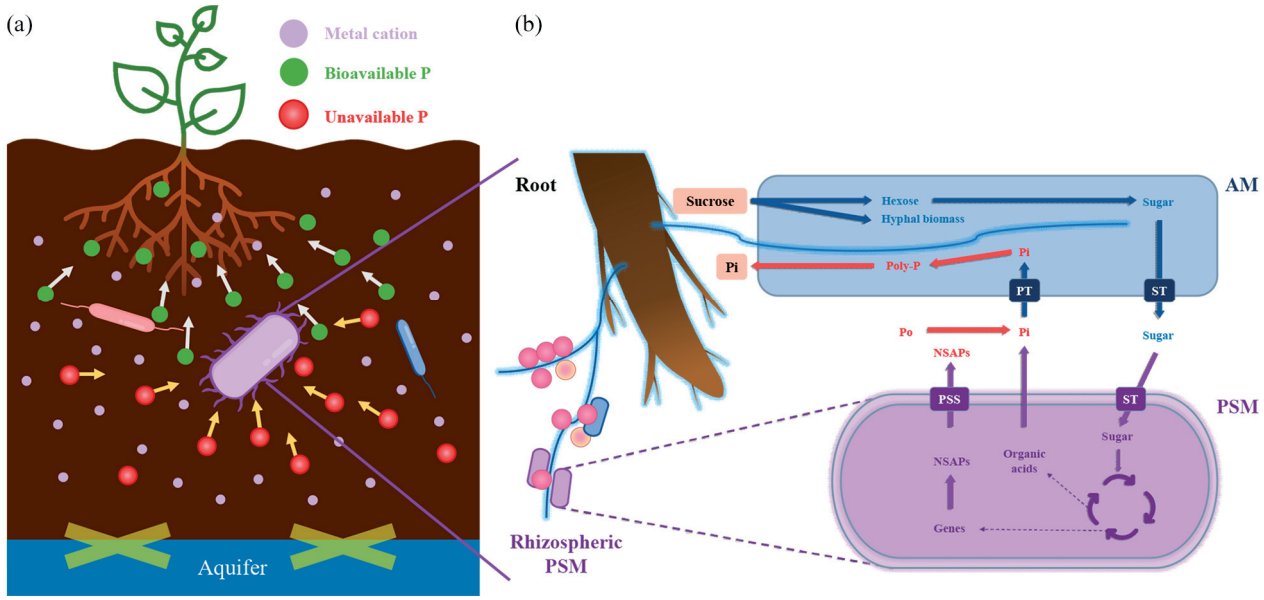

Fig. 5. (a) Conceptual model of phosphorus activation mediated by rhizospheric phosphate-solubilizing microorganisms (PSMs). PSM-driven pathways including acidification, chelation, siderophore secretion, EPS production, and enzymatic mineralization convert unavailable soil P (red) into bioavailable orthophosphate (green); (b) Released Pi is absorbed by plant roots via phosphate transporters (PT), while root-derived sugars sustain microbial metabolism through sugar transporters (ST). Microbial enzymatic systems (nonspecific acid phosphatases, phytases) convert Po to Pi, part of which is stored transiently as polyphosphate (poly-P). The coupled plant–microbe exchanges maintain a dynamic P cycle that might enhance nutrient use efficiency and mitigates P loss.

pools and plant uptake systems [162]. Through the concerted release of organic acids, protons, siderophores, and phosphatases, PSB mobilize both inorganic and organic P forms, transforming them into bioavailable orthophosphate (Pi) that diffuses toward the root surface. In parallel, plants secrete a variety of carbon-rich compounds such as sugars, amino acids, and carboxylates that sustain microbial metabolism and maintain the reducing power necessary for these biochemical transformations [163]. This reciprocal nutrient exchange establishes a finely balanced microbial–plant phosphorus cycle at the root–soil interface.

Recent experimental studies further highlight the practical potential of PSB–biochar–plant systems. In saline–alkaline agricultural soils, the combined application of PSB with biochars derived from *Parthenium* and sewage sludge significantly improved soil pH regulation, cation/anion balance, and cation exchange capacity while enhancing *Spinacia oleracea* biomass and nutrient uptake compared to single amendments. These synergistic effects were particularly pronounced at 1–3% application rates, demonstrating that biochar provides a physicochemical matrix that stabilizes PSB activity and amplifies P mobilization under chemically stressed soil conditions [164]. Complementary evidence comes from studies targeting Fe-bound phosphate, one of the most recalcitrant forms of soil P. The integration of PSB with Mg-modified lignin biochar markedly enhanced $FePO_4$ dissolution by as much as 17-fold due to biochar-induced structural transformation of Fe–P particles and increased microbial organic acid production. Such modifications preferentially exposed crystal planes more susceptible to PSB-mediated dissolution, illustrating how engineered biochars can expand the biochemical niche of PSB beyond Ca-bound P solubilization [165]. These emerging findings demonstrate that PSB–biochar–plant systems can be strategically engineered to overcome multiple soil constraints, including salinity, alkalinity, and Fe-bound P recalcitrance, thereby offering a promising, scalable approach for enhancing P availability, nutrient efficiency, and plant productivity across diverse agroecosystems.

However, PSB performance in field soils often deviates from in vitro expectations because soil matrices are spatially heterogeneous and biologically competitive [166]. Inoculated PSB strains must contend with native microbial communities, fluctuating redox conditions, and rapid re-adsorption of solubilized phosphate onto mineral surfaces [167]. Consequently, the rhizosphere microhabitat where root exudates locally enhance nutrient availability, moisture, and carbon flux is generally more favorable for PSB establishment and activity than bulk soil environments [168]. Within this microenvironment, PSB can persist as rhizosphere resi-

https://doi.org/10.5338/KJEA.2025.44.41
Agric. Environ. Sci. 2025, 44, 422-442

dents or root-associated epiphytes, improving nutrient acquisition and strengthening plant tolerance to abiotic stresses such as salinity, drought, and metal toxicity.

An additional layer of interaction arises from symbioses with arbuscular mycorrhizal fungi (AMF). AMF extend the functional reach of plant roots through dense hyphal networks that scavenge phosphorus from otherwise inaccessible soil domains. Plants engaged in AMF symbiosis can achieve intracellular Pi concentrations several orders of magnitude higher than those in the surrounding soil solution. Yet, many AMF lack genes encoding nonspecific acid phosphatases (NSAPs) and therefore depend on co-associated PSB to mineralize organic P sources [169]. In return, AMF and plant roots release fructose, carboxylates, and amino acids that stimulate PSB growth and phosphatase expression. Such mutualistic feedbacks amplify Po mineralization, accelerate Pi release, and enhance P flux through the mycorrhizal pathway. Metagenomic analyses confirm that AMF hyphospheres harbor enriched populations of PSB and other P-cycling taxa, indicating that fungal hyphae can act as microbial recruitment corridors linking soil P reservoirs to plant tissues [170].

Overall, the rhizosphere serves as the ecological nexus where chemical, microbial, and plant processes governing phosphorus activation converge. Effective P transfer from soil to plant depends on the synchronization of microbial solubilization, enzymatic mineralization, and mycorrhizal transport with root uptake kinetics. Future optimization of these interactions through co-inoculation strategies combining PSB and AMF, selective enrichment of rhizospheric consortia, or integration with engineered carriers such as biochar and bioelectrochemical modules hold strong potential for transforming legacy phosphorus into a renewable, biologically managed nutrient resource in sustainable agroecosystems.

Materials and Methods

This review was developed using a structured literature search and qualitative synthesis approach. Relevant publications were identified through major scientific databases, including Web of Science, Scopus, PubMed, and Google Scholar. Search queries incorporated combinations of keywords such as “legacy phosphorus,” “residual phosphorus,” “phosphorus activation,” “phosphate immobilization,” “biochar,” “microbial fuel cells,” “phosphate-solubilizing microorganisms,” and “soil P transformation.” The search primarily targeted studies published between 2010 and 2024, whenever possible, to capture both foundational concepts and recent technological developments. However, earlier seminal works were additionally incorporated when necessary to contextualize key mechanisms or provide historical perspectives on phosphorus cycling and management.

While a formal meta-analysis was not conducted, quantitative results from individual studies were systematically compared to evaluate recurring patterns, identify converging or diverging outcomes across experimental systems, and enhance the robustness of the synthesized conclusions. Only peer-reviewed journal articles, authoritative reports, and high-quality review papers were included. Studies lacking methodological transparency or analytical rigor were excluded. The final selection reflects a comprehensive body of evidence spanning soil chemistry, microbial ecology, agronomy, and environmental engineering relevant to phosphorus immobilization, activation, and recovery.

Conclusion

Phosphorus management must now transition from a fertilizer-intensive paradigm toward the recovery and reuse of residual and legacy P accumulated in agricultural soils. This review outlines an integrated framework that links redox-driven immobilization with microbial reactivation to establish a self-sustaining phosphorus cycle. Electrochemically induced redox gradients, achievable through bioelectrochemical systems or amendment-driven soil redox modulation, immobilize soluble P via Fe/Mn oxide formation, thereby curbing leaching losses and forming stable yet bio-accessible reservoirs. Subsequent rhizospheric reactivation medi-

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Agric. Environ. Sci. 2025, 44, 422-442

ated by plant–microbe interactions converts these immobilized pools into plant-available forms. Root-associated microorganisms, including phosphate-solubilizing bacteria, mycorrhizal fungi, and heterotrophic decomposers, exude organic acids and phosphatases that liberate P from mineral or biochar-bound complexes. These biotic processes are spatially organized along root exudation zones, where micro-scale redox and pH fluctuations promote both P solubilization and uptake. The resulting rhizospheric feedback loop, in which roots, microbes, and mineral interfaces co-regulate P availability, represents a critical biological lever for sustaining productivity under reduced fertilizer input.

Biochar serves as a structural and electrochemical bridge in this cascade, stabilizing captured P, fostering microbial colonization, and maintaining redox connectivity between soil particles and root surfaces. Integrating these biogeochemical and biological processes yields a closed, redox-responsive P cascade from abiotic capture to biotic activation that redefines legacy phosphorus as a renewable nutrient reservoir rather than a pollutant source. Looking forward, advancing this framework will require multi-scale validation, from microscale electron transfer to field-scale nutrient fluxes, and the development of adaptive agroecosystems that combine engineered amendments, electrochemical control, and rhizosphere engineering. Such systems could ultimately enable precision phosphorus management, turning legacy P from an environmental liability into a regenerative asset for sustainable agriculture.

Data Availability: All data are available in the main text or in the Supplementary Information.

Author Contributions: Y.Y. conceived, designed the research, and wrote the manuscript; K.D., A.J.H., A.S., K.J.J., S.Y., S.J., S.Y. and C.M. reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

Notes: The authors declare no conflict of interest

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Additional Information:

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Agric. Environ. Sci. 2025, 44, 422-442

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