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Review Article

From Soil Nutrient Stocks to Root-Accessible Flux: Rethinking Soil Fertility in Cropping Systems

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Abstract

Soil fertility assessments commonly rely on total nutrient stocks, operationally defined extractable pools, and field-calibrated crop responses. Although valuable for nutrient management, these measurements do not fully explain when, where, or how rapidly nutrients become accessible to active roots. This critical review synthesizes the soil chemical, microbial, and plant processes linking nutrient reserves with crop nutrient acquisition. We distinguish nutrient stocks, soil solution concentrations, resupply rates, root-accessible fluxes, and net plant acquisition, emphasizing their distinct meanings and measurement scales. Mineral dissolution, sorption and desorption, organic matter mineralization, diffusion, mass flow, microbial immobilization, and root activity jointly influence nutrient delivery. We critically compare conventional extractions with ion-exchange methods, diffusive gradients in thin films, isotope tracing, rhizosphere imaging, root observations, and serial plant nutrient budgets. Each approach measures a different component of nutrient availability, and no single indicator reliably captures the complete soil–root system across nutrients and cropping environments. We propose a multiscale, testable framework connecting nutrient release, delivery to active roots, actual plant acquisition, and crop performance. It distinguishes three questions: whether nutrients are released, whether they reach absorbing roots when required, and whether acquisition contributes to growth and yield. Future studies should combine repeated soil measurements, microbial transformation rates, spatial root observations, and whole-plant nutrient accumulation across developmental stages and field conditions. Independent validation against calibrated soil-test baselines is essential to establish when additional measurements improve nutrient diagnosis and management decisions. This process-aware approach offers a practical direction for understanding nutrient accessibility while maintaining long-term soil fertility across cropping systems.

Keywords: Rhizosphere biogeochemistry; Microbial nutrient turnover; Diffusion and mass flow; Root system architecture; Diffusive gradients in thin films; Soil-test calibration

1. Introduction

Soil fertility assessment commonly relies on laboratory measurements of nutrient concentrations and chemically extractable pools [1–3]. These measurements provide practical indices for fertilizer recommendations, but they represent selected properties of a soil sample rather than the complete sequence by which nutrients reach and enter roots [1, 3]. Total nutrient stocks describe the mass present in defined soil pools; routine extractions estimate quantities mobilized by particular reagents under specified conditions [2, 3]. Neither measure, by itself, quantifies the rate of nutrient transfer through soil water to an absorbing root surface [4]. Mechanistic approaches have long linked soil solution concentrations, solid-phase buffering, ion movement, and root geometry to nutrient acquisition [2, 4]. The central challenge is therefore not to replace established soil tests, but to clarify what they measure and when additional process information improves their interpretation.

The distinction between nutrient quantity and nutrient delivery is especially clear for phosphorus (P). A soil can contain substantial P reserves while sustaining a low phosphate concentration in solution because phosphate interacts strongly with mineral surfaces [5, 6]. Conversely, an exchangeable or weakly retained pool can replenish soil solution as roots absorb nutrients, although the rate depends on soil chemistry and transport conditions [5]. Nitrogen (N) illustrates a different set of constraints. Organic N transformations regulate the formation and turnover of potentially available N compounds [7], while nitrate, ammonium, and some organic N forms differ in mobility and in the uptake responses of plant species [8]. Findings from natural plant communities show that the relative availability of N forms can influence uptake preferences, but these

patterns should not be transferred to field crops without crop-specific evaluation [8]. Thus, an estimate of 'available nutrient' has meaning only in relation to a specified nutrient form, soil environment, root system, and observation interval [3, 5].

Conventional soil testing retains considerable agronomic value when a method is calibrated against crop response within an appropriate soil and management domain [3]. Its predictive usefulness does not require the extractant to reproduce the chemical conditions surrounding living roots [2, 3]. Nevertheless, calibration cannot automatically be transferred across contrasting soils, sampling depths, cropping systems, or developmental stages. Evidence from forest ecosystems, where common soil chemical measurements sometimes poorly predicted stand productivity, illustrates the broader limits of using a single chemical index as a universal measure of ecosystem functioning [9,10]. Those forest results do not invalidate calibrated agronomic tests; instead, they reinforce the need to define the system and response variable for which a test has predictive value [9, 10]. Bulk-soil measurements also omit part of the biological environment that determines local nutrient accessibility. Across plant communities, root traits are linked to contrasting fungal collaboration strategies [11]. Roots modify rhizosphere pH, soluble carbon inputs, nutrient concentrations, and microbial processes that influence nutrient transformations near the absorbing surface [12]. Root system architecture and exudation can modify the soil volume explored and the chemical environment encountered by roots, although evidence from perennial and forest systems must be interpreted cautiously when discussing annual crops [13]. Consequently, soil nutrient delivery is neither a purely chemical property of bulk soil nor a fixed attribute of the plant; it arises from the interaction of soil processes, root spatial distribution, and biological activity [12, 13].

Time introduces a further distinction between soil supply and plant requirements. In managed cropping systems, the synchronization of N release with crop demand has been recognized for decades [14]. A recent cross-ecosystem synthesis placed plant–soil nutrient synchrony within a broader account of nutrient cycling and agroecosystem design [15]. Temporal asynchrony has also been documented outside croplands, although such evidence describes ecosystem-level patterns rather than direct delivery rates at root surfaces [16]. Accordingly, this review does not present supply–demand synchrony as a new concept. Its narrower contribution is to evaluate whether information on nutrient release, transport, and access by active roots adds explanatory or predictive value beyond existing, crop-calibrated soil fertility indices.

For clarity, four quantities are distinguished throughout the review. A nutrient stock is the mass in a defined soil pool and sampling domain. A nutrient resupply rate describes the transfer of a nutrient from solid or organic pools toward dissolved, potentially accessible forms over a specified interval. A root-delivery flux describes nutrient movement to an absorbing root interface, with its value dependent on the defined area or root length, time scale, and soil conditions. Root uptake is entry of nutrient into the plant, whereas a change in whole-plant nutrient content measures net accumulation over an interval and may differ from gross uptake if nutrient losses or sources outside soil uptake are relevant [4,17]. The terms 'root-accessible nutrient flux' and 'root-delivery flux' are used here as analytical descriptions rather than as claims that a single standard method directly measures all processes. Their proposed value must be judged by whether they help explain measured nutrient acquisition and crop performance [17].

This critical review brings together soil nutrient chemistry, microbial turnover, root function, and available measurement approaches. It considers where established methods are informative, where mechanistic indicators may add value, and where the evidence is too limited to infer a reliable crop-level benefit. Priority is given to published mechanistic investigations, field-based crop studies, method comparisons, and foundational models. Findings from forests and natural grasslands are identified as contextual evidence rather than treated as direct agronomic validation. No new meta-analysis is undertaken. The review culminates in a testable framework that compares predictions based on conventional soil tests with those informed by dynamic nutrient measurements, root traits, and independently observed plant nutrient accumulation.

2. Soil Processes Governing Nutrient Supply to Roots

Nutrients in soils occur in pools that differ in chemical form, accessibility, and rates of turnover [3,6]. For P, relevant pools include phosphate in soil solution, reversibly sorbed phosphate, mineral-associated forms, and organic P compounds that require transformation before most uptake can occur [6,18]. For N, the distinction includes ammonium and nitrate in solution, dissolved organic compounds, microbial biomass N, and organic matter pools with differing physical protection and decomposition potential [7,19]. These are operational categories rather than isolated compartments: material can move among them through sorption, dissolution, decomposition, mineralization, microbial assimilation, and subsequent turnover [18,19]. Therefore, a large measured stock does not necessarily imply rapid replenishment of the forms available near an active root [3].

Soil solution concentration represents the immediately dissolved fraction, but its interpretation requires knowledge of exchange with solid phases [2]. When uptake lowers the concentration adjacent to a root, desorption or dissolution may replenish the dissolved pool; the speed and extent of replenishment depend on the composition and reactivity of the soil [2,5]. The term buffering should be used precisely: chemical buffering characterizes the change in sorbed or exchangeable quantities associated with a change in solution concentration, whereas a kinetic resupply rate concerns how quickly that adjustment occurs [2,3]. A soil can have appreciable buffering capacity and still supply nutrients slowly if the relevant reactions or transport pathways are limited [5]. Effective diffusion is also influenced by pore-water connectivity, pathway tortuosity, and interactions between the dissolved nutrient and the solid phase [2,4]. For weakly mobile nutrients, jointly considering concentration,

resupply, and transport is therefore more informative than considering any one of these attributes alone [4,5].

Phosphate exemplifies the influence of mineral chemistry on nutrient accessibility. Sorption to iron- and aluminum-bearing surfaces, interactions with calcium-bearing minerals, and soil pH can maintain low dissolved phosphate concentrations even where total P is substantial [5,6]. Rhizosphere processes may alter local pH, release organic ligands, or affect mineral reactions and thereby change phosphate mobilization near roots [5,12]. At the same time, a higher chemically extractable P value does not establish that phosphate is delivered more rapidly to the root surface or accumulated in the plant. That inference requires independent measurements of P uptake or a transport-relevant indicator [5,6]. Organic P adds further complexity because gross mineralization, simultaneous immobilization, and subsequent recycling can occur even when net changes in an extractable pool are small [18]. Mineral-derived nutrient inputs must also be interpreted at the appropriate time scale. Biological activity can contribute to mineral weathering and alter reactive mineral surfaces [20]. At broader spatial scales, the release of P through chemical weathering varies with lithology, solution chemistry, and the environmental setting [21]. Long-term changes in soil development are associated with shifts in plant nutrient-acquisition strategies [22], and comparisons along soil-age sequences show that diverse strategies can coexist during ecosystem development [23]. These findings establish that mineral nutrient reservoirs and plant access are dynamic over long intervals. They do not, by themselves, quantify nutrient release during a single crop season. The seasonal contribution of weathering requires measurements or appropriately tested process estimates in the cropping soil of interest [20,21].

After release into soil solution, nutrients reach roots through interacting transport processes. Mass flow denotes movement of dissolved nutrient with water toward the root system, whereas diffusion results from gradients in dissolved nutrient concentration, including those produced by root uptake [4]. The relative contribution of these processes depends on nutrient form, the spatial pattern of water and nutrient supply, soil structure, and root geometry [2,4]. In particular, phosphate depletion may develop around an absorbing root when local diffusion and chemical replenishment cannot match root removal [5,6]. Depletion zones can overlap as roots proliferate, making their geometry and spacing relevant to acquisition [4]. Functional–structural models such as OpenSimRoot allow root architectural variation to be examined alongside nutrient uptake processes; model behavior, however, should not be interpreted as direct field validation without independent measurements [24]. Soil architecture affects whether nutrient-containing domains are accessible to growing roots. The arrangement of aggregates and pores, nutrient placement, and root spatial distribution jointly determine how closely an active root approaches a nutrient source [4,24]. In field-grown maize, Erel et al. [25] showed that the relationships linking root and rhizosphere traits with P acquisition depend on soil type. This finding cautions against transferring a root trait–uptake relationship unchanged among fields [25]. Comparative work involving perennial grassland and differently managed wheat systems also illustrates that soil properties and root traits vary together across contrasting production contexts [26]. Neither result establishes that root architecture alone controls nutrient uptake; chemistry, biological activity, and root function must be considered jointly [4,25].

Nitrogen cycling differs from phosphate dynamics because microbial processes repeatedly change the chemical forms present in soil. Mineralization releases inorganic N from organic substrates, while microbial assimilation can temporarily retain available N in biomass [7,19]. Nitrification converts ammonium-derived N into nitrate through microbial oxidation and may alter the forms and locations accessible to roots [27]. In certain plant species, root-released compounds can inhibit nitrification, demonstrating that plants can influence the transformation of soil N rather than only absorb its products [27]. Evidence that N-form availability influences plant uptake strategies [8] does not mean that an increase in one inorganic N pool will invariably increase crop acquisition. Uptake must be interpreted against simultaneous microbial immobilization, transport, root activity, and crop demand [7,8].

Soil organic matter is both a source of nutrients and a substrate for microorganisms, but its total quantity does not directly specify the rate at which plant-accessible N is produced [19,28]. Mineral-associated organic matter may participate in N cycling when microbial and chemical interactions facilitate access to its constituents [28]. The relative contribution of different organic N pools can differ among soils, as shown by evidence that nominally more resistant fractions can participate in microbial immobilization and plant N acquisition [19]. Decomposition rates also depend on substrate properties and biological processes rather than following one fixed trajectory [7,29]. Broad patterns observed during long-term decomposition are informative but should not be substituted for crop-season estimates of mineral N release [29].

These examples suggest a practical sequence for interpreting soil fertility: nutrient pools must provide potentially accessible forms; reactions and organisms must replenish the solution; water-linked transport must deliver dissolved nutrients toward roots; and roots must take up those nutrients under the prevailing developmental conditions [2,4,17]. A limitation at any one stage can weaken the relationship between a soil-test value and plant acquisition. However, the sequence should not be mistaken for four independent steps, because roots and microorganisms also modify solution chemistry and the rates of nutrient transformation [12,17]. The conceptual process map in figure 1 summarizes these connections and indicates where complementary measurements could distinguish chemical limitation, transport limitation, and uptake limitation. Such distinctions are hypotheses to be tested against plant nutrient accumulation and crop performance, not conclusions that can be inferred from soil concentrations alone.

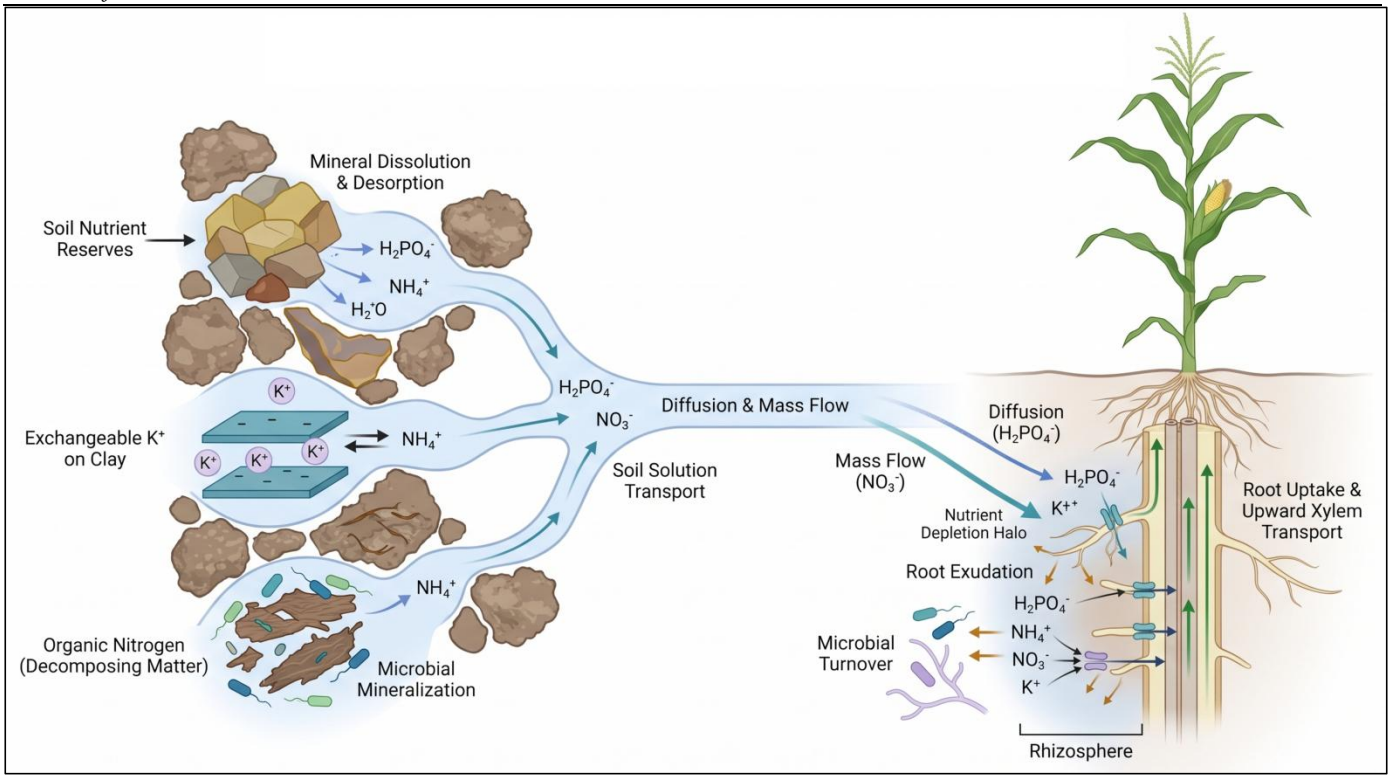

Figure 1. Conceptual processes linking soil nutrient pools to nutrient delivery and acquisition by roots. Mineral dissolution, desorption, and microbial mineralization contribute to the replenishment of dissolved nutrients, while diffusion and mass flow transport nutrients through soil water toward active root surfaces. Root exudation, microbial assimilation and turnover, and root architecture modify these pathways. Arrows represent potential processes rather than measured rates or a universal direction of net nutrient change. The figure is a synthesis of established soil nutrient chemistry and rhizosphere mechanisms [2, 4, 12, 17]. The figure was created using BioRender: Scientific Image and Illustration Software (Toronto, Canada; app.biorender.com).

Table 1. Key processes connecting soil and microbial transformations to root-accessible nutrient supply.

Process	Mechanistic link	Useful measurement	Interpretive limitation
Mineral release and exchange	Dissolution and reversible exchange replenish dissolved nutrients [3,5].	Solution chemistry over time; release or sorption kinetics.	A laboratory release rate may differ from root-zone delivery.
P sorption and desorption	Mineral surfaces retain or release phosphate [5,6].	Sorption measurements; labile-P resupply tests.	Extractable P is not equivalent to flux at a root.
Organic nutrient mineralization	Organic substrates are converted to inorganic nutrient forms [18,19].	Gross and net turnover; isotope tracers.	Net change can conceal simultaneous opposing fluxes.
Microbial immobilization and turnover	Microbial biomass retains nutrients and can release them during turnover [30–34].	Microbial biomass plus isotope-based turnover.	Biomass alone does not demonstrate plant transfer.
Extracellular enzyme activity	Enzymes contribute to conversion of selected organic nutrient forms [36,42].	Substrate-specific phosphatase or related assays.	Assays indicate potential activity under test conditions.
Rhizodeposition and priming	Root-derived C can modify decomposition and microbial nutrient cycling [38–40].	Rhizosphere sampling; isotope tracing; gross rates.	Chemical mobilization need not increase plant uptake.
Mycorrhizal nutrient pathways	Fungal hyphae extend nutrient exploration and may transfer nutrients to roots [47,48].	Hyphal-access contrasts; isotopes; plant nutrient content.	Fungal abundance does not establish net agronomic benefit.
Diffusion and mass flow	Nutrients move through soil water toward absorbing roots [2,4].	Solution gradients; diffusion estimates; water flux.	Transport to a sampler is not identical to uptake by a root.

3. Rhizosphere Microorganisms as Regulators of Nutrient Availability

Soil microorganisms regulate nutrient accessibility by transforming organic and inorganic compounds and by competing with roots for some of the same dissolved resources [30]. They can release inorganic nutrients through decomposition and mineralization, but they may also incorporate them into growing biomass and microbial residues [7,31]. The resulting effect on root supply depends on the balance between release and retention, the location of microbial activity, and its timing relative to active root uptake [30,31]. A larger microbial biomass or a change in community composition is therefore not, by itself, evidence of improved crop nutrient acquisition [31]. Nitrogen (N) cycling illustrates why gross transformations need to be distinguished from net changes [17,32]. Depolymerization of organic N, ammonification, microbial immobilization, and nitrification contribute to the identity and turnover of soil N pools [7,19]. Net mineralization, commonly estimated from changes in inorganic N during an incubation, reflects the balance between concurrent mineralization and immobilization; a small net value can coexist with rapid gross turnover [32]. Isotope pool-dilution approaches can help quantify these underlying fluxes, although interpretation depends on tracer mixing and the pools represented by the measurement [17, 32]. To connect microbial transformations with plant nutrition, measurements should be paired with soil inorganic N dynamics and crop N accumulation during corresponding sampling intervals [19].

Microbial nutrient retention depends partly on the balance of carbon (C) supply and nutrient requirements [33]. Stoichiometric adjustments in microbial N-use efficiency may alter how much N enters biomass rather than remaining in the surrounding solution [33]. Nutrients incorporated into microbial biomass are not necessarily lost to the crop system: microbial death, turnover, and subsequent decomposition can return some of them to cycling pools [31, 34]. Nevertheless, the formation of microbial-derived soil organic matter does not demonstrate that the same N will become available within a particular crop season [34]. The agronomic consequence depends on the rates, location, and timing of retention and release, not solely on the amount of microbial biomass [30, 33]. Phosphorus (P) cycling presents related, but chemically distinct, processes. Some microorganisms solubilize mineral-associated phosphate through changes in local solution chemistry, while phosphatases can catalyze hydrolysis of particular organic P compounds [35, 36]. These capacities have been documented extensively, but successful solubilization in culture or a high potential enzyme activity does not establish improved P uptake by field-grown crops [36, 37]. Released phosphate can be sorbed again by minerals, incorporated into microbial biomass, or remain outside the actively explored rooting volume [18,37]. Methods that estimate gross P mineralization or isotope exchange help separate internal cycling from net changes in extractable phosphate, although no single assay measures the complete plant-accessible flux [18].

Roots influence microbial nutrient transformations by releasing soluble C compounds, mucilage, and other rhizodeposits into nearby soil [38]. This supply can modify microbial growth, enzyme production, and decomposition of existing soil organic matter [38,39]. Rhizosphere priming is a change in the decomposition of soil organic matter associated with living roots, not a synonym for increased crop nutrient uptake [39]. Experimental evidence shows that rhizosphere activity can mobilize certain soil nutrients while promoting the retention of others, so the direction of response must be measured for each nutrient rather than inferred from microbial activity alone [40]. Model-based work further suggests that the relationship between plant N requirements and priming can differ with mycorrhizal association, but these relationships require direct tests in cropping soils [41]. Microbial allocation of C to extracellular enzymes and other resource-acquisition activities also affects its growth efficiency [42]. Greater measured potential enzyme activity may indicate increased capacity to process substrates under assay conditions, but it does not directly quantify in situ nutrient release or transfer to the plant [42]. Accordingly, extracellular enzyme assays are most informative when interpreted alongside gross transformation rates, microbial biomass turnover, and plant nutrient measurements [32, 42]. This distinction matters because the same measured enzyme potential may correspond to different nutrient outcomes when substrates or mineral surfaces differ among soils [18, 37]. Root exudation itself varies with root identity, developmental stage, morphology, and microbial associations [43, 44]. Evidence from mature beech forests, for example, links exudation with root traits and fungal activity, but the observed relationships should not be transferred uncritically to annual crops [43]. Research on plant nutrient-acquisition strategies indicates that rhizosphere regulation of N cycling can be part of broader plant functional strategies [45]. For cropping systems, the immediate research need is to establish whether root-derived C inputs change nutrient delivery within root-accessible soil domains and whether those changes measurably affect crop accumulation [38, 44].

Arbuscular mycorrhizal fungi can extend the zone explored for relatively immobile nutrients through extraradical hyphae and transfer nutrients to host roots through specialized symbiotic interfaces [36,47]. Their net contribution depends on the host, fungal partner, nutrient distribution, and exchange of plant C for fungal services [47]. A field-based study of millet and chickpea reported context-specific benefits from common mycorrhizal networks, illustrating a possible pathway rather than a general rule for all intercrops [48]. The agronomic importance of managing mycorrhizal communities remains debated: one critical review found insufficient evidence to recommend management based on fungal abundance or diversity alone [46], whereas a published response argued that the symbiosis may warrant management when its function and context are considered [49]. These positions are best reconciled by measuring actual nutrient transfer and crop response rather than using fungal abundance as a stand-alone proxy [46,49].

Evidence from ectomycorrhizal trees further indicates that fungal associations can influence nutrient recovery from decomposing litter [50]. However, the processes and

symbiotic partners in those systems differ from arbuscular mycorrhizal associations in most cereal crops; a forest litter result cannot be treated as direct evidence for cereal nutrient uptake [50]. This distinction between mechanistic plausibility and crop-specific validation is equally important when interpreting microbial diversity. Soil biodiversity can support multifunctionality, but diversity indices do not quantify the nutrient flux reaching roots [51,52]. Biodiversity experiments in grasslands identify potentially relevant nutrient-retention pathways [53], whereas critical appraisals of soil biodiversity approaches caution against translating broad ecological metaphors into untested management prescriptions [54]. For field-oriented synthesis, Table 1 distinguishes the processes governing root-accessible supply from the measurements that reveal their operation. It emphasizes that each microbial indicator is conditional and should be combined with direct nutrient transformation measurements and plant nutrient accumulation before a causal contribution to crop acquisition is inferred [17,37].

4. Root Development and Nutrient Acquisition Across Crop Growth Stages

The distribution and activity of roots determine which soil domains contribute to plant nutrient acquisition at a particular stage of development [4, 13]. Root length, branching, depth, diameter, and root hairs influence contact with soil and the distance nutrients must travel to absorbing surfaces [4, 25]. These traits should not be interpreted as interchangeable indicators of acquisition: extensive total root length may provide little access to a localized nutrient pool if much of it occurs outside the relevant soil volume or in root segments with different transport activity [24, 25]. Root architecture must therefore be considered together with nutrient distribution, transport through soil, and physiological uptake capacity [4, 24]. For phosphate, movement through soil is often limited by sorption and slow diffusion, which makes the spatial arrangement of fine roots and root hairs particularly important [5, 6]. Root hairs can increase the effective absorbing surface and shorten diffusion pathways between phosphate-containing soil and root epidermal cells [13]. Nitrate is generally more mobile in soil water, so its acquisition is also shaped by root depth and distribution within the water-transport domain [8]. These contrasts are conditional rather than universal: soil pore connectivity, root uptake kinetics, and changes in solution concentrations can alter the relative importance of root traits for each nutrient [4, 24].

Root systems develop unevenly through time, with newly formed axial and lateral roots, active elongation zones, and older root segments contributing differently to exploration and acquisition [55]. Structural–functional models such as CRootBox provide a representation of three-dimensional root development and can be linked with process descriptions to formulate hypotheses about spatial access [55]. Their architecture outputs do not, by themselves, prove accurate predictions of nutrient influx under field conditions. Such predictions require nutrient-specific transport and uptake assumptions, appropriate soil parameterization, and validation against measured root distributions and crop nutrient accumulation [24, 55]. Developmental changes in the canopy and reproductive structures affect plant requirements for nitrogen, phosphorus, potassium, and other nutrients [8, 14]. However, a tissue concentration measured on one date does not identify when or from which soil pool the nutrient entered the plant [56]. Concentration reflects the combined effects of nutrient content and dry matter accumulation, while nutrient content requires both tissue concentration and organ biomass [56]. Sequential whole-plant nutrient budgets are therefore preferable for estimating net nutrient accumulation during a defined interval [8,56]. Redistribution from vegetative tissues to developing grain changes the distribution of nutrients within the plant but should not be counted again as new uptake from soil [56].

Uptake also requires movement across root membranes, after nutrients have reached the root surface [57]. For P, transporter-mediated influx and soil-mediated replenishment are connected processes operating at different scales [5,57]. A genotype may display substantial phosphate uptake capacity in nutrient solution yet acquire little P in a soil if delivery through pore water is inadequate [5,57]. Conversely, improved soil P resupply may not translate into greater plant acquisition if the relevant roots are absent or physiologically inactive [24, 57]. Evaluating root traits without soil delivery measurements, or measuring soil delivery without uptake capacity, risks attributing an observed crop response to the wrong mechanism [4, 57]. Roots can also modify local nutrient availability through ion exchange, exudation, and chemical changes in their immediate surroundings [5,12]. The nature of this influence depends strongly on the soil environment. For instance, a 2025 study in rice paddy systems showed that rhythmic radial oxygen loss can modify iron-associated P transformations and local P bioavailability [58]. That finding identifies a system-specific root-mediated mechanism rather than a mechanism that should be assumed in well-aerated upland soils [58]. Root-driven changes in nutrient availability therefore require measurements that resolve the relevant chemical conditions and plant–soil interface [5, 58].

For N, the chemical form reaching roots is also important. Plants can acquire nitrate and ammonium, and uptake of some organic N compounds has been documented in diverse plant systems [8, 59]. The contribution of each pathway depends on soil transformations, competing microbial uptake, and the methods used to estimate plant acquisition [8, 30]. Evidence from natural vegetation helps establish mechanistic possibilities but cannot determine the relative contributions of N forms in a cereal field without crop-specific measurements [8, 59]. Where the question is N-source attribution, sequential biomass measurements alone are insufficient; appropriately designed isotope tracing or other source-specific evidence is needed [56]. Interactions with fungal partners and neighboring crops can further alter the portion of soil explored by roots and hyphae [47, 63]. A recent intercropping study connected root traits to several rhizosphere functions under differing P inputs, emphasizing the dependence of these interactions on crop mixture and management [60]. Long-term intercropping experiments have

also reported improvements in grain productivity and selected soil fertility attributes in particular systems [61]. A meta-analysis found gains in P-use efficiency for some cereal–legume combinations [62]. Nevertheless, improved productivity in mixed stands can arise from several processes; it should not be assigned solely to enhanced nutrient flux without measurements that separate root competition, complementarity, and nutrient acquisition [60, 63].

The temporal dimension provides the link between these mechanisms and figure 2. Earlier work established that aligning soil N supply with crop demand is an important agronomic objective [14,15]. Field observations in maize further show that N mineralization and crop N accumulation can change over the growing season, making the timing of measurements consequential [64]. Figure 2 therefore presents supply, plant demand, and actual uptake as separate conceptual rates on a comparable spatial and temporal basis. Their illustrative trajectories are not universally applicable to all nutrients or cropping systems. The testable question is whether measurements of resupply and root function explain changes in crop nutrient accumulation beyond the information obtained from a calibrated soil test [15,64].

5. Measuring nutrient availability beyond conventional soil tests

The choice of a nutrient test must follow the scientific question rather than the availability of an instrument [3]. Routine soil extraction measures an operationally defined pool, whose agronomic meaning arises mainly from calibration against crop response [1,3]. Soil-solution sampling characterizes dissolved concentration at a specified place and time [3,5]. Resin devices and diffusive gradients in thin films (DGT) accumulate analytes at a sink during deployment and therefore characterize a different aspect of nutrient supply [65,66]. Isotope methods estimate selected transformations or transfers, whereas repeated plant nutrient budgets evaluate changes in the nutrient content of the crop [8,18,67]. Disagreement among these indicators can reveal differences in the processes and timescales measured rather than analytical failure. Conventional tests remain indispensable benchmarks because they are comparatively accessible and may have a long history of locally calibrated fertilizer recommendations [1,3]. Their interpretation nevertheless depends on extractant chemistry, soil mineralogy, sampling depth, and the response variable used in calibration [3,5]. A test that predicts fertilizer response need not measure the instantaneous rate at which nutrients move to a root.

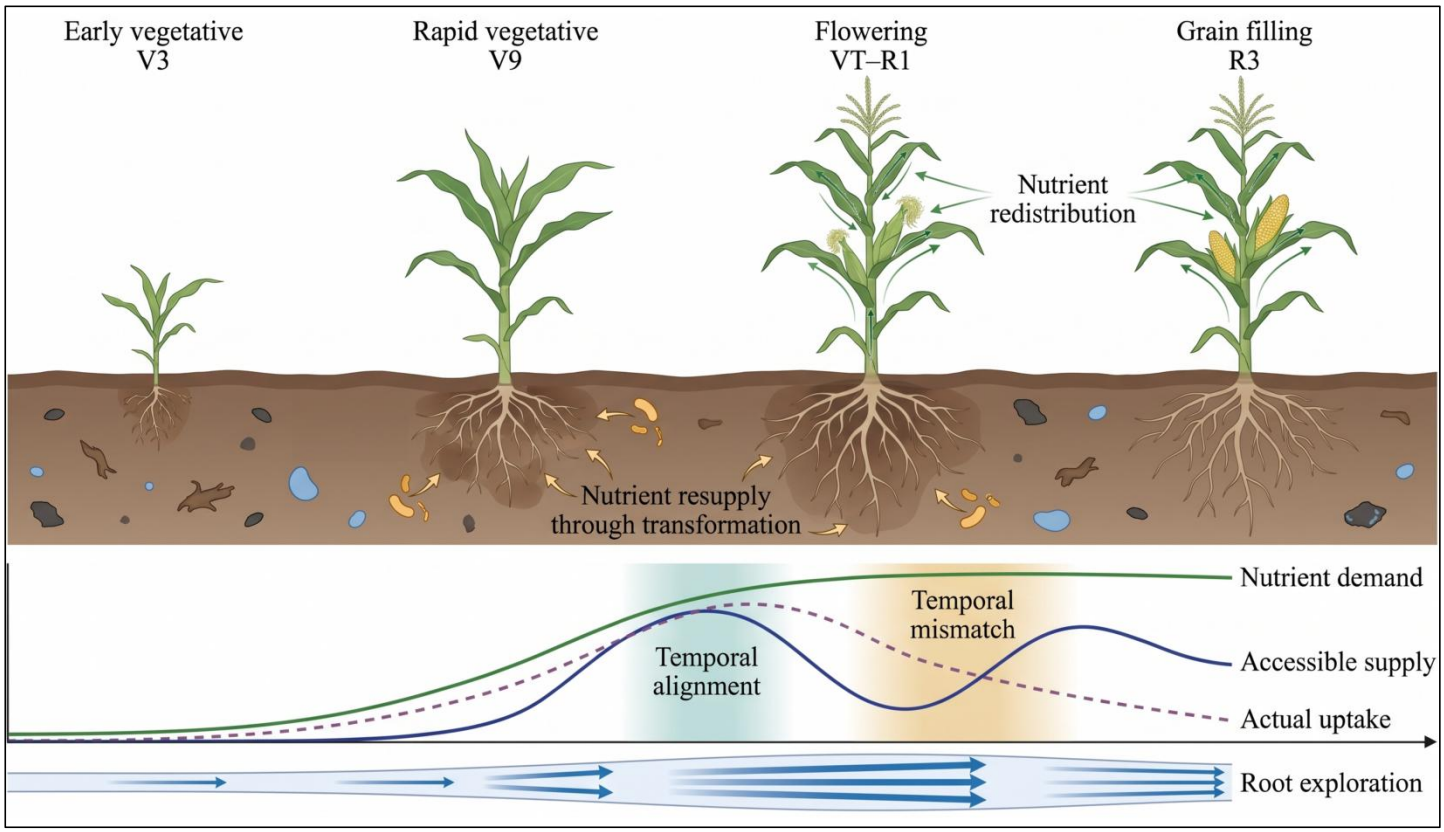

Figure 2. Conceptual relationships among root-accessible nutrient supply, plant nutrient demand, and actual root uptake during crop development. The trajectories are illustrative, not measured data; nutrient-specific patterns depend on resupply, root activity, and the observation interval. Redistribution among plant organs is distinct from new uptake from soil [14, 15, 64]. The figure was created using BioRender: Scientific Image and Illustration Software (Toronto, Canada; app.biorender.com).

Conversely, a detailed mechanistic measurement is not necessarily more useful for management unless it improves predictions or decisions beyond an appropriate conventional baseline. Evidence from forest-soil comparisons [9,10] illustrates system-specific limitations but must not be treated as direct validation or invalidation of crop-soil tests. For phosphate, DGT deploys a diffusive layer and a selective binding phase that lower local dissolved concentration and draw solute toward the device [65]. Accumulation over a known time reflects diffusion through the deployment geometry and, in soils, replenishment of dissolved analyte from labile pools [65, 66]. DGT can therefore complement chemical extractions in appropriately calibrated soil–crop settings, but its sink is not a growing root. It lacks changing root architecture, biological uptake regulation, and root-derived chemical inputs; its signal also depends on diffusion-layer thickness, deployment duration, contact with moist soil, and binding chemistry [65, 66]. DGT-derived flux should consequently be called a probe flux, not a direct measure of root uptake. Resin membranes face related constraints concerning soil contact, deployment time, and sink selectivity [3, 65]. Temporal alignment is equally important. A laboratory extraction samples an operational pool at one time, whereas an in situ probe integrates accumulation during deployment [3,65]. An incubation estimates processes under its imposed conditions, and a tissue sample reflects nutrient acquisition and internal allocation before harvest [8,14]. A direct comparison should therefore pair a documented supply interval with sequential plant nutrient-content measurements over a biologically relevant interval. The intervals need not be identical, but any lag between release, transport, and acquisition must be stated and tested rather than silently ignored [14,15].

Gross nutrient-transformation methods address another question. Isotope pool dilution can distinguish gross production and consumption even when net pool change is small [19,32]. For phosphorus, Wanek et al. [67] developed an isotope-dilution approach that explicitly accounted for abiotic sorption and desorption alongside biological transformations. Its tested systems included forest and grassland soils, so transfer to cropped fields requires nutrient-specific validation. Tracer additions, sampling disturbance, and incubation conditions may influence the estimated rates [18,67]. Gross mineralization or immobilization is not itself a measurement of the amount delivered to roots. Spatial methods provide information that bulk samples cannot. Rhizosphere imaging and microsensors can reveal local concentration patterns, while root mapping identifies whether active roots intersect a nutrient-bearing domain [13,25]. Their strength is mechanistic resolution; their weakness is that a small observed interface may not represent the entire field root system. Composite sampling has the opposite limitation, providing broader coverage while masking gradients. A defensible multiscale design records root class, soil depth, position, sampling time, and the volume or area represented, rather than assuming that observations at one scale automatically extrapolate to another [24,25].

Plant-based measurements are essential endpoints. Nutrient concentration multiplied by sampled dry biomass yields nutrient content; changes in whole-plant content across dates approximate net external acquisition when plant losses are negligible or quantified [8,56]. Internal remobilization changes organ contents without necessarily changing total plant content, which is why shoot-only sampling may misrepresent acquisition if root pools change substantially. Isotope tracers can help partition nutrient sources but require attention to tracer recovery and dilution [56]. Crop yield is an important secondary endpoint, not a substitute for uptake measurements, because multiple processes jointly determine harvest output. Table 2 compares these methods and identifies the evidence each can and cannot provide [3, 65, 67].

6. Integrating soil nutrient supply, root uptake, and crop productivity

A process-aware assessment must join measurements made at different scales without equating them [2,17]. At the soil scale, nutrient pools, reactions, and gross transformations characterize potential supply [3,18]. At the soil–root interface, solution concentrations, water movement, and local depletion influence delivery [4,24]. The absorbing root surface adds membrane transport capacity and developmental variation [5,13]. Whole-plant nutrient content then records the integrated consequence of acquisition, losses, and internal allocation [8,56]. Figure 3 organizes these levels as linked hypotheses and validation targets rather than as a new empirical law. The first necessary distinction is between nutrient release and delivery. Rapid mineralization may coexist with substantial microbial immobilization [17,19]. Release into solution can also occur in soil domains that roots do not occupy, while phosphate released from a surface may be re-adsorbed before reaching a root [5,28]. An increase in soluble nutrient concentration therefore identifies an intermediate process, not proof of increased acquisition. The relevant test combines a measured release or transformation rate with local transport information and a subsequent plant nutrient increment [17,24]. Evidence on mineral-associated nitrogen transformations supports the importance of tracking multiple pathways; the specific response to added ammonium or nitrate described by Ren et al. [69] should not be generalized to all cropped soils.

A second distinction concerns root contact and membrane uptake. Nutrient delivery to the root exterior can differ from influx across the root membrane, and either can differ from changes in whole-plant nutrient content [4,5]. The mechanistic OpenSimRoot model contains root growth, soil solute-transport, and nutrient-uptake routines and is suitable for testing root-trait hypotheses [24]. CRootBox provides a structural–functional root framework [55], whereas published CPlantBox studies emphasize whole-plant structure and coupled water and carbon transport [70,71]. These tools do not have identical nutrient-process modules, calibration requirements, or independent field validation. A simulated nutrient uptake pattern is therefore evidence of model behavior, not an experimentally established crop response [24,55,70].

A third distinction separates nutrient acquisition from agronomic performance. Tissue concentrations may decrease through biomass dilution even while absolute nutrient uptake increases [3]. More acquisition can support growth when

nutrient availability is consequential, but a change in nutrient content does not automatically imply a proportional grain-yield response [3,56]. Metrics such as uptake efficiency, fertilizer recovery, physiological utilization efficiency, and partial factor productivity use different numerators and denominators and should not be conflated. A predictor of plant nutrient content may be scientifically valuable even when it adds little predictive power for final yield. Studies of national nutrient budgets, including Zhang et al. [68], provide broader accounting context but are not direct tests of these field-scale response relationships.

The framework can be tested through a sequence of linked questions. Does a particular pool release or replenish nutrient on a timescale relevant to crop growth [18,67]? Does nutrient movement place that nutrient within reach of active roots [4,24]? Does the resulting delivery coincide with a measurable increase in plant nutrient content [8,14]? Each question needs its own observation: kinetic or isotope methods for transformation, spatial and root measurements for delivery, and serial plant budgets for acquisition. A convincing field study should integrate these observations rather than infer an entire pathway from one strong correlation. Minimum reporting should include nutrient form, soil classification and relevant mineralogy, sampling depth, extraction or probe protocol, fertilizer placement and timing, root distribution, crop stage, and organ-level biomass and nutrient concentrations [3,25,65]. Where microbial activity is central to a hypothesis, gross transformation rates and microbial biomass are preferable to community composition alone [17,32]. Replicated plots and separate calibration and validation datasets are needed to distinguish mechanism from incidental association. Paired observations across developmental stages can then identify whether a temporal mismatch arises from release, transport, root exploration, or uptake capacity [14,15].

Model evaluation should occur at several levels, but each level represents a different target. Reproducing observed soil concentrations or gross transformation rates tests pool dynamics; matching measured root distributions tests structural assumptions; matching local uptake or whole-plant nutrient increments tests acquisition [24,55]. Independent predictions of uptake and crop outcomes constitute stronger evidence of practical utility. Calibration success cannot be reported as independent validation. To establish added value, a process-aware predictor should be compared with the best locally calibrated soil-test baseline using the same held-out observations, transparent error metrics, and an appropriate measure of prediction uncertainty. This is the proposed evaluation standard, not a claim that existing studies have already demonstrated universal superiority. Management comparisons provide feasible tests. Fertilizer bands change the location of nutrient supply relative to roots, whereas residue additions and cover crops can alter the timing of nutrient release and retention [14,72]. Root traits and cropping patterns can modify explored soil volume and belowground nutrient cycling [61,62,73]. Factorial experiments that measure both supply processes and plant uptake can help identify which mechanism explains a management response. Evaluating sustainability also requires a longer perspective: rapid supply within one season should be interpreted alongside nutrient inputs, harvest exports, and changes in soil reserves across rotations [22,29,68].

The central proposal is therefore selective integration, not replacement of routine soil testing. Dynamic probes, isotope methods, root observations, and models should be added where they resolve a specific uncertainty or improve an externally tested prediction [3,24,65].

Table 2. Complementary methods for assessing soil nutrient pools, dynamic supply, root distribution, and plant acquisition.

Method	Measured quantity	Best use	Main limitation
Routine extraction	Operationally extractable pool [3]	Calibrated crop response	Not a direct supply rate
Soil solution sampling	Local dissolved concentration [3,5]	Immediate solution chemistry	Time and position sensitive
Ion-exchange resin	Ions captured by resin over time [3]	Relative labile supply	Contact and sink effects
DGT	Diffusive flux to selective sink [65,66]	Resupply index for suitable analytes	Probe is not a living root
Isotope pool dilution	Selected gross transformation rates [19,67]	Separate production from consumption	Tracer/incubation assumptions
Rhizosphere imaging	Local chemical gradients [13,25]	Mechanistic microsite tests	Limited representativeness
Root mapping	Root location and architecture [24,55]	Match roots with nutrient zones	Presence is not uptake activity
Serial plant budget	Change in organ/plant content [8,56]	Evaluate net acquisition	Account for loss and allocation

Such evidence could identify conditions in which root-accessible nutrient supply conveys information unavailable from pool measurements, while also establishing where conventional tests remain sufficient. Figure 3 summarizes this progression from soil measurements to process attribution and independent crop-level validation.

6. Knowledge Gaps and Future Research Priorities

The leading research gap is not the existence of nutrient-supply processes, but evidence of when measuring them improves agronomic inference beyond calibrated tests [3,15]. Paired studies should compare conventional extractions with dynamic resupply measures on the same soils and report predefined outcomes, including serial whole-plant nutrient content and harvested yield. Independent validation across soil classes and growing seasons is essential because an improvement observed in one calibration dataset may not transfer [25,65]. A second priority is to couple microbial turnover with plant acquisition. Gross N or P transformation measurements should be collected alongside microbial biomass, root distribution, and plant nutrient increments [17,67]. Experiments must distinguish temporary immobilization from subsequent release within the crop uptake period; shifts in microbial abundance alone are insufficient evidence of improved supply [30,31]. Third, studies should test where and when active roots intersect nutrient supply. Contrasting root architectures, fertilizer-placement patterns, and crop stages offer tractable experiments [24,25]. Plant trait-based hypotheses are promising [73], but measured uptake must remain the endpoint. Finally, model comparisons should explicitly distinguish fitting from independent prediction and assess the additional field value of each new measurement [24,70]. A relatively simple method that remains accurate across soils may be more useful than a complex model requiring inputs that cannot be measured reliably.

7. Conclusions

Soil fertility cannot be fully explained by nutrient stocks or extractable concentrations alone. Effective plant nutrient acquisition depends on the coordinated processes of nutrient release, microbial transformations, transport through soil, and uptake by active roots. These processes vary across soil environments and crop developmental stages, making nutrient availability a dynamic property of the soil–root system. Conventional soil tests remain essential for fertility assessment, but their interpretation can be strengthened by complementary measurements of nutrient resupply, rhizosphere activity, root function, and plant nutrient accumulation. Future research should prioritize integrated field experiments and independently validated models to determine when these measurements provide meaningful improvements over established soil fertility indicators. Particular attention should be given to distinguishing nutrient release from actual plant acquisition and linking short-term nutrient delivery with long-term soil fertility maintenance. Ultimately, a process-based understanding of nutrient accessibility can support more reliable fertility assessment, efficient nutrient management, and sustained crop productivity.

Author contributions

Lingwen Shan: Writing-original draft, writing-review and editing, conceptualization, figure preparation, and visualization. Yang Song: Writing-original draft, writing-review and editing, conceptualization, funding, and visualization. Quan Zhao: Writing-review and editing, conceptualization, resources, and software. All authors have reviewed and approved the final version of the manuscript for publication.

Ethical approval

Not applicable.

Conflicts of Interest

The authors report no conflicts of interest.

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Declaration of Generative AI and AI-assisted technologies in the writing process

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