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REVIEW

Soil water status shapes nutrient cycling in agroecosystems from micrometer to landscape scales

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Abstract

Soil water status, which refers to the wetness or dryness of soils, is crucial for the productivity of agroecosystems, as it determines nutrient cycling and uptake physically via transport, biologically via the moisture-dependent activity of soil flora, fauna, and plants, and chemically via specific hydrolyses and redox reactions. Here, we focus on the dynamics of nitrogen (N), phosphorus (P), and sulfur (S) and review how soil water is coupled to the cycling of these elements and related stoichiometric controls across different scales within agroecosystems. These scales span processes at the molecular level, where nutrients and water are consumed, to processes in the soil pore system, within a soil profile and across the landscape. We highlight that with increasing mobility of the nutrients in water, water-based nutrient flux may alleviate or even exacerbate imbalances in nutrient supply within soils, for example, by transport of mobile nutrients towards previously depleted microsites (alleviating imbalances), or by selective loss of mobile nutrients from microsites (increasing imbalances). These imbalances can be modulated by biological activity, especially by fungal hyphae and roots, which contribute to nutrient redistribution within soils, and which are themselves dependent on specific, optimal water availability. At larger scales, such small-scale effects converge with nutrient inputs from atmospheric (wet deposition) or nonlocal sources and with nutrient losses from the soil system towards aquifers. Hence, water acts as a major control in nutrient cycling across scales in agroecosystems and may either exacerbate or remove spatial disparities in the availability of the individual nutrients (N, P, S) required for biological activity.

KEYWORDS

catchments, molecular chemistry, microbiology, nitrogen, phosphorus, plants, sulfur

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1 | INTRODUCTION

Water is critical for all life on Earth and its availability in terrestrial systems is highly variable and dynamic. The water cycle upon which terrestrial life relies for replenishment has been scrutinized in the context of climate change due to recurrent extreme events such as droughts and floods (Huntington, 2006; Marengo & Espinoza, 2016; Samaniego et al., 2018). Recent evidence suggests that the availability of terrestrial freshwater resources is declining, largely due to diversion and use of water for irrigation to meet the needs of a growing global population (UN-Water, 2021). In addition, not all of the water stored in soil is usable for biological processes. For instance, water films and water in very fine pores are largely inaccessible to plant roots and microorganisms. In contrast, mid-size and large pores provide water usable for organisms, but can also be prone to rapid infiltration and water flux through the soil matrix (see also, e.g., Vereecken et al., 2022, for a recent review on soil hydrology).

Soil water status refers to the wetness or dryness of the soil and it is most importantly controlled by atmospheric (e.g., rainfall, evaporative demand) and hydrologic (e.g., infiltration, soil water redistribution) processes but also by soil properties and related soil processes, land use and cover, and topography. The soil water status is typically described by the soil moisture content expressed on either a volumetric or gravimetric basis. The soil moisture content is related to the soil matric potential through the moisture retention characteristic function. The matrix potential of unsaturated soil is by definition negative. It describes the strength by which soil moisture is retained in the pore space and it is mainly controlled by capillary forces. The soil moisture retention function states that with decreasing soil moisture, the matric potential becomes more negative as larger pores are drained and capillary forces increasingly retain the remaining water in smaller pores. Under very dry conditions, especially beyond the wilting point, soil water is mainly found in films around soil grains and mineral surfaces or internal surfaces (Vereecken et al., 2022). This relationship controls the storage of soil moisture and is key to quantify soil water flow and the fate of soil nutrients. Soil water status further affects microbial processes and abiotic or biotic transformation of nutrients. Despite these regulating functions of water in nearly every aspect of soil nutrient cycling and availability, it is not yet an integral part of the conceptualization of nutrient cycles across scales from microbial processes in soil pores to nutrient transformation and transport within catchments.

The nutritional elements nitrogen (N), phosphorus (P), and sulfur (S) are required by biota at specific stoichiometric ratios, which are constrained to a small range across many ecosystems and scales (Cleveland & Liptzin, 2007; Kirkby et al., 2011; Sterner & Elser, 2002). In soils, N and S are predominantly found in soil organic matter (SOM), whereas especially P, and to a lesser extent also N and S, can also be derived from inorganic forms, such as ammonium fixed within clay mineral layers, or from primary minerals containing S and P (Cross & Schlesinger, 1995; Frossard et al., 2011; Nieder et al., 2011). The utilization of these elements for plant and microbial growth thus relies on the mineralization rates of SOM, which is critically controlled by water supply (W. Huang & Hall, 2017; Moyano et al., 2013) and nutrient stoichiometry (Eberwein et al., 2015; Gan et al., 2020; Meyer et al., 2018), and the ability of plants and microbes to acquire nutrients from mineral phases. As the different sources of N, P, and S are distributed heterogeneously within soils, transport with water flux can act as a bridging agent to overcome spatial disparities or, vice versa, a lack in water flux will maintain spatial disparities.

In this review, we aim to provide a coherent account across scales of how water affects soil nutrient cycling within agroecosystems and discuss how it modulates interactions among different soil nutrients. These scales consider the molecular level, where nutrients and water are consumed, microscale variations in water and nutrient availability within the soil pore system and microhabitats, as well as between different soil horizons and at larger scales within or between catchments.

2 | MOLECULAR-SCALE PROCESSES INCORPORATING WATER INTO NUTRIENT CYCLING

In the complex living system of soil, water plays a similar role as in other multicellular organisms such as the human body. In organisms, water acts (1) as a critical constituent of the cells; (2) as a solvent and reaction medium for all hydrophilic compounds, such as essential ions, carbohydrates, and amino acids; (3) as a reactant and/or reaction product in various reactions, such as hydrolysis, polymerization, oxidation, and reduction; and (4) as a transport medium for gases, nutrients, and waste products (Jéquier & Constant, 2010). The same functions can also be attributed to water in soils.

Further, soil water content or, vice versa, the lack of oxygen under conditions of high water contents can change redox conditions and thereby induce a change in element speciation within the soil. For example, under reducing conditions, that is, with low or no supply of oxygen as an electron acceptor, electrons can instead be transferred to, for example, Fe(III) (Megonigal et al., 2004; Reddy & DeLaune, 2008), resulting in Fe reduction into soluble Fe(II), along with release of nutrients previously adsorbed to the Fe(III) oxides. As a result, a release of organic P compounds was observed in temperate arable soils with a shift from oxic to reducing conditions due to increased soil moisture (Baumann et al., 2020). Thus, water level and associated redox conditions may influence the availability of nutritional elements for biological processes, the consequences of which will be discussed in more detail in the following chapters. Overall, a sufficient water level in the soil is essential for most physical, chemical, and biological processes.

Interactions among nutrients and soil water are detectable by isotope exchange. Particularly oxygen is of interest here due to its occurrence in many nutrient species and water. Oxygen has three stable isotopes, ^{16}O (99.76%), ^{17}O (0.037%), and ^{18}O (0.20%), where the standardized ratio of the two most abundant isotopes can be applied as an environmental tracer (^{18}O/^{16}O relative to the Vienna Standard Mean Ocean Water; conventionally expressed as δ^{18}O).

Nitrate as the anion of the very strong nitric acid (pK_a −1.38) is reported to not readily exchange oxygen atoms with water (Hall & Alexander, 1940), but its nitrification precursor nitrite, the anion of the much weaker nitrous acid (pK_a 3.15), readily does so in at least slightly acidic aqueous medium (Kool et al., 2007). This also determines the isotopic signature of nitrate, which is formed from nitrite in the final step of nitrification (Kool et al., 2011). Microbial-derived nitrate, that is, nitrate formed in the soil during nitrification, generally has a very distinct oxygen isotope signature compared with atmospheric nitrate, which is mostly derived from industrial sources. This information can be used to trace atmospheric N deposition in ecosystems, provided that the nitrate is not reduced to nitrite again and thus susceptible to oxygen isotope exchange with soil water (Ohte, 2013).

For P, the exchange of oxygen in water with oxygen in phosphate is negligible at temperatures below 70°C and in absence of biological activity (O'Neil et al., 2003). However, enzymes in the biological P cycle, so-called phosphatases, catalyze oxygen exchange at ambient temperatures. Ubiquitous intracellular pyrophosphatases cause a complete oxygen exchange between phosphate and water (Blake et al., 2005; Cohn, 1958). The kinetics of oxygen isotope exchange mainly depend on temperature (Chang & Blake, 2015) and pH, with rate constants ranging from 1.51×10^{-5} to 3.13×10^{-4} s^{-1} (Chang et al., 2021; von Sperber et al., 2017). Extracellular phosphoesterases in turn, such as alkaline and acid phosphatases, nucleotidases, phosphodiesterases, and phytases exchange one or more oxygen atoms between water and phosphate during the hydrolysis of organic phosphate-bearing compounds (Y. Liang & Blake, 2006; von Sperber et al., 2014, 2015; Wu et al., 2015). Due to the complete oxygen exchange, the high reaction rate, and the large isotope fractionation, the activity of pyrophosphatase is often assumed to dominate the oxygen isotope composition of phosphate in the soil–plant system (Bauke et al., 2021; Helfenstein et al., 2018; Tamburini et al., 2012). Hence, oxygen isotope exchange in phosphates can be used to locate hotspots of P cycling, for example, within different soil compartments (Bauke et al., 2017; Siebers et al., 2018), plant compartments (Bauke et al., 2021; Pfahler et al., 2013), or within catchments (Bauke et al., 2022; Pistocchi et al., 2017).

Similar to phosphate, sulfate does not exchange oxygen isotopes with water under ambient abiotic conditions, but this reaction is catalyzed during microbial sulfate reduction (Brunner et al., 2005). During the mineralization of S from organic compounds, oxygen atoms from soil water (or microbial cell water, which is typically in equilibrium with soil water isotope values) are incorporated into the resulting sulfate ion. As soil water δ^{18}O values are generally depleted in ^{18}O compared with most biological compounds, such mineralization processes should result in a shift in δ^{18}O of sulfate toward lighter values relative to δ^{18}O values of the sulfate source in organic matter and S-oxides from atmospheric deposition (Mayer et al., 1995). However, there appears to be no study that has tested δ^{18}O values as an indicator of S mineralization in soil samples.

Across all three nutrient cycles, changes in the isotopic signature of nutritional ions thus evidence intimate coupling of water and nutrient cycling. This allows for isotope-based identification of contact points where these reactions occur, which biological cycling pathway was used and how cycling patterns change under varying environmental conditions such as changing moisture conditions. The spatial overlap of all three required components for such reactions (water, nutrients, and enzymes for biological cycling) is largely defined by the microscale spatial organization of soil compartments.

3 | COUPLING OF WATER AND NUTRIENT DYNAMICS AT THE MICROBIAL SCALE

3.1 | Chemical and physical heterogeneity of soils

The structural organization of soils at the microscale of organo-mineral associations is summarized in the concept of aggregate hierarchy, which suggests that soil aggregates can be hierarchically composed of small microaggregates (<20 μm), large microaggregates (20–250 μm), and macroaggregates (>250 μm) (Waters & Oades, 1991). The assembly of organic and mineral building blocks into aggregates of various sizes forms a three-dimensional structure with connected and dead cavities and pores of various shapes, sizes, and geometries. This continuous network of the pore system is a dynamic biogeochemical interface, as it enables the flow of gases and fluids (Totsche et al., 2010). Aggregate architecture and stability, and thus its function to provide niches for water storage and microbial nutrient metabolism, is strongly dependent on the spatial organization of the individual building units, their specific elemental composition, and the spatial distribution of metal oxides (cementing agents) and organic matter (gluing agents).

The distribution patterns of elements on the surface and inside of aggregates may be highly variable. For example, it has been shown that microbial cell residues probably serve as a nucleus for the formation of organo-mineral associations, and that organic matter is entrapped by mineral particles (Chenu & Plante, 2006; Ladd et al., 1996), but also that organic excretions accumulate on the surface of aggregates (Amelung et al., 2002). In a systematic study of microaggregates, these contradictory findings could be verified as there were no reproducible structures or spatial distribution of elements, binding agents (microbial organic matter, pedogenic oxides), and clay minerals in microaggregates originating from the same soil (Lehndorff et al., 2021). Thus, these studies point to extreme small-scale heterogeneity in nutrient distribution, which is further complicated by differences in the accessibility and availability of nutrients to microorganisms.

The accessibility of nutrients is strongly limited by the size of pores and cavities. In various studies, it was shown that due to pores of a diameter smaller than the size of microbial organisms, organic matter and nutritional elements inside aggregates were protected from microbial turnover (Kaiser & Guggenberger, 2003; Nunan et al., 2003; Siebers et al., 2018). However, when high water levels cause reducing conditions and a reductive dissolution of metal oxides, soil aggregates can be destabilized, leading to a break-down and exposure of previously inaccessible areas (De-Campos et al., 2009; Huang & Hall, 2017). Especially S is sensitive to aggregate break-down, as reduced S forms (especially with sulfur in oxidation state −2) at the newly exposed surfaces can be oxidized (Siebers & Kruse, 2019; Solomon et al., 2003) ultimately yielding soluble sulfate. Also, P speciation shifted from labile toward more stable P-pools due to immobilization within microbial biomass after aggregate break-down (Siebers & Kruse, 2019), thus reflecting the indirect effects of soil water status on nutrient accessibility and availability.

The dynamic nature of the soil aggregate system in combination with variations in soil moisture and soil porosity over time lead to functional biogeochemical heterogeneity in the soil at very small scales. This is reflected in microscale differences in redox potential (Wanzek et al., 2018), oxygen availability, and pH (Uteau et al., 2015), but also in differences in availability of the individual nutrients (Li et al., 2016), thus creating multiple niches for the soil microbiome (Young & Crawford, 2004).

3.2 | Microbial habitats at the micro-scale

In recent years, the characterization of biological microhabitats contributed to an improved understanding of the immense heterogeneity of biogeochemical processes in soils. In this context, the concept of hotspots and hot moments is gaining importance (Kuzyakov & Blagodatskaya, 2015; Tecon & Or, 2017). Hot moments are time intervals during which microbial activity is increased for as long as water, carbon (C) and nutrients are available in sufficient amounts. Hotspots are defined as small soil volumes with 10–100 times higher microbial abundance and much faster process rates compared with the bulk soil. The dimension of these specific spheres ranges from one micrometer to several millimeters (Marschner et al., 2012; see Figure 1A). We propose that both the spatial extent of hotspots (Figure 1B) as well as the duration of hot moments within individual spheres such as the rhizosphere, detritusphere, and mineralosphere is fundamentally controlled by the availability of water.

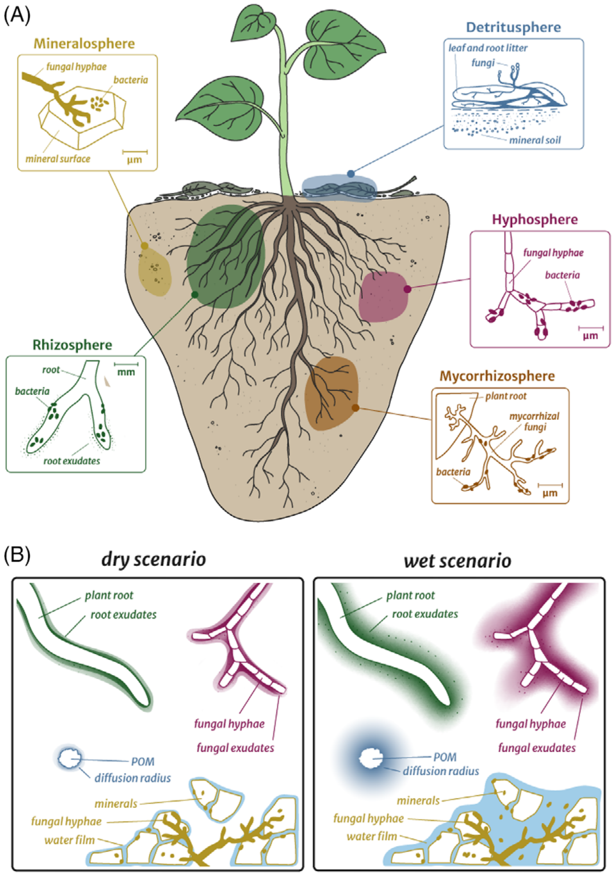

FIGURE 1 (A) Overview of microhabitats in soils representing hotspots with intense interaction between different organisms occurring from the micro- to the millimeter scale. (B) Effect of dry or wet soil conditions on the diffusion of root and hyphal exudates, the diffusion radius around particulate organic matter (POM), and the connectivity of mineral particles through water films with implications for microbial colonization. Under dry conditions (left), diffusion of exudates and POM is limited, whereas under wet conditions (right) it is generally enhanced. Greater connectivity of mineral particles under moist conditions further promotes bacterial movement across water films and thus the ability of bacteria to actively colonize new habitats, whereas under dry conditions only fungal hyphae and their associated bacterial communities are able to bridge air gaps in the soil to explore the adjacent environment.

Each of the individual spheres is characterized by specific features that control their susceptibility to changes in soil water status. High availability of C-rich material derived from leaf and root litter stimulates the development of the detritusphere, where microbial community composition and C turnover differ considerably from their surrounding micro-environment (Poll et al. 2006, 2010). Imaging of microaggregates further revealed spatial correlation between plant detritus and microbial organic matter, suggesting that there is a close link between source and consumer (Lehndorff et al., 2021). In the detritusphere, an increased water content favors the mineralization of plant residues and results in a higher transfer of residue-C to the surrounding soil (Védère et al., 2020). The rhizosphere, by comparison, is a narrow region of soil directly influenced by root secretions and associated soil microorganisms. This root–soil interface is characterized by gradients of nutrients, protons, C resources, and living microorganisms. Increasing water content in the rhizosphere potentially enhances the diffusion radius of exudates, especially in dry soils, and their microbial decomposition (Holz et al., 2018). This affects exudate distribution and root exudation rates (Jones et al., 2009) with implications for overall rhizosphere carbon distribution (Tan et al., 2021). The mycorrhizosphere is further defined as the zone of intense interaction between roots, symbiotic fungi, and soils (Timonen & Marschner, 2006), while the hyphosphere encompasses not only symbiotic but also nonsymbiotic fungi and is characterized by intense fungal–bacterial–soil interactions (Kohler et al., 2017). Mycorrhizal fungi have a positive effect on soil aggregation, ultimately improving water retention and nutrient-holding capacity in the soil, leading to enhanced resilience to, for example, soil drying, flooding, compaction, and/or nutrient leaching (Audet, 2014).

In contrast to spheres characterized by high C availability, the mineralosphere provides a low-C and mineral-rich environment (Uroz et al., 2022), where the surface attachment of microbes to soil particles modifies a range of biogeochemical processes, such as SOM decomposition and soil-borne pathogenicity (Ahmed & Holmström, 2015;

Chenu & Stotzky, 2002; Kandeler et al., 2019; Wu et al., 2014). Also, microorganisms that are specifically adapted and preferentially colonize this habitat contribute to mineral weathering (Ahmed et al., 2017; Colin et al., 2017; Uroz et al., 2012, 2015; Vieira et al., 2020), thus releasing nutritional elements into the soil solution that are then potentially available for transport to and microbial transformation in other microhabitats.

Although most of the above-mentioned studies focus on only one sphere, the conceptual paper of See et al. (2022) gave evidence that different spheres might overlap under natural soil conditions and might, consequently, be modified by water status. However, even if different spheres, such as detritusphere and rhizosphere exist in close proximity (less than 10 mm distance) they often support very different bacterial communities (Borer et al., 2022). Furthermore, in a compartmented microcosm experiment, only limited microbial-driven energy and C transfer existed between the two spheres (Marschner et al., 2012), while redistribution of soil C from the rhizosphere to soil minerals by fungi is common due to extensive exploration by fungi as well as rapid hyphal turnover and promotes the formation of mineral-associated organic matter (See et al. 2022). In order to reconcile these different observations, there is an urgent need for explicit studies or modelling approaches taking into account the temporal dynamics of individual microhabitats in response to soil water status, as well as distances between microhabitats considering their extent under conditions of different soil water contents.

3.3 | Connectivity of microbial habitats

Severe soil desiccation leads to a decrease in microbial activity due to cytoplasmic dehydration that decreases enzyme activity, but also due to substrate limitation as a result of reduced diffusion rates in thinner water films of the soil matrix (Schjønning et al., 2003; Skopp et al., 1990; Stark & Firestone, 1995). With soil drying, water films become disconnected and the continuously hydrated neighborhoods shrink (Bickel & Or, 2020; Tecon & Or, 2017). As a consequence, diffusion times rapidly extend when diffusion mainly occurs within water films along surfaces while direct pathways, for example, across a pore, are becoming increasingly unavailable. Additionally, diffusion lengths shrink given the limited spatial extent of the water film (Figure 1B). Such microscopic effects have been observed in experiments demonstrating decreasing ranges of cell motility with film thickness (Tecon & Or, 2016) and the fragmentation of the aqueous phase even under moderate wetness conditions.

A practical way to illustrate the effect of wetness on nutrient transport and accessibility is via the effective diffusion in soil, often expressed as a function of volumetric water content (θ), pure diffusion in bulk water D_0 ($\approx 10^{-10}$ m^2 s^{-1}) and porosity or the saturated water content (θ_s):

$$D_e(\theta) = D_0 \frac{\theta^{\frac{10}{3}}}{\theta_s^2}. \qquad (1)$$

A characteristic diffusion time t_D can be calculated for comparative assessment of how water content affects access or exchange among neighboring bacterial colonies that are L_D distance apart:

$$t_D = {L_D}^2 / D_e(\theta). \qquad (2)$$

Considering a fertile soil in temperate regions with a high bacterial cell density of 10^{10} cells g$^{-1}{}_{\text{soil}}$ and a specific surface area of 100 m^2 g$^{-1}{}_{\text{soil}}$ (loamy soil), we expect up to 10^2 cells per mm^2 surface area (Raynaud & Nunan, 2014). Assuming for simplicity that bacterial cells are uniformly distributed, the average separation distance between cells is about 100 µm. For wet conditions, with $\theta = 0.25$, $\theta_s = 0.5$, and $D_e \approx 0.04\ D_0$ the characteristic diffusion time for nutrients between neighboring cells (assuming no mass flow) is about 2500 s (0.7 h). However, considering a dry soil with water content of $\theta = 0.05$, t_D would increase to 25 days for the same cell spacing. In the same manner, the effective radius of nutrient acquisition for an hour, day, or month can be estimated for different hydration conditions using the characteristic diffusion length

$$L_D = \sqrt{D_e(\theta) \times t}\,). \qquad (3)$$

In other words, the soil water status affects the connectedness of the aqueous phase as reflected in diffusion distances or diffusion times (we ignore mass flow that persists for short times after rainfall or irrigation). This is a critical ingredient for considering soil metabolic exchanges and nutrient cycling and may limit metabolic processes such as microbial C and N transformation if water films in drying soils become increasingly isolated in disconnected pores of the soil matrix (Kim & Or, 2019) to the point of full disconnection between areas of nutrient supply and demand (Butcher et al., 2020; Querejeta et al., 2021).

Soil drying further creates a strongly altered biogeochemical environment in which solute concentrations can be increased by several orders of magnitude, which may include an accumulation of protons and can thus result in a decrease in pH in the remaining water films (Kim & Or, 2019), depending on the buffer capacity of the soil. Upon rewetting, these highly concentrated (potentially acidic) brines, which contain not only ions but also organic compounds, are suddenly mobilized from the soil pores and, by reconnection of the water films, can interact with each other or with the soil matrix, that is, their solutes can either be rapidly taken up and metabolized by microorganisms that have survived the drought, or they can directly chemically react with each other at concentrations that are much higher than in soils at intermediate or higher soil moisture levels.

Such fluctuations in soil moisture do not uniformly influence different microbial groups, their microbial colonization patterns and their functionality. Soil bacteria require direct contact with liquid water for their life function (nutrient uptake occurs primarily via diffusion through the liquid phase) and for different modes of motion, and can produce osmoprotective substances to survive dry conditions (e.g., Iturriaga et al., 2009). By comparison, fungal hyphae can bridge gaps across empty pores and can access resources under drier conditions than bacteria (Waring et al., 2013; Figure 1B). This may give fungi an advantage over bacteria in colonizing microhabitats such as the mineralosphere (Boeddinghaus et al., 2021; Kandeler et al., 2019). Moreover, fungi exhibit stronger resistance to soil desiccation than bacterial communities (Barnard et al., 2013) highlighting their ability to function even when diffusion no longer supplies sufficient nutrients to sessile cells.

3.4 | Microbial nutrient acquisition as controlled by soil water status

The bulk soil microbial response to environmental factors is often measured as heterotrophic soil respiration, which represents an aggregated response to various small-scale physical and biochemical processes taking place at the interface between microbes and substrate at the pore scale (Becker & Holz, 2021; Moyano et al., 2013; Schimel & Gulledge, 1998). Soil water availability represents one of the most important factors in this context: It is well established that soil respiration peaks at an intermediate range of soil moisture and decreases when soils are either drier or wetter than the optimum, explainable by deficiency of water or oxygen, respectively (Orchard & Cook, 1983; Skopp et al., 1990). A prediction of soil respiration in the context of coupled water and nutrient dynamics is further complicated by highly nonlinear relationships. The underlying small-scale mechanisms may include microbial cell lysis (Borken & Matzner, 2009; Van Gestel et al., 1992) associated with the release of intracellular solutes (Fierer & Schimel, 2003; Halverson et al., 2000), or aggregate disruption (Denef et al., 2001) with previously immobilized organic matter becoming available. Similarly, it was already recognized by Birch (1958) that rewetting of dry soil causes large pulses in nutrient and C mineralization, which is the so-called “Birch effect” (Orchard & Cook, 1983).

Purely chemical reactions can contribute to the sudden increase in CO_2 emission upon rewetting of soils. For example, nitrite tends to accumulate in soils during drying (Liu et al., 2018) and can react chemically with lignin-derived aromatic carboxylic acids. This leads to the formation of nitroso compounds and considerable CO_2 release, especially at high nitrite concentration and low pH, where up to 8% of lignin-derived carboxylic acids reacted with nitrite within 24 h with CO_2 release (Wei et al., 2017). Also, the frequently observed flush of NO and N_2O emissions after rewetting of dry soil has been attributed to a concerted action of a very fast abiotic mechanism, so-called chemodenitrification, and has been found to substantially contribute to total N_2O and NO emissions from soils in a recent meta-analysis (Wei et al., 2022). This process is responsible for the rapid release of NO and N_2O within minutes after rewetting, whereas the microbiological processes of nitrification and denitrification act over a few hours up to a few days (Harris et al., 2021; Homyak et al., 2017; Krichels et al., 2022).

Changes in soil water status further induce changes in redox conditions as outlined in the previous sections, which requires an adaptation of microbial metabolism, as available electron acceptors change. Nitrate, manganese (IV) oxide, iron (III) oxide, sulfate, and CO_2 are alternative electron acceptors in soils to sustain microbial growth, which are progressively less energy-efficient than O_2 (Schink, 2006) and directly alter nutrient pools. A switch from oxygen to nitrate might occur between 5 and 17 µM remaining O_2 depending on the O_2 tolerance of the dominating microorganisms (Lycus et al., 2017). Additionally, organic C and nitrate concentrations determine if the denitrification cascade is truncated or not (Philippot & Hallin, 2005; Skiba & Smith, 2000) and are positively correlated with emissions of N_2O or N_2. Although the energy gain is still relatively high during denitrification, it leads to a net nitrate loss, because at the same time provision of new nitrate via nitrification is hampered under low O_2 concentrations (Schleper, 2010). Besides the reduction in energy production along the redox chain, also the diversity of involved microorganisms and the oxygen tolerance decreases significantly (Kallistova et al., 2017; Muyzer & Stams, 2008; Philippot & Hallin, 2005), which severely reduces functional redundancy and metabolic flexibility as an emerging property under fluctuating redox conditions. Whether fluctuating redox conditions cause a shift in microbial community composition or only in microbial activity, primarily depends on the duration of the redox change compared with the relative reproduction rate of the microbial community (Pett-Ridge & Firestone, 2005). Regular changes in redox conditions facilitate the establishment of versatile microbial communities, which quickly switch to alternative resource utilization (DeAngelis et al., 2010). The water-mediated interplay or competition between microbial activity and purely chemical reactions of reactive substrates in the soil thus highly depends on the soil conditions, the drying history and the frequency of drying-rewetting cycles of the soil (Birch, 1958; L. L. Liang et al., 2016), and can also play an important role in soil N retention (Matus et al., 2019; Wei et al., 2022), but also for the availability of other nutritional elements.

3.5 | Integrating soil water status with stoichiometric controls of nutrient cycling

Predicting the microbial response to coupled water and redox dynamics and linking them to the availability and connectivity of resources in microbial habitats is complicated by highly contrasting effects of nutrient availability on soil respiration. Increasing supply of nutrients, such as N or P, has been shown to increase soil respiration in several studies (Cleveland & Townsend, 2006; Meyer et al., 2018), while others report a decline (Bowden et al., 2004; Janssens et al., 2010). This variable response is assumed to be regulated by “stoichiometric decomposition” and “microbial N mining.” According to stoichiometric decomposition, increased nutrient availability may increase soil respiration, especially in nutrient-limited soils rich in available C (Eberwein et al., 2015; Meyer et al., 2018). On the other hand, a decrease in soil respiration with increasing nutrient supply has often been explained by a reduction of microbial nutrient mining, that is, an increased SOM decomposition for nutrient acquisition under C-rich conditions (Craine et al., 2007; Moorhead & Sinsabaugh, 2006). These partially opposing effects of microbial N mining and stoichiometric decomposition may coexist and interact in soil depending on C and nutrient availability (Chen et al., 2014).

Despite the differences in soil nutrient stoichiometry, microbial nutrient stoichiometry is considered stable on a global scale (Griffiths et al., 2012). Cleveland and Liptzin (2007) proposed a C:N:P ratio of 60:7:1. No specific ratio relative to S has been proposed yet. However, Khan and Joergensen (2019) suggested that the microbial S metabolism has specific importance under P-limiting conditions. This stability might be achieved by the ability of microbiota to selectively coregulate the expression of genes (for examples, see Kasahara et al., 1991; Merrick & Edwards, 1995; Robichon et al., 2000) involved in C, N, P, and S mobilization, uptake and storage (Santos-Beneit, 2015). Consequently, depending on the current C:N:P ratio in soils, microbial growth strategies (Allison, 2012; Kaiser et al., 2014) may switch from a limitation of energy (C) to a limitation of nutrients or vice versa (Zechmeister-Boltenstern et al., 2015), which has been described as the “threshold elemental ratio” or “breakpoint ratio” (Townsend et al., 2007).

In this regard, the soil water content becomes an important mediator for the supply of C and nutrients in sufficient amounts and at adequate ratios. As outlined in the previous sections, water saturation might induce the use of nitrate as electron acceptor under oxygen limiting conditions and its (energy demanding) mobilization from organic N pools in soil. Together with the overall reduced energy gain from organic C sources under anoxic conditions, it becomes obvious that C and N might be the limiting factors for microbial activity, independent from the available P pools. Thus, increased (C:N):P ratios might induce microbial activities under reducing conditions. In contrast to the differential effects of redox status on nutrient availability, drought will affect all processes related to C, N, and P mobility in the same way, resulting in an overall reduced activity pattern of the soil microbiome independent from the soil nutrient C:N:P ratio. Rewetting after a prolonged period will change soil C:N:P ratios as a result of the release of nutrients from dead biomass and thus also influence microbial activity mainly in terms of nutrient mobilization depending on the new nutrient ratio. However, these are also determined by climatic conditions, especially precipitation (Andrade-Linares et al. 2021), thereby complicating a prediction of nutrient effects on soil respiration. At present, the theories on both nutrient mining or stoichiometric controls still do not account for the mediating effects of water on nutrient availability for microbial metabolism.

4 | WATER AND NUTRIENT DYNAMICS AT THE PLANT SCALE

The transport of water and nutrients toward a plant root is in many ways controlled by the same processes as described in the previous section for the microbial scale. Inside the pores of minerals and microaggregates with a typical size of <200 nm, water is not available to plants (“dead water”), because it is retained by too strong capillary and molecular forces. However, nutrients released into these small-scale pores by weathering of mineral sources or microbial mineralization of organic compounds can be transported to the plant root by diffusion processes (Figure 2). In larger scale pores between aggregates, water is available to the plant and the water flux toward the root can deliver additional nutrients by convective transport. Both of these transport mechanisms will determine the coupling of water and nutrient cycling processes immediately around individual plant roots.

Considering a whole root system within a soil profile, additional complexity arises from the fact that concentrations of SOM typically decrease with depth, resulting in an accumulation of nutrients in organic form in the upper part of the soil profile. In deeper parts of the soil profile, nutrients are mainly present in mineral forms, such as P or S derived from the minerals contained in the parent material or as nutrients contained in leachate, such as nitrate and sulfate (Jobbágy & Jackson, 2001). In agroecosystems, these spatial patterns can be additionally modified by the input of mineral or organic fertilizer into the topsoil. However, during the growing season, the soil first dries out in the topsoil, and therefore decreased availability of water may limit nutrient uptake from the topsoil (Javaux et al., 2013). By comparison, subsoils frequently maintain elevated water contents for prolonged periods. The subsoil water reservoir additionally can be refilled by either preferential flow through the soil profile via macropores, for example, after rainfall events, or by capillary rise from groundwater, depending on the texture and hydraulic properties of the soil (Vereecken et al., 2022). Additionally, plants may develop specific adaptations of their root system architecture or benefit from mechanisms such as hydraulic lift of water from the subsoil to the topsoil, to overcome an uneven distribution of water and nutrients in the soil profile. Hence, at the plant scale, the extent to which water availability modifies nutrient cycling is determined by spatial separation of water and nutrients both for individual roots and for a full root system.

4.1 | Water-driven nutrient transport to plant roots

Classical rhizosphere models simulate rhizosphere gradients around individual roots in 1D radially symmetric geometry. In the context of solutes and microorganisms in the rhizosphere, this was extensively reviewed by Kuppe et al. (2022). For diffusion-dominated systems, the Péclet number (the ratio of diffusion versus convection time) is often small (Roose et al., 2001). Thus, the extent of the rhizosphere can be assessed by using the characteristic diffusion lengths similar to Equation 3, but using the apparent diffusion coefficient that accounts for retardation due to sorption, which is different for different solutes, that is:

$$L_D = \sqrt{\frac{D_e(\theta)}{\theta + b} \times t}. \tag{4}$$

Table 1 shows the characteristic diffusion lengths for different nutrients. We can expect a rhizosphere gradient to extend from the root surface to a distance in the order of centimeters for mobile nutrients such as nitrate, and millimeters for less mobile nutrients such as

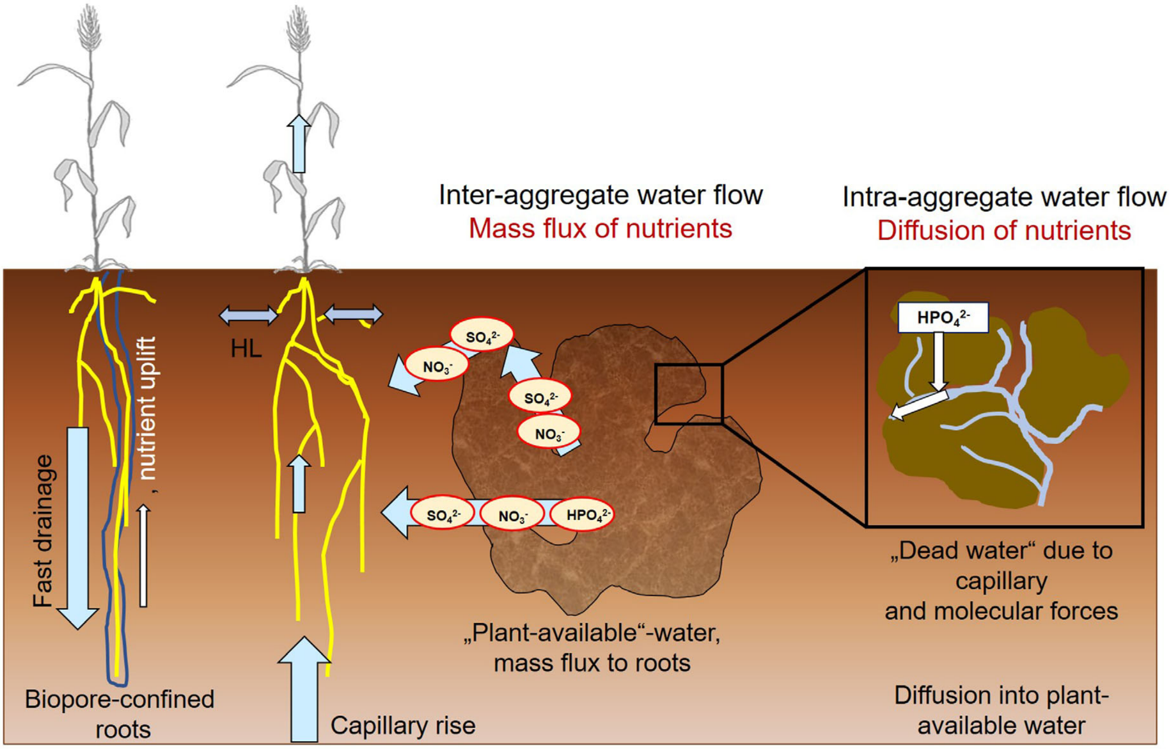

FIGURE 2 Integrated water and nutrient flux from small-scale flux within soil pores to redistribution within the soil profile (HL = hydraulic lift, leading to temporal moistening of the topsoil with subsoil water during nighttime).

TABLE 1 Rhizosphere extent as estimated by the diffusion length L_D for different nutrients at two different levels of volumetric water content

		L_D (cm)	
Nutrient	***b*** **(–)**	**θ: 0.03**	**θ: 0.01**
NO_3^-	1.0	1.34	0.23
SO_4^{2-}	2.0	1.01	0.17
NH_4^+	39.0	0.24	0.03
PO_4^{3-}	239.0	0.10	0.02

Parameters taken from Roose et al. (2001): liquid diffusion coefficient D_l, 1.0×10^{-5} (cm^2/s); volumetric water content θ, 0.3 or 0.1 (cm^3/cm^3); tortuosity factor f, 0.3 (–); buffer power b (-) as listed above. The diffusion time t_D was taken to be 24 days in this example, the lower boundary of the mean root lifespan of annual crops in the temperate zone as found by Pritchard and Rogers (2000) and also the mean value of root lifespan of four annual crops found by van Noordwijk et al. (2004).

phosphate. This strongly influences the soil volume available for plant nutrient uptake. For a large root system of 70 m root length and an average root radius of 0.02 cm, the rhizosphere volume would be 39.6 L versus 0.2 L for mobile and immobile nutrients, respectively. Depending on the distances between individual roots and the mobility of the nutrients, the rhizosphere volumes of individual roots may overlap so that the net rhizosphere volume is reduced accordingly (Landl et al., 2018). The rhizosphere volume is further reduced by a low volumetric water content θ (Table 1). The shape of the gradient is also influenced by the root radius (see, e.g., Vetterlein et al., 2020) and the boundary conditions at the inner (interface with the root surface) and outer (interface with the bulk soil) boundaries.

The extent of the rhizosphere gradient depends in a highly nonlinear way on the water content of the soil. The unsaturated hydraulic conductivity drops significantly in dry conditions (Schröder et al., 2008) and this needs to be taken into account for modelling of root water and nutrient uptake processes (Khare et al., 2022). In moist conditions, there are no significant rhizosphere gradients for water because the redistribution of water is fast compared with the development of the gradients. Conversely, in dry conditions, the hydraulic conductivity becomes so small that rhizosphere gradients become significant, that is, the rhizosphere dries out compared with the bulk soil (Carminati et al., 2010). These water dynamics influence the nutrient dynamics via facilitating or impeding the transport of nutrients toward the root surface and via the soil water content and thus the amount of nutrients available to the plants.

In addition to the focus on individual rhizosphere compounds, it is important to consider the interplay between multitudes of processes taking place in the rhizosphere at various spatial and temporal scales (Schnepf et al., 2022). For instance, plants can alter their rhizosphere by releasing organic substances that affect the hydraulic and/or chemical nature of the soil surrounding them. The release of gel-like substances such as mucilage alters the soil hydraulic properties, which in turn affects the fate of nutrients in the soil. The release of low-molecular organic acids or protons changes pH and nutrient mobility directly. The exudation of citrate, for example, is known to increase the plant availability of sparingly available phosphate. The increased concentration of anions in the rhizosphere is then buffered by a concomitant change in cation concentration to maintain charge balance. Often this is achieved by an increase in H^+ concentration, but it may also induce an accumulation of other mobile cations, such as K^+ and Na^+ (McClure et al., 1990; Raddatz et al., 2020). Further, the release of all organic compounds, including sugars, affects the local microbial population (Dupuy & Silk, 2016), which in turn may alter nutrient availability.

Root growth lengthens and narrows the rhizosphere as shaped by rhizodeposition (Landl et al., 2021). This can be described using the dimensionless Péclet number of the rhizosphere, which describes the time scale of root growth relative to diffusion:

$$\mathrm{Pe}_{\mathrm{rhizo}} = \frac{v\, r_0}{D_l \theta f}, \tag{5}$$

where v is the root elongation rate and r_0 is the root radius. For $\mathrm{Pe}_{\mathrm{rhizo}} > 1$, the extent of the rhizosphere is largely determined by how fast the root grows, whereas for $\mathrm{Pe}_{\mathrm{rhizo}} < 1$ the rhizosphere extent is mainly determined by diffusion. Plants can also alter the rhizosphere volume at their disposal by developing root hairs (Leitner et al., 2010; Zygalakis et al., 2011), or by forming symbioses with mycorrhizal fungi (Kobae, 2019). This will determine the rhizosphere hotspot volume in which the relevant chemical changes of the soil take place that may improve nutrient availability.

Once at the root or hyphal surface, nutrients are taken up actively or passively (Hopmans & Bristow, 2002; Jorda et al., 2021). Water enters the roots passively according to the total water potential gradients, although the root water uptake paradigm has recently shifted toward the recognition of symplastic osmotic potential gradients that may actively drive root water uptake (Couvreur et al., 2021). With this water influx, solutes may enter the root either by advection via the transpiration stream, or by diffusion across the root membrane according to a concentration gradient between roots and soil. However, solutes can also be excluded from uptake, a mechanism known to protect plants from pollutants. Active nutrient uptake is often described by Michaelis Menten kinetics, a nonlinear function of the nutrient concentration in the soil solution at the root surface (Cushman, 1982). This type of nutrient uptake is independent of any concentration gradient between roots and soil. Finally, a combination of both active and passive nutrient uptake is also possible (Somma et al., 1998).

After uptake, nutrients are translocated in the xylem via the transpiration stream toward the shoot (e.g., Bauke et al., 2021; Jorda et al., 2021) but can also be back-transported from the shoot to roots via the phloem (Bauke et al., 2021), thereby significantly influencing the redistribution of nutrients into the soil upon decomposition of above- or below-ground plant residues.

4.2 | Overcoming depth gradients in water and nutrient distribution

If limitations in nutrient availability cannot be overcome by modifications of the rhizosphere around an individual root, plants can also respond with a specific adaptation of the architecture of the whole root system (e.g., de Bauw et al., 2020; Dathe et al., 2016; Lynch, 2019). These variations in root system architecture determine the overlap of the rhizosphere around individual roots, but will also affect the overlap of rhizosphere with other microhabitats as described in the previous chapter. Root system architecture further specifically interacts with the different distribution of water and nutrients in the soil profile and again depends on the mobility of a nutrient and its transport within the soil profile. For immobile nutrients such as P, enhanced growth of thin and long roots especially in the topsoil, so-called topsoil foraging, has been observed. For mobile nutrients that are easily leached to deeper layers of the soil profile, such as N in form of nitrate, the growth of a few deep roots is preferred (Lynch, 2019). S limitation has been reported to result in enhanced growth of the primary root (Joshi et al., 2019), although no specific results from field studies are available. Especially foraging via deep roots is also beneficial for water acquisition from deeper soil layers (Lynch, 2019).

When deep roots, especially those of tap root systems, decompose they leave large cavities in the soil, which can serve as preferential flow paths (Jarvis, 2007). These preferential flow paths may on the one hand exacerbate the discrepancy between water and nutrient distribution within the soil profile, if, for example, after a precipitation event large quantities of water are quickly transferred from the nutrient rich topsoil into deeper layers of the soil profile with lower amounts of plant-available nutrients. On the other hand, preferential flow paths have also been identified as hotspots of microbial activity (Franklin et al., 2019; Fuhrmann et al., 2019) and can be enriched with nutrients from the decomposing root or faunal activity in the pore. Hence, moistening of these hotspots during preferential flow events may also provide a short-term increase in nutrient availability for roots growing in the pores (for a more detailed account of the interaction of root growth and microbial activity in soil pores see Wendel et al. [2022]).

In the reverse direction, water uptake from deeper soil layers will also acquire nutrients from the subsoil, thus re-allocating them to the topsoil with litter fall. The ecological significance of such vegetation controlled nutrient cycling in ecosystems is well known for forests (e.g., Bullen & Chadwick, 2016; Buxbaum et al., 2005; Uhlig et al., 2020), and is now increasingly considered also as a management strategy in agricultural systems utilizing, for instance, subsoil access from deep rooting pre-crops (Perkons et al., 2014; Seidel et al., 2019). However, water uptake from the subsoil can also result in a spatial separation of water and nutrient acquisition. In perennial shrub species, the addition of water and N to dry topsoil (by irrigation) resulted in species-specific resource use patterns. Some species utilized both the additional water and the additional N, whereas others took up N only (Gebauer & Ehleringer, 2000), suggesting that water required by the plants was supplied via root uptake from other parts of the soil profile.

The water taken up from deep soil may also directly be redistributed via the roots to the topsoil (Figure 2). This upward transport of water from wetter subsoil areas to drier topsoil areas via plant roots is commonly denoted as hydraulic lift or hydraulic redistribution (Neumann & Cardon, 2012; Prieto et al., 2012; Richards & Caldwell, 1987). Hydraulic lift is generally driven by the same mechanisms as root water uptake and occurs when transpiration losses from plant leaves are reduced, for example, during the night when stomata are closed (Prieto et al., 2012; Richards & Caldwell, 1987) and leaf water potential is near zero (Schmidhalter, 1997). As a consequence, the water potential of the dry topsoil can be lower than the water potential of the roots that are within the topsoil (Meunier et al., 2017; Prieto et al., 2012). In this case, following this gradient, water taken up by the roots in the subsoil will not ascend into the shoot, but will be released into the dry topsoil instead (Vereecken et al., 2022).

We are not aware of significant evidence that this water release includes a release of nutrients from the plants into the soil. However, the released water becomes temporarily available to microbes and may stimulate microbial mineralization processes releasing nutrients into the soil solution. As increased water availability usually improves nutrient availability and uptake, it was also suggested that hydraulic lift improves plant nutrient acquisition in the rhizosphere (Liste & White, 2008; Prieto et al., 2012). For trees, Dawson (1997) observed indeed that soil N availability increased around roots when they engaged in hydraulic lift. By contrast, Snyder et al. (2008) did not find a significant effect of hydraulic lift on ^{15}N uptake of shrubs when minimal amounts of N in aqueous solution were added to the soil. Similar mechanisms can be assumed to occur for crop species, for the acquisition of N as well as any other nutrient element from soil, such as P and S, when accounting for limitations of the different mobility of these elements in soils, although this has not been specifically studied yet. In many cases, studies on water redistribution via roots also only consider effects on individual plants or plant species, but rarely consider implications for the full ecosystem.

5 | ECOSYSTEM-SCALE COUPLING OF WATER AND NUTRIENT DYNAMICS

5.1 | Water-driven nutrient inputs at ecosystem scale

Rain, snow, hail, and other forms of precipitation act as one of the major components linking nutrient dynamics and fate across larger distances within agroecosystems, as nutrients exported from one catchment, for example, via gaseous losses or to a lesser extent by dust transport, can be imported to other catchments with precipitation via "wet deposition" and thus transfer nutrients from atmospheric sources to the soil. The trends of atmospheric deposition of N, P, and S can be very broadly characterized for temperate regions as a strong increase in N deposition, but relatively less for P and regionally differentiated decline or increase for S (Ackerman et al., 2019; Gao et al., 2018; Mahowald et al., 2008). Moreover, in addition to any wet deposition, poorly quantified dry deposition can add half or more of annual atmospheric nutrient inputs to soils (Huang et al., 2011), which are not immediately effective, but may later be mobilized from deposition surfaces with the next precipitation event. Additionally, nutrients can also be added to ecosystems with direct water transport, for example, by overland or subsurface flow. In either form, these inputs may provide a useful addition for crops deficient in certain nutrients or an unwanted nutrient excess not utilized by the plants (Cui et al., 2014; Karimi et al., 2020). For agroecosystems, the relative impact of atmospheric deposition compared with fertilizer inputs on agricultural crop performance is often not fully quantified (He et al., 2007; Pieri et al., 2010; Tositti et al., 2018).

The response of catchments to these nutrient inputs additionally depends on the microbial composition. Waring et al. (2013) have discussed how changes in soil conditions across biomes and land use affect the ratio of fungal to bacterial biomass, as differences in physiology affect the biogeographic distributions of these two groups. A recent study (Yu et al., 2022) showed that fungi with their generally slower growth and turnover rates (Rousk & Bååth, 2007), greater carbon to nutrient stoichiometry (Waring et al., 2013), and greater capacity to degrade more recalcitrant substrates (Strickland & Rousk, 2010) dominate in high latitudes with low mean annual temperature and high net primary productivity relative to soil bacteria that dominate in the tropical regions and in arable lands with frequent tillage disturbances. By comparison, another global study of fungal and bacterial groups (Bahram et al., 2018) pointed to limitations of available data and limited consideration of the role of water when comparing ecosystems at a global scale. Bickel et al. (2019) have shown the critical role of water status in mediating bacterial diversity and explaining the origins of its pH dependency (climatic water regime determines soil pH), thus resulting in diverse microbial responses to nutrient input across ecosystems.

At global to local scales differential water-driven input of N, P, and S leads to modifications of stoichiometric ratios in the soil (Figure 3), which in turn may result in feedbacks on agricultural ecosystem performance. Finally, surplus additions of single or multiple nutrients may temporarily be retained in the receiving soils, but later on still end up in nearby connected water bodies via water-mediated transfer (Gurmesa et al., 2022; Verma & Sagar, 2020). These processes are especially critical in riparian ecosystems where soils are more or less directly connected to adjacent surface water bodies.

5.2 | Water-driven exports from agroecosystem catchments

Water-driven losses of nutrients from arable land can be manifold, ranging from surface runoff due to precipitation, subsurface transport, particulate transport in the form of aerosols, or gaseous emission. Especially fertilizer N and P in agroecosystems can pose a severe risk as there is an imbalance between applied nutrients in the form of fertilizer and the uptake by plants, resulting in a large fraction that can potentially be mobilized and either enter the freshwater system or, especially in the case of N, be emitted to the atmosphere (Vitousek et al., 2009).

As described in the previous chapters, soil water content and water filled porosity greatly affect the production of N_2O and N_2 emissions. In agroecosystems, especially rainfall or irrigation are drivers of such short-term emission of N_2O when the concentration of mineral N in the soil is high (Wang et al., 2010). The volatilization of NH_3—occurring at the soil surface when NH_4^+ from organic fertilizers (mainly urea) is converted to NH_3 gas at high pH values—is increased with increasing

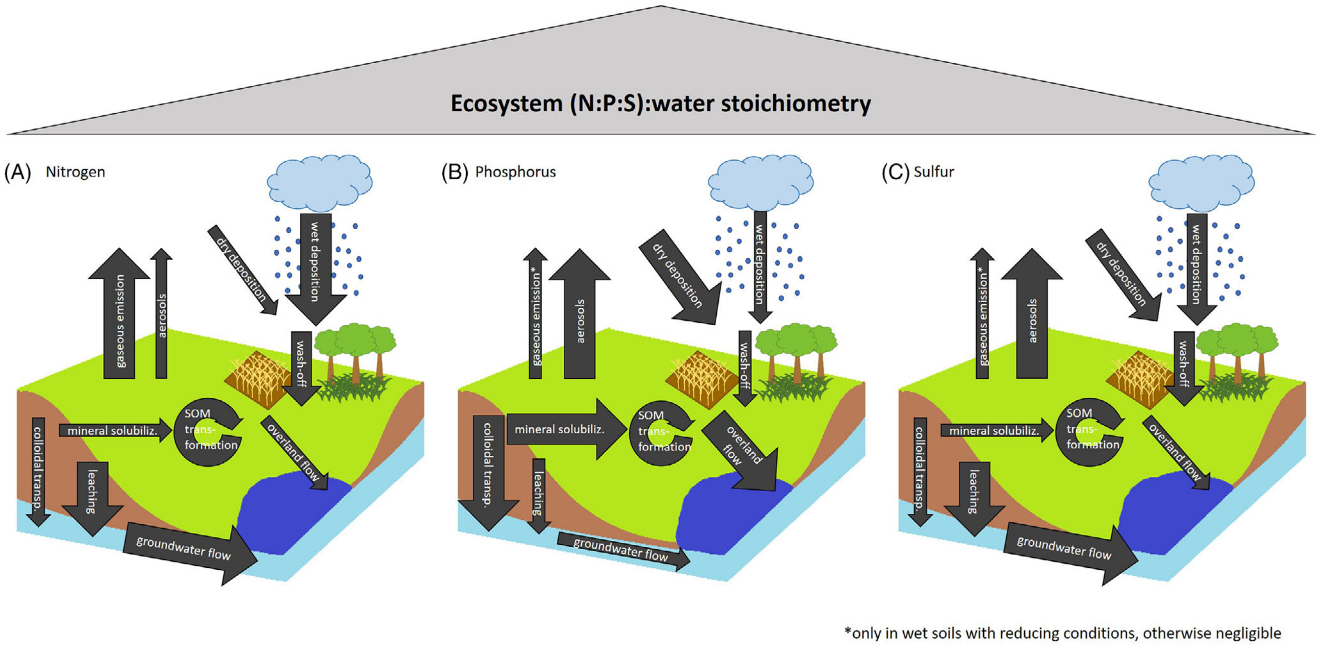

FIGURE 3 Water-related processes at the catchment scale driving soil water status and cycling of nitrogen (N), phosphorus (P), and sulfur (S) in soils, resulting in a climate- and ecosystem-specific N:P:S to water stoichiometry. The size of the arrows indicates the relative importance of each process for the respective element.

soil moisture. In water-saturated soil, NH_3 volatilization is high as the movement of fertilizer N into the soil is reduced and fertilizer-derived urea that remains at the soil surface is hydrolyzed at a higher rate in wet conditions (Bock & Kissel, 1988). Similar to N, the cycle of S in agroecosystems is not closed, especially to the atmosphere, and soils can act as a sink but also as a source of atmospheric S (Eriksen, 2008). There are various volatile S compounds produced during the decomposition of SOM, especially under wet, anaerobic conditions, including H_2S, carbonyl sulfide, dimethyl sulfide, or C disulfide (Maynard, 1998). Similarly, gaseous emissions of phosphorus, in form of phosphine, only occur in wet conditions and are often considered negligible (Young et al., 2021).

In addition to soil moisture effects on the amount and form of gaseous emissions, exports with water fluxes play an essential role for N, S, and P (Figure 3). The leaching of NO_3^- is one of the most important N loss pathways leading to increasing contamination of surface and groundwater, particularly in areas with arable land (Li et al., 2021). In arable land, the most critical season for losses of dissolved N is the fall and winter period, when plant N uptake is low or zero but soil microorganisms involved in N turnover (mainly mineralization and nitrification) are still active and convert SOM to NH_4^+ and NO_3^- (Sieling & Kage, 2006). Further, the amount and distribution of precipitation across the landscape determine N leaching losses (Bijay-Singh & Craswell, 2021; Singh & Sekhon, 1979). Temperate soils with low mean annual precipitation have lower soil moisture, higher O_2 availability, and thus higher nitrification activity, thereby promoting the accumulation of NO_3^- (Li et al., 2021). However, losses in irrigated cropland were observed to be much higher than in rain-fed agriculture (Bijay-Singh & Craswell, 2021). Leaching losses of dissolved S mostly dominate the overall S losses in temperate regions (Bristow & Garwood, 1984; Eriksen & Askegaard, 2000; Riley et al., 2002), and factors influencing leaching losses of SO_4^{2-} are probably similar to NO_3^- (Riley et al., 2002). For P, there is already a considerable number of reviews reporting on P transport and P management in arable soils (e.g., Kadlec, 2016; Sharpley et al., 2015; E. O. Young et al., 2021). In brief, the influence of precipitation or temperature via, for example, heavy rain events, dry–wet cycles, or freezing–thawing cycles have a major impact on the mobilization and transport of both dissolved and particulate P. Losses of dissolved P may even be greater than previously assumed (Hahn et al., 2014; Jordan-Meille & Dorioz, 2004; Kleinman et al., 2007), contributing between 16 and 69% of total P losses from arable catchments (Jiang et al., 2021; Nausch et al., 2017). Studies estimating the losses of dissolved P from catchments are rare, but, for example, Gottselig et al. (2017) reported in a comprehensive study of stream water of five forest catchments that dissolved P exports from catchments were between 0 and 17% of total P loss. There is a rising awareness that during stormflow events the amount released as dissolved P can be substantial, accounting for up to 61% of total P losses (Gu et al., 2017; Gu, 2017), although it is widely accepted that P is mainly transported in particulate form, for example, bound to colloids, during heavy rain events and high discharge periods.

Natural colloids (particles of 1–1000 nm diameter), as well as their subset of natural nanoparticles (1–100 nm), are highly mobile in soils, and the colloid-facilitated transport of elements is highly dynamic as the transport is closely connected to the water movement in the soil. Colloids have a large specific surface area and consist of primary building blocks such as organic matter, Fe/Al-(hydr)oxides, clays, or calcium carbonates with potential adsorption sites for nutritional ions (Burger et al., 2021; Gottselig et al., 2017; Philippe & Schaumann, 2014). Phosphate has the highest potential for colloidal exports due to its high adsorption affinity compared with nitrate and sulfate (Johnson & Cole, 1980). Especially high discharge events can cause substantial particulate P exports (Burger et al., 2021; Jiang et al., 2021; Tiemeyer et al., 2009). Even though the export of dissolved nitrate and sulfate is exceeding colloidal N and S exports (Burger et al., 2021), there is evidence that colloidal export of S can be substantial. Mainly organic S in different oxidation states (e.g., reduced species in sulfides, thiols; intermediately oxidized species in sulfoxides, sulfones, and sulfonates; and fully oxidized S in sulfate esters) are released and transported (Adediran et al., 2021; Fakhraee et al., 2017), with the redox state being dependent on the redox conditions of the soil (Adediran et al., 2021; Boye et al., 2011). The scale of nutrient loss via dissolved or colloidal transport finally further depends on the connection of a given soil profile or site within the catchment to the aquifer.

5.3 | Riparian systems as control points of water-driven nutrient exports

Riparian zones are the land–freshwater interface at rivers, lakes, and estuaries. As such, they have important ecological functions because they often directly control the export of N, P, and S from the terrestrial to aquatic ecosystems by a combination of physical, chemical, and biological processes. In agricultural systems that receive excessive amounts of fertilizers, vegetated riparian buffer zones have been implemented as a strategy to reduce the transfer of N and P to aquatic ecosystems to avoid eutrophication and toxic algal blooms. While multiple studies have shown that this strategy is effective in reducing N inputs to surface water bodies (Hill, 2019; Mayer et al., 2007; Zhao et al., 2021), the effect of riparian buffer zones on P transfer is less clear (Gu et al., 2017; Hoffmann et al., 2009; Young et al., 2019). Vegetated riparian buffer zones provide a physical barrier that slows down the overland flow, which allows for stronger infiltration of P into the soil, where it is retained in geochemical pools (e.g., through sorption and precipitation processes) and biological pools (e.g., through uptake by roots and microorganisms) (Dosskey et al., 2010; Hoffmann et al., 2009; Zhang et al., 2010). However, the accumulation of P in the biomass and geochemical pools of the riparian zone is finite. When plants die and decompose, part of the P will be remobilized as organic P (Dodd et al., 2018). Further, the adsorption sites in soils might become saturated and/or reduced, resulting in a slow but continuous release of legacy P into freshwater systems (Haygarth et al., 2014; Sharpley et al., 2013). Indeed, studies have indicated that legacy P in subsoils of riparian buffer zones might be the driving force for the ongoing eutrophication of river and lake ecosystems (Andersson et al., 2015; Carlyle & Hill 2001; Weihrauch et al., 2021). At the same time, riparian buffer zones can help to mitigate the contamination of groundwater with nitrate and phosphate, a persisting problem compromising the quality of drinking water in many parts of the world (Hill, 2019; Warrack et al., 2021).

Sulfur in riparian zones presents a particular case, because, in contrast to N and P, the inputs of S have been reduced in many terrestrial ecosystems over the past decades due to the decline of sulfuric acid deposition (H_2SO_4) from the combustion of fossil fuels, although regional exceptions exist. However, S is still an important regulatory element in riparian buffer zones, for example a decline in sulfate deposition may coincide with a (partial) reversal of soil acidification. Reduced levels of soil acidity, in turn, stimulate microbial activity and initiate increased export of dissolved organic matter from riparian zones (Evans et al., 2006), thus contributing to water mediated redistribution of carbon and nutritional elements within the catchment.

Hydrological flow paths in riparian zones mix these nutritional elements with C leading to biogeochemical processes that either promote or impede the export of nutrients (Bauke et al., 2022; Hedin et al., 1998; Vidon et al., 2010). Having generally high but also strongly fluctuating water tables, redox processes at the microbial scale (see previous chapters) are especially critical in soils of riparian zones. These redox processes create a dynamic system that might change over the course of days, months, or even years, creating hotspots and hot moments at the ecosystem scale (Mansfeldt, 2003; Nogueira et al., 2021; Bernhardt et al., 2017), depending on the availability and distribution of nutrients at the smaller scales and on their susceptibility to different export pathways such as colloidal and dissolved but also gaseous losses.

6 | CONCLUSION—COUPLING OF NUTRIENT CYCLING TO SOIL WATER STATUS ACROSS SCALES

At the smallest scale, nutrient cycling within agroecosystems is controlled by the availability of water as a reaction partner. Especially water-related limitations of oxygen availability lead to redox effects that determine the speciation and reactivity of elements. With increasing scale, these underlying mechanisms are modified and partially overridden by additional processes, such as the spatial organization of water, nutrients, and microorganisms within the soil pore system, the redistribution of nutrients via plant uptake and release from litter and larger scale transport processes with atmospheric circulation, overland flow, drainage, and subsurface flow.

Considering that N, P, and S as the major nutritional elements in agroecosystems are differentially sensitive to changes in water status and different transport pathways, water-driven nutrient transport and turnover can either mitigate or exacerbate imbalances in nutrient stoichiometry. Further, the availability of nutrients is indirectly affected by soil water controls on the activity of microorganisms and plants. Especially fungal hyphae and plant roots can act as additional mediators of nutrient cycling by compensating for differences in availability and concentration of various nutrients within the soil. At catchment or even larger scale, nutrient inputs via precipitation, but also overland flow carrying nutrients in dissolved or particulate form, may balance or at least alter stoichiometric ratios in soils. Vice versa, inputs mediated by precipitation may also increase nutrient limitation if deposition induces an excess of the deposited element, without concomitant increase in the availability of other nutrients.

An overall understanding of water status effects on nutrient cycling within agroecosystems should thus aim to integrate these processes across scales. Experimental work, which is often restricted to observations at individual scales, should consider soil water status and associated variation in nutrient availability and mobility as an additional factor, for example, in concepts of nutrient stoichiometry and nutrient mining. Also, more multifactorial experiments are needed to obtain a better understanding of the interacting effects of soil water status, as well as water residence time and related C fluxes and redox potentials on nutrient cycling across scales. Novel modeling approaches are becoming available to upscale the effect of spatial and temporal variations of environmental properties on smaller scales to describe larger scale processes (Chesson, 2012; Fritsch et al., 2020). These models consider nonlinear processes, feedback mechanisms, scale breaks and/or spatial and temporal variations on smaller scales that affect properties observed at larger scales. In combination with experimental approaches, we thus increasingly approach a mechanistic understanding of nutrient turnover processes across scales in soils of agroecosystems under a changing climate or as a consequence of extreme events.

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