



Review

Nutrients in the rhizosphere: A meta-analysis of content, availability, and influencing factors



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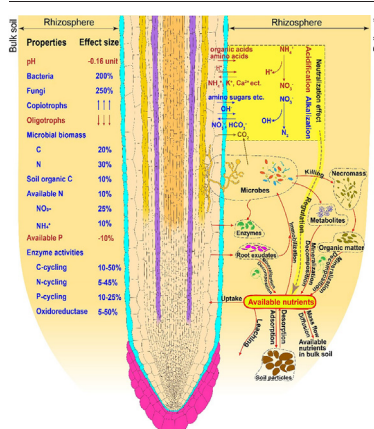
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HIGHLIGHTS

- Rhizosphere nutrient availability was quantitatively identified using a meta-analysis.
- Available nitrogen was approximately 10% higher in the rhizosphere than in bulk soil.
- Available phosphorus in the rhizosphere decreased by 12% compared to bulk soil.
- In the rhizosphere, microbial population densities increased more than the microbial biomass.
- Copiotrophic microorganisms were more dominant than oligotrophs in the rhizosphere.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrient deficiency in most terrestrial ecosystems constrains global primary productivity. Rhizosphere nutrient availability directly regulates plant growth and is influenced by many factors, including soil properties, plant characteristics and climate. A quantitatively comprehensive understanding of the role of these factors in modulating rhizosphere nutrient availability remains largely unknown. We reviewed 123 studies to assess nutrient availability in the rhizosphere compared to bulk soil depending on various factors. The increase in microbial nitrogen (N) content and N-cycling related enzyme activities in the rhizosphere led to a 10% increase in available N relative to bulk soil. The available phosphorus (P) in the rhizosphere decreased by 12% with a corresponding increase in phosphatase activities, indicating extreme demand and competition between plants and microorganisms for P. Greater organic carbon (C) content around taproots (+17%) confirmed their stronger ability to store more organic compounds than the fibrous roots. This corresponds to higher bacterial and fungal contents and slightly higher available nutrients in the rhizosphere of taproots. The maximal rhizosphere nutrient accumulation was common for low-fertile soils, which is confirmed by the negative correlation between most soil chemical properties and the effect sizes of available nutrients. Increases in rhizosphere bacterial and fungal population densities (205–254%) were much higher than microbial biomass

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increases (indicated as microbial C: + 19%). Consequently, despite the higher microbial population densities in the rhizosphere, the biomass of individual microbial cells decreased, pointing on their younger age and faster turnover. This meta-analysis shows that, contrary to the common view, most nutrients are more available in the rhizosphere than in bulk soil because of higher microbial activities around roots.

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1. Introduction

The global agricultural productivity must increase by up to 70% to meet the food demand of nearly 10 billion people expected to populate Earth by 2050 (Hunter et al., 2017). This onerous challenge must be met without the expansion of arable land and by using lower inputs of fertilizers and pesticides, or we may risk increasing natural ecosystem loss and causing the depletion of rock phosphate reserves (Abelson, 1999; Chowdhury et al., 2017; Sattari et al., 2012; Tilman et al., 2011). Nutrient deficiency, extensively confirmed in most terrestrial ecosystems, threatens plant production and ecosystem stability (Elser et al., 2007; Hou et al., 2020). One of the ways by which plants attempt to overcome this stress is by reinforcing nutrient availability in the rhizosphere (Hinsinger et al., 2003; Kuzyakov and Razavi, 2019). The rhizosphere is one of the most pivotal microbial hotspots determining the dynamics and cycling of nutrients; therefore, the plant-microbial interactions are very intense in this critical zone (Kuzyakov and Blagodatskaya, 2015). The interplay between roots and microbes determines the available nutrient content by regulating three process groups: (1) the rate of nutrient uptake by plants, immobilization by microorganisms, or release from organic matter decomposition; (2) nutrient mobility in soils; (3) the conversion between unavailable and available forms of nutrients (Darrah, 1993).

Many interrelated factors, such as original soil properties, plant characteristics, and climate factors, influence the three process groups and their interplay, and modulate the rhizosphere nutrient status (Jones et al., 2004). For instance, in low-fertile environments, a range of mechanisms (e.g., exudation of organic compounds and protons) are activated to increase the solubilization of nutrients in the rhizosphere (Rengel and Marschner, 2005). In acidic soil, plants elevate pH and optimize rhizosphere nutrient availability by releasing various root exudates, enhancing the uptake of anions (e.g., nitrate) or excreting OH^- from nitrate reduction (Sugihara et al., 2016). In contrast, in alkaline soils, roots secrete organic anions (e.g. citrate and malate) and protons, leading to rhizosphere acidification (Sun et al., 2020). In addition, compared with plants with fibrous root systems, taproots are more strongly colonized by arbuscular

mycorrhizal fungi, contributing to greater nutrient acquisition by accessing soil micropores and transporting nutrients (e.g. phosphorus (P) and nitrogen (N)) to plants (Hodge et al., 2001; Hodge and Storer, 2014; Yang et al., 2015). The formation of root nodules in legumes allows the conversion of N_2 to ammonia and amino acids and induces a divergent nutrient status in the rhizosphere, as compared to non-legumes (Day et al., 2001; Moreau et al., 2019). Furthermore, moisture and temperature also strongly regulate nutrient acquisition by plants by influencing the diffusion rate, cell membrane permeability, root physiology, and interactions with microorganisms (Praeg et al., 2019; Warren, 2009). For instance, the root uptake of NO_3^- is more preferential relative to NH_4^+ or glycine under warmer temperatures (Warren, 2009). The colonization of arbuscular mycorrhizal fungi is higher under drier conditions, inducing positive mycorrhizal P responses in plants (Cavagnaro, 2016). In summary, individual studies have identified differences between the rhizosphere and bulk soil in terms of their nutrient content and availability (Li et al., 2020; Marschner et al., 2002; Massaccesi et al., 2015; Steer and Harris, 2000). Similarly, the mechanism by which rhizosphere nutrient availability is modulated by only one or several interrelated factors has long been unraveled. However, a thorough and quantitative understanding of the effects of these factors on rhizosphere nutrient availability is still lacking and strongly recommended for further clarification (Cheng et al., 2014; Jones et al., 2004; Marschner et al., 2004; Pii et al., 2016).

Bacteria and mycorrhizal/saprotrophic fungi are the dominant components of rhizobiomes. They play important roles in improving nutrient acquisition, facilitating plant growth by exuding enzymes and organic molecules, and inhibiting fungal pathogens (Artursson et al., 2006; Philippot et al., 2013). For instance, in P-depleted soil, P-mobilizing bacteria release available P from organic compounds, which provides a P pool for plant growth and arbuscular fungal hyphae to extend to roots (Kucey et al., 1989). Even though the mobility and dispersal of bacteria and fungi are different, specific bacteria can migrate via fungal hyphal structures and colonize novel microhabitats (e.g., the rhizosphere). Many bacteria also feed on living saprotrophic and pathogenic fungi, as well as fungal remains (Ballhausen and de Boer, 2016). These relationships suggest that bacteria

and fungi have specific survival and colonizing strategies, which may contribute to diverse changes in their densities in the rhizosphere compared to bulk soil. Microbial densities in the rhizosphere, are two to three orders of magnitude greater than those in bulk soil (Ramos et al., 2000). The classification of microorganisms based on their life strategies (i.e., copiotrophs and oligotrophs) suggests that copiotrophs (grow faster and rely on resource availability; r strategists) are more abundant in the rhizosphere, whereas oligotrophs (efficiently exploit resources at the expense of growth rate; K strategists) are abundant in resource-poor environments (such as bulk soil; Ho et al., 2017; Liu et al., 2021; Ling et al., 2022). For instance, the abundances of the copiotrophic phyla Bacteroidetes and β -Proteobacteria are generally greater in the rhizosphere than those in the surrounding bulk soil (Fan et al., 2017; Kavamura et al., 2018). The fungal phylum Ascomycota, a copiotrophic taxon, is more abundant in the rhizosphere by utilizing a higher number of resources compared to Basidiomycota (Egidi et al., 2019; Pascual et al., 2018). While the shift of microbial communities in the rhizosphere has been acknowledged, a quantitative elucidation of the relative abundance of bacterial and fungal communities in the rhizosphere is still seldom (Ling et al., 2022).

We collected studies on nutrient content and availability in the rhizosphere, depending on plant characteristics, soil properties, and climatic factors. These studies mainly reported nutrients (e.g., N, P, and K) content, organic carbon (C) content, microbial C, activity of enzymes, bacterial and fungal population densities, and other original soil properties (e.g., pH, total N, and P). Plant species information (e.g., legumes/non-legumes, fibrous roots/taproots, trees/herbaceous plants/forbs), and climate factors (mean annual precipitation (MAP) and mean annual temperature (MAT)) were recorded. A meta-analysis was performed to elucidate the rhizosphere effects on nutrients (i.e., N, P, and potassium (K)) content. Our main aims were to (1) quantify nutrient availability in the rhizosphere compared to bulk soil, (2) identify how plant characteristics, original soil properties, and climatic factors influence nutrient availability in the rhizosphere relative to bulk soil, and (3) quantitatively elucidate the relative abundance of bacterial and fungal communities in the rhizosphere compared to bulk soil. We hypothesized that (1) available pools of nutrients are more depleted in the rhizosphere than in bulk soil due to intensive root uptake and microbial immobilization; (2) Plants with taproots accumulate more organic C and nutrients compared to plants with fibrous roots owing to stronger interactions with arbuscular mycorrhizal fungi during their longer life; (3) copiotrophic groups are more abundant than oligotrophs in the rhizosphere than in bulk soil.

2. Materials and methods

2.1. Data collection and extraction

Peer-reviewed research articles were collected from the ISI Web of Science search engine. China National Knowledge Infrastructure (CNKI) search engine was also used to increase the number of studies for the meta-analysis. The searching keywords included: either “rhizosphere soil or rhizospheric soil,” either “bulk soil” or “non-rhizospheric soil” and either “soil nitrogen”, “soil phosphorus”, “organic carbon”, “organic matter”, “enzyme*” or “microbial community”. The articles had to meet the following criteria to be included in the database: (i) data from bulk soil were included for comparison with data from rhizosphere soil; (ii) at least one of the variables presented in Table S1 should be included; (iii) the mean and replicate numbers for each variable were reported. A total of 123 articles, including 1030 observations, were found and included in the database for further analysis (Fig. S1; Table S1).

The data in the tables or main text were directly derived from the articles. The data illustrated in the figures of the articles were extracted using the WebPlotDigitizer (v.4.4) software (<https://automeris.io/WebPlotDigitizer>). The mean value, standard deviation (SD), and numbers of replicates (n) of each variable were extracted from the original sources. When standard error (SE) was reported, it was converted to SD by using the following equation: $SD = SE \times n^{0.5}$. When SD or SE were not available,

a SD approximated value as one-tenth of the mean was adopted (Gattinger et al., 2012; Luo et al., 2006; Xu et al., 2019).

In addition to the aforementioned variables, other information, such as geographical coordinates, climate factors (MAT and MAP), plant characteristics, original soil properties (pH, soil organic carbon (SOC), total nitrogen (TN), total phosphorous (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), and available potassium (AK)) were also collected from the articles. The methods to collect rhizosphere and bulk soil or analyze soil nutrients content are all commonly used, which ensures the observations are comparable. Only data reported as population densities ($\text{CUF} \cdot \text{g}^{-1}$) were collected to calculate the effect size of microbes (i.e. bacteria and fungi) between rhizosphere and bulk soil. When the articles reported soil organic matter content, we converted it to SOC content by using a factor of 1.724 (Swanepoel et al., 2016). When articles did not include MAT or MAP data, we downloaded these from WorldClim (<http://worldclim.org/version1>) using the reported coordinates and ArcGIS 10 software (Hijmans et al., 2005). Detailed information on plant characteristics was further examined, including plant types (herbaceous plants, shrubs, and trees), legumes/non-legumes, and root system types (fibrous roots and taproots). Descriptive statistics of climate factors and original soil properties in primary studies revealed that the studies cover broad climatic zones and have very diverse original soil properties. Consequently, the results are relevant for broad range of ecosystems (Table S2).

ΔpH was calculated by subtracting the bulk soil pH from the rhizosphere pH. The relationship between ΔpH and original soil pH was tested using a linear regression model. As soil pH is an important factor influencing nutrient availability, this relation shows the pH modification in rhizosphere by plants and microbes, which helps to understand the mechanisms of nutrient mobilization, accumulation or depletion in the rhizosphere. The average and SE of ΔpH were also calculated. Data regarding the relative abundance of bacteria and fungi in the rhizosphere and bulk soil were extracted from seven research articles using the above-mentioned approach. These data were used to quantitatively evaluate the relative abundance of bacteria and fungi in the rhizosphere compared to bulk soil. The difference in microbial phyla was calculated by subtracting the relative abundance of individual phyla in bulk soil (bacteria, archaea, or fungi) from that in the rhizosphere soil (Ren et al., 2021). The average value of the difference for individual phyla was calculated as \bar{D} . The equation for calculating the average value is as follows:

$$\bar{D} = \frac{\sum_{i=1}^N D_i}{N} \quad (1)$$

where \bar{D} is the average value of the difference between individual phyla. N is the number of observations for each phylum. D_i is the difference in the phyla between the rhizosphere and bulk soil for the i th observation. The SE of the difference for individual phyla was also calculated.

2.2. Data analysis and statistics

Effect size was calculated as the natural log of the response ratio (RR) to represent the difference of individual variables between the rhizosphere and bulk soil (Hedges et al., 1999):

$$\ln\text{RR} = \ln \left(\frac{\bar{X}_R}{\bar{X}_B} \right) \quad (2)$$

where \bar{X}_R and \bar{X}_B are the means of a variable in the rhizosphere and bulk soil, respectively. The positive or negative $\ln\text{RR}$ represented an increase or decrease of the variable in the rhizosphere compared with bulk soil. The variance of $\ln\text{RR}$ was determined as follows (Curtis and Wang, 1998; Ren et al., 2018):

$$V_{\ln\text{RR}} = \frac{S_R^2}{n_R \bar{X}_R^2} + \frac{S_B^2}{n_B \bar{X}_B^2} \quad (3)$$

where S_B and S_R are the SDs of the variables in the bulk and rhizosphere soils, respectively. n_B and n_R are the sample sizes of the variables in the bulk and rhizosphere soils, respectively. To elucidate the overall rhizosphere effect, the weighted mean response ratio ($\ln RR_{++}$) was determined using a random-effects model (Curtis and Wang, 1998; Ren et al., 2018) as follows:

$$\ln RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^n w_{ij} \ln RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^n w_{ij}} \quad (4)$$

where m is the number of compared groups, j is the number of comparisons in the i th group, and w is the weight of $\ln RR$ (i.e., $w_{ij} = 1/\sqrt{\ln RR_{ij}}$). The SEs of $\ln RR_{++}$ were calculated as follows:

$$s(\ln RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^n w_{ij}}} \quad (5)$$

Accordingly, the percentage change can be derived using the equation: $[(\exp(\ln RR_{++}) - 1) \times 100\%]$. When 95% confidence intervals did not overlap with zero, the rhizosphere effect on individual variables was significant. Otherwise, the increase (or decrease) of the variable in the rhizosphere was insignificant compared to that in bulk soil. Kendall's tau rank correlation and Spearman's rank correlation were used to test the publication bias within each variable (Table S3). Rosenthal's fail-safe numbers suggested that possible publication bias within some variables does not influence the results (Rosenberg, 2005). During the categorical moderator analysis, the significance of the heterogeneities between groups (Q_{between}) and within groups (Q_{within}) was applied using the Chi-square test. For instance, a p -value of Q_{between} smaller than 0.05, represents significant heterogeneity of the effect size between categories of individual explanatory variables. Spearman's correlation coefficients were calculated to analyze the relationships between the effect sizes of available nutrients (AN, AP, AK, NH_4^+ , and NO_3^-) and other factors (i.e., original soil properties, MAT, and MAP). Only field experiments which were directly affected by climate factors were included when calculating the correlation coefficients between MAT and MAP and the effect sizes of available nutrients (AN, AP, AK, NH_4^+ , and NO_3^-). The meta-analysis was performed using MetaWin 2.1 (Rosenberg et al., 2000). Other data analyses were performed using Origin 2020b (OriginLab Inc.) software.

3. Results

3.1. Available nutrients in the rhizosphere vs. in bulk soil

The available N (AN) was 10% higher in the rhizosphere than in the bulk soil (Fig. 1A). The NH_4^+ (11%), NO_3^- (24%), TN (14%), and MBN (32%) contents in the rhizosphere increased (Figs. 1 and 2). Higher enrichment of NH_4^+ and NO_3^- was observed in the rhizosphere when either MAT or MAP was relatively low (Fig. 3, $p < 0.05$), which generally represents boreal or relatively dry conditions. The effect size of AN increased at high original soil pH or when the original SOC, TN, and TP were low, while the opposite trends were found for the effect size of NO_3^- (Fig. 3, $p < 0.05$).

Unlike AN, AP decreased by 12% and was more depleted in the rhizosphere than in the bulk soil (Fig. 1B). The effect size of AP increased at high original soil pH, but decreased with an increase in the original TP and AP (Fig. 3, $p < 0.05$).

The available K (AK) increased by 15% in the rhizosphere compared to the bulk soil (Fig. 1E), whereas the TK content was similar in the rhizosphere and bulk soil (Fig. 2D). The effect size of AK decreased at high precipitation (Fig. 3, $p < 0.05$).

3.2. Soil biochemical and biological factors in the rhizosphere vs. in bulk soil

The increase in pools with fast turnover, for example, MBC and MBN, was approximately twice stronger in the rhizosphere (19% and 32%,

respectively) compared to SOC (9%) and TN (14%) (Fig. 2). The activities of all enzymes were greater in the rhizosphere than in the bulk soil (Fig. 4). Remarkably higher bacterial (205%) and fungal (254%) population densities in the rhizosphere were also confirmed (Fig. 2G–H), emphasizing the importance of the rhizosphere as a microbial hotspot. Positive relationships between MBC and bacterial population density, MBC and fungal population density, and effect sizes of bacterial and fungal population densities were also confirmed (Fig. 5).

The relative abundances of bacteria and archaea, such as Proteobacteria, Bacteroidetes, and Firmicutes, were greater in the rhizosphere than in the bulk soil (Fig. 6A). In contrast, the relative abundance of Crenarchaeota, Actinobacteria, and Acidobacteria in the rhizosphere decreased.

3.3. Rhizosphere nutrient status as affected by plant characteristics

Most available nutrients (AP, AK, NH_4^+ , and NO_3^-) were more enriched in the rhizosphere of taproots than in fibrous roots, as indicated by their larger change around taproots (Fig. 1). Similar strong enrichments were also found for the SOC, TN, TP, TK, MBC, and MBN contents around taproots (Fig. 2). Further, bacteria and fungi were more abundant in the rhizosphere of taproots than in fibrous roots (Fig. 2G–H).

AN and AP were more exhausted in the rhizosphere of legumes than in non-legumes (Fig. 1A–B). In contrast, the MBC and MBN contents were higher in the legume than in the non-legume rhizospheres (Fig. 2E–F). Similarly, the effect size of bacterial and fungal population densities was also higher in the rhizosphere of legumes than in that of non-legumes (Fig. 5C).

3.4. Shift of rhizosphere pH as related to original soil pH and plant characteristics

ΔpH decreased with increasing original soil pH (Fig. 7A), indicating a neutralizing effect and buffering capacity of plant roots in both acidic and alkaline soils. On average, the soil pH in the rhizosphere was 0.16 ± 0.02 units lower than in bulk soil (Fig. 7B). Plant characteristics strongly influenced the rhizosphere soil pH (Fig. 7C–E). Leguminous species induced a much higher reduction in rhizosphere pH (-0.44 units) than non-legumes (-0.11 units).

4. Discussion

This meta-analysis demonstrated that the availability of most nutrients was higher in the rhizosphere than in bulk soil (Figs. 1 and 8). Exceptionally, the AP was more depleted in the rhizosphere, indicating extreme P demand for plants (especially for legumes) and microorganisms. Among the interrelated factor groups, the increase in nutrient availability in the rhizosphere as compared to bulk soil was higher for low-fertile or acidic soils because of stronger root-microbial interactions and acidity neutralizing effects. Plants with taproots have greater SOC than plants with fibrous roots, which provide sufficient substrates for microbial growth and enzyme synthesis. This leads to a very strong increase in bacterial (+352%) and fungal (+483%) population densities and slightly higher AP, AK, NH_4^+ , and NO_3^- contents around taproots than fibrous roots (Figs. 1, 2, and 8). A much larger increase in bacterial and fungal population densities in the rhizosphere than in the microbial biomass (indicated as MBC, +19%) demonstrated that the average biomass of individual microbial cells decreased. We proposed that the higher dominance of copiotrophic microorganisms in the rhizosphere, which have faster growth rates in response to higher availability of C resources than oligotrophs, could be responsible for this decrease (Figs. 2 and 8).

4.1. Effects of climatic factors and original soil properties on available nutrients in the rhizosphere

Climatic factors, such as precipitation and temperature, have specific effects on nutrient availability within the rhizosphere. While NH_4^+ and NO_3^- enrichments were strongly regulated by precipitation and temperature,

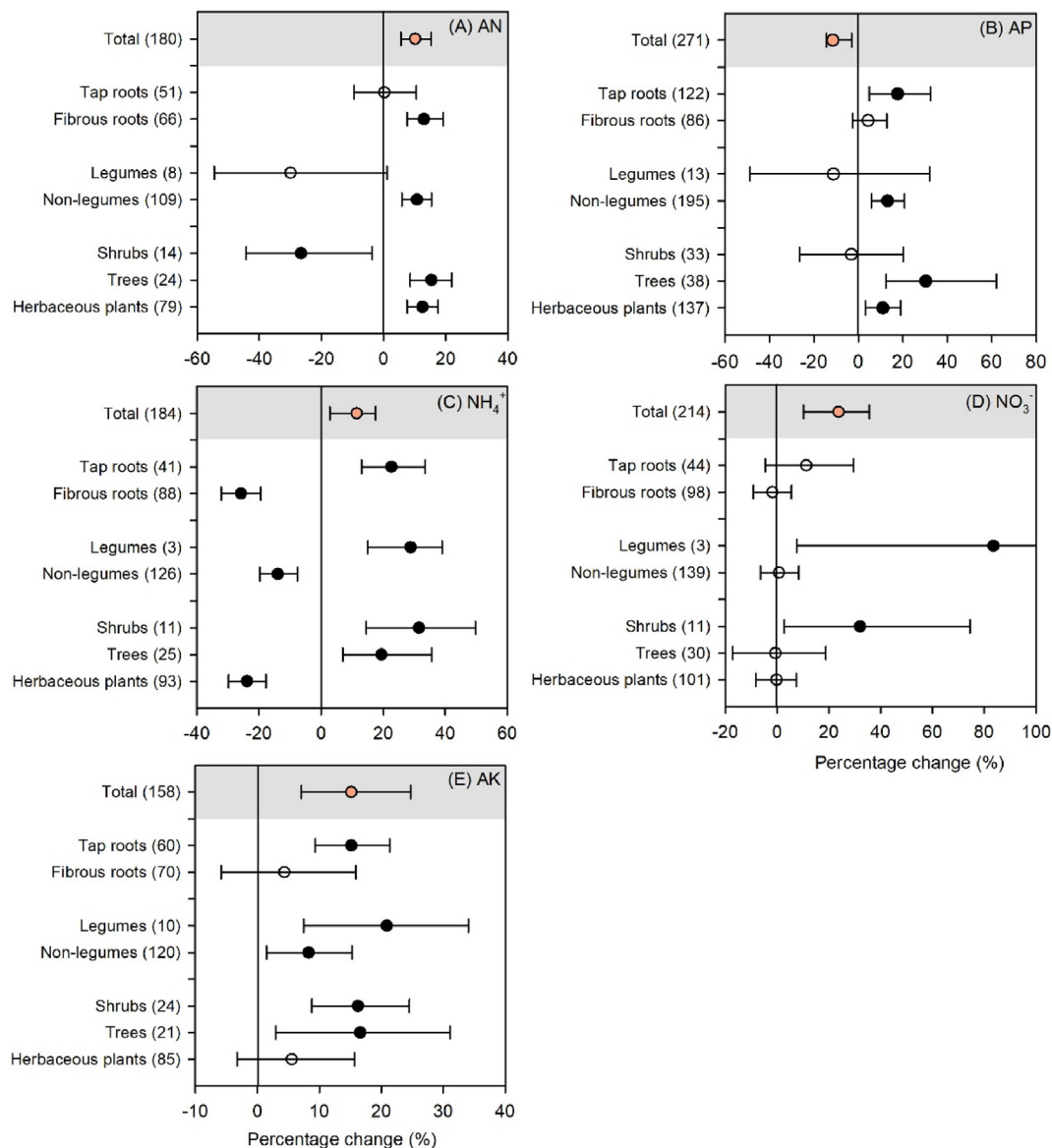


Fig. 1. Changes of available nutrients in the rhizosphere compared with bulk soil. The negative and positive values represent the depletion and accumulation, respectively, of the nutrients in the rhizosphere compared to bulk soil. The open symbols indicate that the value is not significantly different from zero. The number in the parentheses beside each available nutrient is the sample size. Error bars represent bootstrapped 95% confidence intervals. Note that the total effect size of each available nutrient does not reflect the means from individual groups, because approximately 17–34% of the observations cannot be subdivided to one of these groups, owing to the absence of sufficient information in the original articles. AN: available nitrogen; AP: available phosphorus; AK: available potassium.

these did not influence AP in the rhizosphere (Fig. 3). NH_4^+ and NO_3^- are the two most important N forms for root uptake, the contents of which are mediated by soil moisture and temperature. For instance, the transformation between NH_4^+ and NO_3^- , as well as the plant preference for N uptake, strongly increases with temperature (Clarkson, 1986; Ganmore-Neumann and Kafkafi, 1980; Kafkafi, 1990). Warming increases soil organic matter decomposition (Kuzayakov and Bol, 2006), thereby also N mineralization, but also stimulates N uptake by plants and immobilization by microorganisms (Dong et al., 2001), which depletes NH_4^+ and NO_3^- in the rhizosphere. The effects of temperature on the root uptake of either NH_4^+ or NO_3^- differs because of N diffusion, root physiology, membrane permeability, presence of mycorrhizal symbionts, and competition with microorganisms for N (Clarke and Barley, 1968; Warren, 2009). Clarkson (1986) suggested that 85% of N uptake is in the form of NH_4^+ rather than NO_3^- at temperatures below 9 °C. High NO_3^- uptake is more common under warmer conditions (Warren, 2009). NH_4^+ can be adsorbed on and in clay particles, which strongly decreases its diffusivity compared to NO_3^- and influences the effect of temperature change on

NH_4^+ uptake. N availability in the rhizosphere is greater under drought conditions due to decreased plant and/or microbial N uptake (Cregger et al., 2014; Deng et al., 2021). This explains the negative relationship between MAP and the effect sizes of NO_3^- (Fig. 3). Similar to NO_3^- , drought-induced reduction in K uptake by roots also contributes to K enrichment in the rhizosphere (Ge et al., 2012), leading to a negative relationship between MAP and the effect size of AK.

Compared to the effects of climatic factors, the original soil properties (pH, SOC, TN, TP, AP, and AK) were more important for the effect sizes of AN, AP, and AK (Fig. 3). Soil with originally high fertility (high contents of SOC, TN, TP, AP, and AK) provides sufficient available nutrients for both plant and microbial communities (Tang et al., 2021; Tian et al., 2020). Nutrient delivery from bulk soil to the roots by diffusion and mass flow meets the plant and microbial demand. In contrast, when soil is less fertile (lower SOC, TN, and TP contents), the mass flow from the bulk soil to the rhizosphere is low. Microorganisms and roots release more enzymes and carboxylates to increase nutrient mineralization from organic pools to maintain their growth (Rengel and Marschner, 2005).

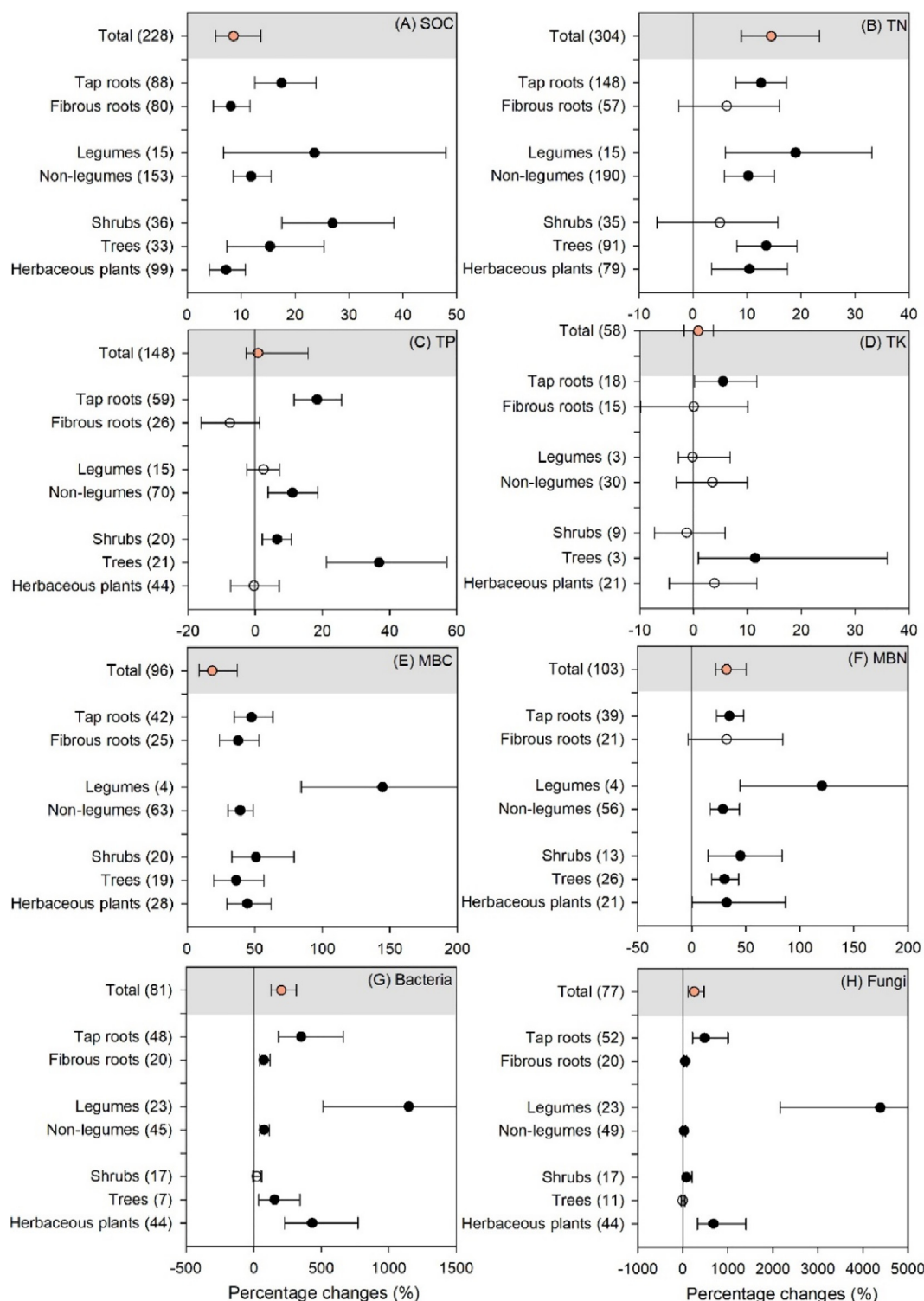


Fig. 2. Changes of chemical and biochemical properties in the rhizosphere compared with bulk soil. The negative and positive values represent the decrease and increase, respectively, of the properties in the rhizosphere compared to bulk soil. The open symbols indicate that the value is not significantly different from zero. The number in the parentheses beside each property is the sample size. Error bars represent bootstrapped 95% confidence intervals. Note that the total effect size of each soil property does not reflect the means from individual groups, because approximately 5–42% of the observations cannot be subdivided to one of these groups, owing to the absence of sufficient information in the original articles. SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; TK: total potassium; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen.

4.2. Acidity and alkalinity neutralization in the rhizosphere modulates nutrient availability

Although most plant species acidify the rhizosphere, the ability of plants to influence the rhizosphere pH depends strongly on the original soil pH

(Fig. 7A). Specifically, the plant increases or decreases the rhizosphere pH to maintain the equilibrium between cations and anions at the root-soil interface (Figs. 7 and 8). Roots acidify rhizosphere soil through the following processes: i) uptake of cations coupled with proton release, ii) release of organic acids (Jones, 1998), and iii) CO₂ release via root respiration (Rao

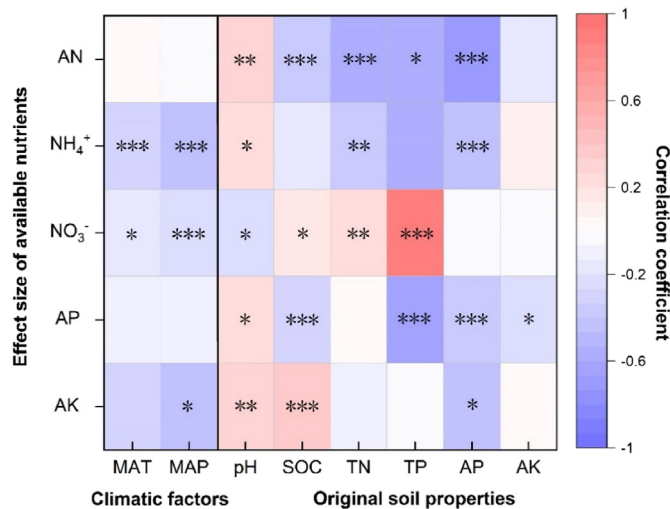


Fig. 3. Spearman's rank correlation coefficients between effect sizes of available nutrients and climatic factors and original soil properties. SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; AN: available nitrogen; AP: available phosphorus; AK: available potassium; MAT: mean annual temperature; MAP: mean annual precipitation. Cells colored with pink or blue indicate that the relationship is positively or negatively significant, respectively. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

et al., 2002), and iv) release of chelates removing cations from exchange sites. Microorganisms acidify the rhizosphere through similar processes. In particular, legumes strongly acidify the rhizosphere (-0.44 unit, Fig. 7D) because of the release of protons following the excess uptake of cations over anions during biological N_2 fixation (Haynes, 1983; Israel and Jackson, 1982; Liu et al., 1989), as well as nitrification of NH_4^+ to NO_3^- (Ma et al., 2019; Raza et al., 2020). These processes help overcome the deficiencies of P and Fe as well as micro-nutrients in soil (Custos et al., 2020).

In contrast, in acidic soil, plants generally increase the rhizosphere soil pH to tackle Al stress (Bagayoko et al., 2000) and increase the availability of all macro- and most micro-nutrients. The plant uptake of anions (e.g., NO_3^-) in excess of cations often causes the roots to secrete HCO_3^- . The excretion of OH^- from NO_3^- reduction is also the main mechanism to increase rhizosphere pH (Sugihara et al., 2016). For legumes, the reduction of protons to H_2 by nitrogenase during biological N_2 fixation also contributes to an increase in rhizosphere pH (Mahon, 1979). In summary, these neutralizing effects of the rhizosphere contribute to higher contents of AN, NH_4^+ , AP, and AK in the rhizosphere when the original soil pH is low (Fig. 3).

4.3. Nutrient depletion and accumulation in the rhizosphere

The rhizosphere volume is crucial for plant nutrition, as it defines the total amount of each nutrient immediately available to the plant. The rhizosphere is expected to be depleted with nutrients compared to bulk soil (Joner et al., 1995; Wang et al., 2007). However, the global meta-analysis confirmed this trend only for AP and AN in the rhizosphere of shrubs (Fig. 1B), which contradicts our first general hypothesis. Low P availability in the rhizosphere coupled with high acid and alkaline phosphatase activity (Fig. 4A–B) compared to bulk soil, shows extreme P demand for plants and microorganisms. P availability in the rhizosphere is limited at low and high soil pH (Haynes, 1982). For instance, calcium phosphate precipitates in an alkaline environment (i.e., $pH > 8.0$). At pH values lower than 5.0, iron or aluminum phosphates are formed, and P is adsorbed onto Fe or Al (oxyhydr)oxides. Neutralization of acidity and alkalinity in the rhizosphere increases P availability. It should be noted that when we calculated the total effect size of AP (Fig. 1B), all cases (including monoculture and polyculture) were included, but only monocultures were considered when analyzing the

influence of plant characteristics (e.g., taproots and fibrous roots). The negative total effect size of AP, compared to the positive influence of most plant characteristics (Fig. 1B), indicates that increased plant species richness may exacerbate P depletion in the rhizosphere.

In contrast to AP, high nutrient content (i.e., AN, AK, NH_4^+ , and NO_3^- ; Fig. 1) in the rhizosphere could be because mass flow (the movement of nutrients with water) is faster than the nutrient uptake by roots (Barber, 1962). If the nutrient supply from mass flow exceeds their uptake, those nutrients will increase around the root, which creates accumulation zones (Barber and Ozanne, 1970; York et al., 2016). This is common especially for Ca^{2+} uptake from calcareous soils (Zamanian et al., 2016), or by Fe accumulation around the roots in iron-rich water-saturated soils (Hoefer et al., 2017; Jeewani et al., 2020; Williams et al., 2014). However, if nutrients are more enriched in the rhizosphere than in bulk soil, diffusion may occur opposite to the mass flow because of the concentration gradient. The diffusion rate of a nutrient is influenced by the exchange of nutrients between soil particle surfaces and surrounding water (Kuzyakov and Razavi, 2019). Organic compounds excreted by roots (i.e., low and high molecular weight organic compounds) also affect the diffusion rate through acidification, reduction/complexation, or ligand exchange reactions (Hoefer et al., 2017; Kramer-Walter et al., 2016; Terzano et al., 2014), but are mainly defined by microbial utilization (Kuzyakov et al., 2003). These effects on diffusion can reduce the nutrient uptake of roots by 13–61% compared to roots in a stirred nutrient solution (Drew et al., 1969). Therefore, even though nutrients are enriched in the rhizosphere, the diffusion from the rhizosphere to the soil is diminished. On the other hand, the stronger soil organic matter decomposition and mineralization rate—the rhizosphere priming effects (Huo et al., 2017; Pausch et al., 2013) as indicated by increased enzyme activities (Sanaullah et al., 2016), MBC, and microbial abundance—increases nutrient mineralization and their availability (Figs. 2 and 4).

4.4. Nutrient availability within the rhizosphere is mediated by plant and root characteristics

Plant nutrient exploitation depends on root morphology (e.g., taproots or fibrous roots), interaction with symbionts (e.g., mycorrhiza and rhizobia), and release of root exudates and enzymes (Dinkelaker and Marschner, 1992; Moreau et al., 2019). Taproots acquire more water and nutrients from deeper horizons (Kautz et al., 2013). Lateral roots growing from taproots extend the nutrient exploring capacity of the plants and enhance their interactions with beneficial microorganisms. A larger increase in bacterial (+352%) and fungal (+483%) population densities around taproots also implies stronger microbial activities in their rhizosphere than plants with fibrous roots (Fig. 2G–H), contributing to the slightly higher AP, AK, NH_4^+ , and NO_3^- in the rhizosphere of taproots than fibrous roots. The stronger increase in the rhizosphere SOC of taproots, in accordance with our second hypothesis, demonstrates the stronger ability of taproots to store C and energy sources during their longer life, which provides abundant substrates for enzyme synthesis and thus a larger release of available nutrients (Fig. 2A). It should be noted that plants with fibrous root systems have much larger absorptive surface areas than taproots because of more highly branched fine roots and active root hairs, which facilitate direct nutrient acquisition (Holz et al., 2018). In contrast, the ability of taproots to absorb nutrients is limited because of their coarser system; therefore, assistance from microbial symbionts (e.g., arbuscular mycorrhizal fungi) is required, explaining the larger increase in bacterial and fungal population densities. This indicates that both root systems have different absorptive strategies for nutrients from soils (Yang et al., 2015).

Legumes create symbiotic relationships with N-fixing bacteria to increase N availability. However, to effectively form symbiotic relationships with bacteria and fix N_2 , leguminous plants acquire more P (Magadlela et al., 2016; Stevens et al., 2019), which explains why AP is more exhausted in the rhizosphere of legumes than of other species (Fig. 1B). This was supported by the increased alkaline (42%) and acid (108%) phosphatase activities in the rhizosphere of legumes (Fig. 4A–B) and also suggested stronger

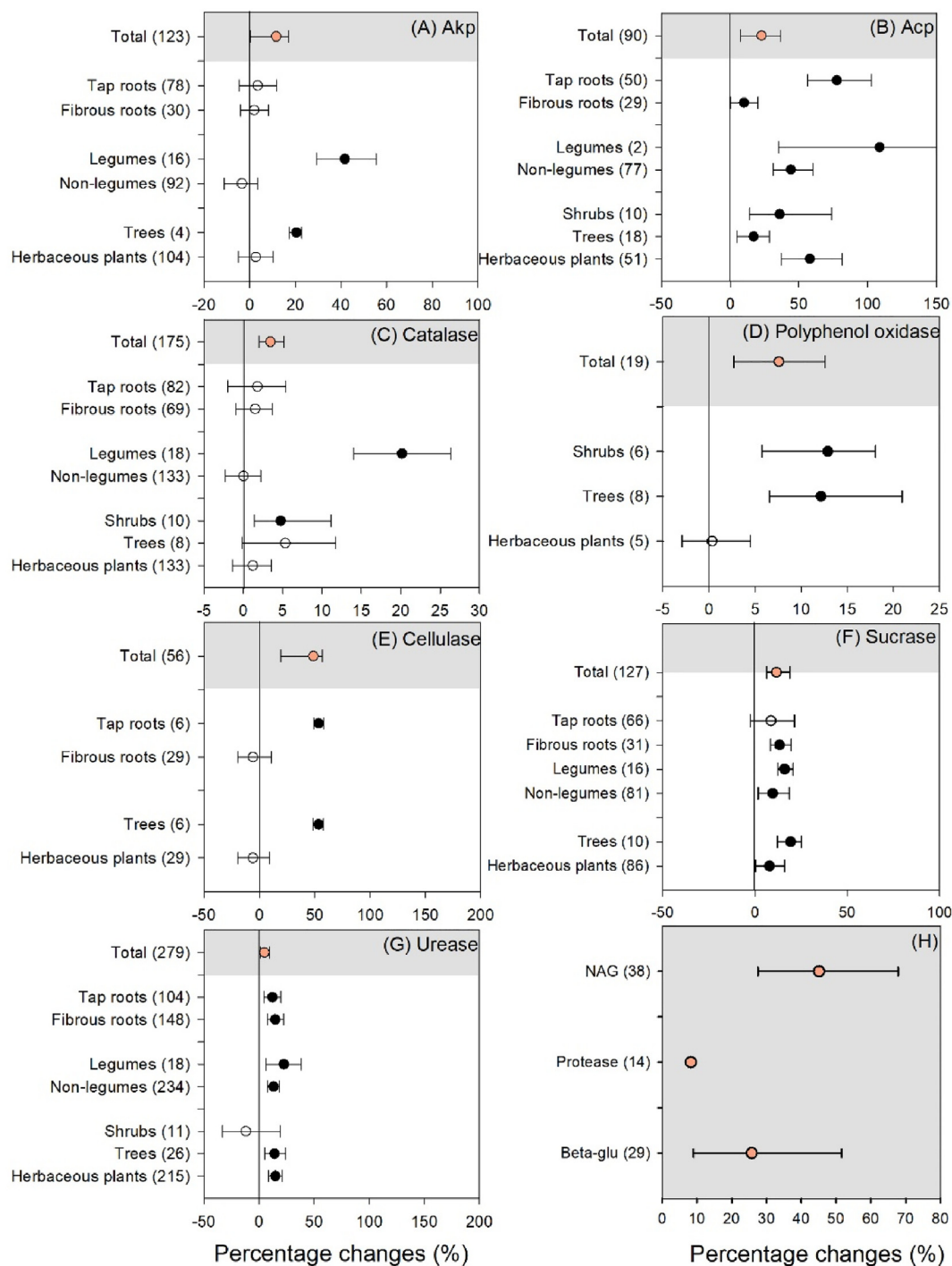


Fig. 4. Changes of enzyme activities in the rhizosphere compared with bulk soil. The negative and positive values represent the decrease and increase, respectively, of the enzyme activities in the rhizosphere compared to bulk soil. The open symbols indicate that the value is not significantly different with zero. The number in the parentheses beside each enzyme is the sample size. Error bars represent bootstrapped 95% confidence intervals. Note that the total effect size of the activity of each enzyme does not reflect the means from individual groups, because approximately 9–36% of the observations cannot be subdivided to one of these groups, owing to the absence of sufficient information in the original articles. Acp: acid phosphatase; Akp: alkaline phosphatase; NAG: *N*-acetyl- β -D-glucosaminidase; Dehydro: dehydrogenase; β -glu: β -glucosidase.

mineralization of organic P in legume plants (Maltais-Landry, 2015). Contrary to our expectation, the effect size of AN in the rhizosphere of legumes was not different from zero (Fig. 1A). Even though the number of observations (8 vs. 109) for the AN of legumes and non-legumes is imbalanced, individual studies have shown either increased (Dai et al., 2016; Qiu et al., 2014) or decreased AN (Ding et al., 2017; Xu et al., 2020; Zhou, 2014) in

the rhizosphere of legumes. It has been argued that legumes could be either “altruistic” or “self-serving” (Xu et al., 2020). These divergent results can be attributed to the shift in the N-acquisition strategy of plants between N_2 -fixation and mineral N uptake pathways, depending on whether the canopy accumulates enough N to support photosynthesis and rhizodeposition (Henneron et al., 2020).

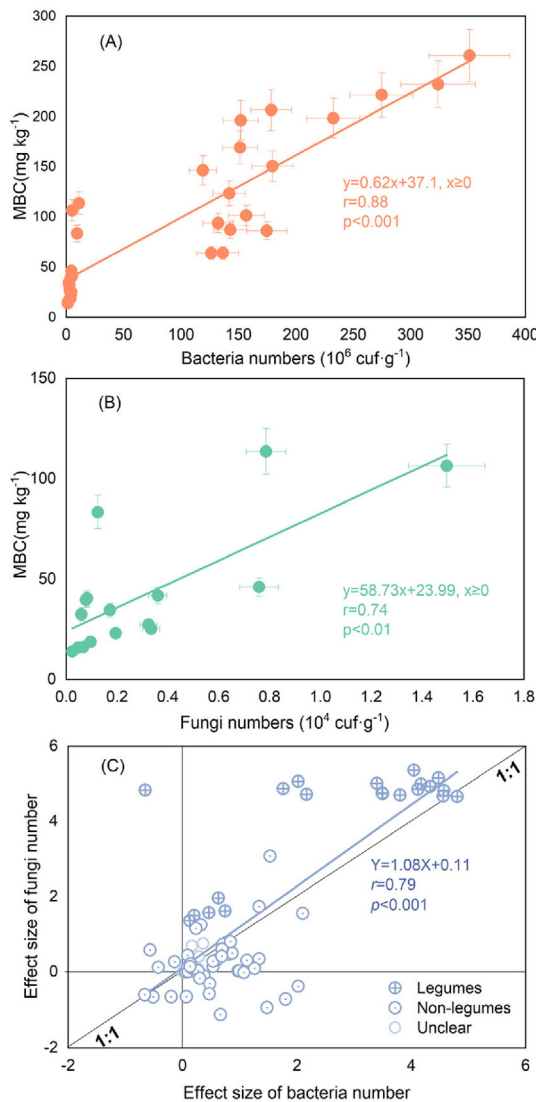


Fig. 5. Relationship between bacterial population densities and MBC (A), fungal population densities and MBC (B), and effect sizes of bacterial and fungal population densities (C). Error bars represent standard deviations.

While AN decreased in the rhizosphere of legumes, NH_4^+ and NO_3^- increased, as was the case in non-legumes. This inconsistent trend could be explained by the low proportion of NH_4^+ and NO_3^- in AN (Fig. S2). The AN content was approximately equal to 5.5–6.0% of the TN, while NH_4^+ and NO_3^- accounted for only approximately 1% and 0.5% of the TN, respectively. This indicates that the remainder of AN, for example, peptides and amino acids, accounts for approximately 4–4.5% of the TN, which equals approximately 73–75% of AN. This is consistent with the findings of previous studies (Jämtgård et al., 2010; Young and Aldag, 2015), which demonstrated that the contents of soluble organic N forms are higher than that of mineral N, especially in natural ecosystems. The significantly higher proportion of soluble organic N content in AN suggests that the change in organic N content, not mineral N, mainly reflects the variation in rhizosphere AN.

4.5. Microbial activities and community shift in the rhizosphere

The enzyme activity in the rhizosphere increased by 3–52% compared to that in the bulk soil (Fig. 4) and demonstrates an enzyme-specific pattern. Catalase and polyphenol oxidase are two defense-related antioxidant enzymes (Babu et al., 2015) and their activities increased by 3.4% and 7.6%, respectively, in the rhizosphere. These enzymes can be expressed

by plant growth-promoting bacteria (e.g., *Pseudomonas*) or other beneficial biota, such as endophytes, which in turn not only strengthen the resistance of plants to diseases induced by pathogenic fungi (Hayden et al., 2018; Lazcano et al., 2021), but also facilitate the transfer of nutrients to the host plant by colonizing root surfaces. For instance, endophytic bacteria (e.g., *Bacillus tequilensis* belonging to the Firmicutes phylum) stimulate root hair development and N uptake by roots (Beltran-Garcia et al., 2014). Increased polyphenol oxidase facilitates the degradation of phenolic compounds and induces the breakdown of polyphenol-protein complexes, which enables the availability of a large portion of N contained in the complexes (Hättenschwiler and Vitousek, 2000). Catalase is related to the redox ability of soil and is associated with aerobic microbial activity (Nowak et al., 2004). In particular, catalase activity in the rhizosphere of legumes increased by 20% because of the stronger increase in bacterial and fungal population densities (Figs. 2 and 5), indicating that leguminous species have a stronger ability to resist environmental stress and protect nodules from pathogens.

The increase in bacterial population density in the rhizosphere was similar to that of fungi (Fig. 2G–H), consistent with the close correlation between the effect size of bacterial and fungal population densities (Fig. 5). A much larger increase in bacterial and fungal population densities (205–254%) in the rhizosphere than in microbial biomass (indicated as MBC, +19%) (Figs. 2 and 5A–B) suggests that the average biomass of individual microbial cells decreased. This could be attributed to the greater dominance of copiotrophic microorganisms (e.g., Proteobacteria, Bacteroidetes, and Firmicutes) in the rhizosphere (Fig. 6A), which have much faster growth rates in available C rich environment than oligotrophs (Fierer et al., 2007; Gharechahi et al., 2021). Copiotrophs invest more resources to proliferate instead of increasing the biomass of each microbial cell. In contrast, Acidobacteria and Actinobacteria, mostly belonging to oligotrophic microorganisms (Lebeau, 2011), showed decreased relative abundance of approximately 3.0% (Fig. 6A). The shift to copiotrophic microorganisms is important for plant-microbial interactions and nutrient availability because some members of the phylum (e.g., *Mucilaginibacter* belonging to Bacteroidetes and *Pseudomonas* belonging to Proteobacteria) can produce large quantities of polysaccharides to optimize the rhizosphere microenvironment, e.g. aggregate soil particles (Agnihotri et al., 2022), provide an energy source for microorganisms, and promote the uptake of trace elements (Danhorn and Fuqua, 2007; Naseem et al., 2018). Ascomycota and Basidiomycota were the dominant fungi in the rhizosphere soil (Qin et al., 2017). Basidiomycota can degrade lignocellulose organic matter more easily (Yelle et al., 2008), whereas Ascomycota are more prone to use easily degradable organic compounds for fast-growing fungi (Lundell et al., 2010). The higher relative abundance of Ascomycota (+4%; Fig. 6B) in the rhizosphere ensures greater production of organic matter-degrading enzymes and the facilitation of symbiotic associations (Challacombe et al., 2019). Furthermore, Crenarchaeota is an ammonia-oxidation archaeon that colonize roots (Simon et al., 2000). Its relative abundance in this meta-analysis decreased by 10% in the rhizosphere compared to that in bulk soil (Fig. 6), corroborating the results of Xu et al. (2018). Strong competition from plants for N may constrain the diversification and growth of Crenarchaeota (Liu et al., 2019; Treusch et al., 2005). It should be noted that even though relative abundance of some phyla in the rhizosphere compared to bulk soil was revealed based on the data extracted from the seven studies, a more comprehensive systematic review is required to elucidate the shift of relative abundance and functions of microbial communities.

5. Conclusions

The findings of our review have important implications for the elucidation of rhizosphere nutrient regulation by plant-microbial interactions. Firstly, the available N and K are enriched in the rhizosphere, while the available P is depleted compared to the bulk soil. Plants trigger a variety of mechanisms to acquire nutrients, including intensive root exudation and neutralization of the acid or alkaline environment. Secondly, plants

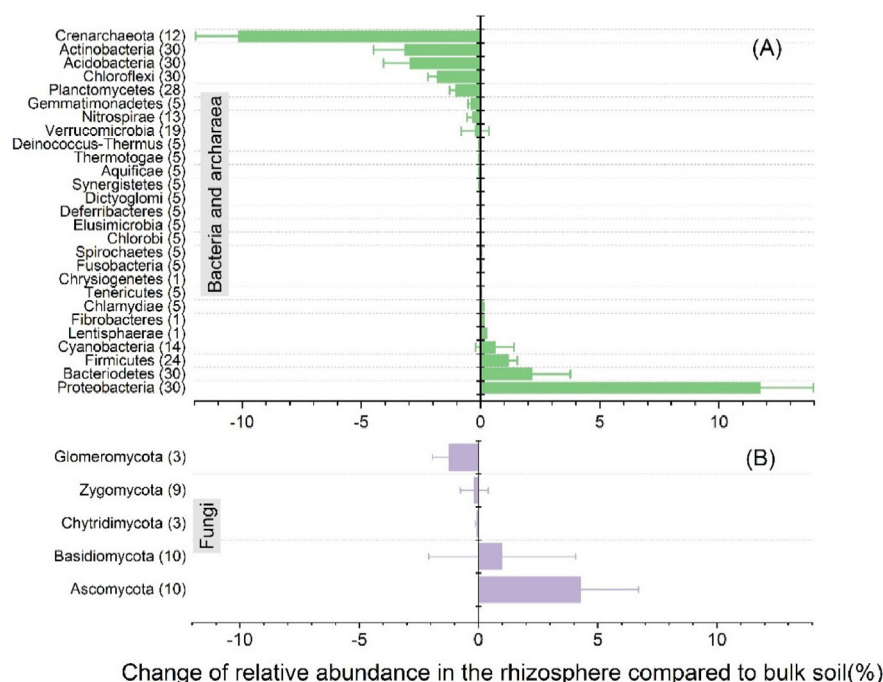


Fig. 6. Relative abundance of bacteria (A) and fungi (B) presented as a difference between the rhizosphere and bulk soil. The data were extracted from seven articles (Bakker et al., 2015; Fonseca et al., 2018; García-Salamanca et al., 2013; Mendes et al., 2014; Pascual et al., 2018; Ren et al., 2021; Sugiyama et al., 2014).

have various levels of interactions with microorganisms to acquire nutrients. For instance, plants with taproot systems will accumulate more organic compounds in the rhizosphere and induce greater microbial density relative to plants with fibrous roots, which provide microorganisms with enough substrates to synthesize enzymes and produce polysaccharides beneficial for the microenvironment. Legumes create symbiotic relationships with N-fixing bacteria and facilitate the release of root exudates and H^+ ,

leading to greater microbial number in the rhizosphere and alleviating serious P deficiency. Bacterial and fungal population densities increase much more than the total microbial biomass. Together with the more abundant copiotrophs in the rhizosphere, these findings suggest that microorganisms in the rhizosphere invest more resources to proliferate instead of increasing their size. Even though small cells are presumed to be favored in oligotrophic settings, specific rhizosphere environments (e.g., stronger microbial activities and higher resource availability) may induce specific microbial growth strategies in this critical zone. For more comprehensive analysis of the drivers determining nutrient content and availability in the rhizosphere, the effects of various types and concentration of root exudates and other soil properties (e.g. moisture, texture and types) on rhizosphere nutrient availability require generalization. Furthermore, examination of processes controlling nutrient content and availability from the perspective of molecular genetics of plants and microorganisms is necessary. Finally, considering that most primary studies were performed in China or written in Chinese, the consistency and generalization from these primary studies need to be verified for other ecologies or other countries.

CRedit authorship contribution statement

Shibin Liu: Conceptualization, Methodology, Software, Validation; **Shibin Liu, Fakun He and Huxuan Xiao:** Data curation, Writing-Original draft preparation, Funding acquisition; **Yakov Kuzyakov:** Writing-Reviewing, Editing and Funding acquisition; **Shengyan Pu:** Supervision, Funding acquisition; **Bahar Razavi:** Writing-Reviewing, Editing. **Duyen Thi Thu Hoang:** Visualization, Investigation.

Declaration of competing interest

No conflict of interest exists in the submission of this manuscript, and manuscript is approved by all authors for publication.

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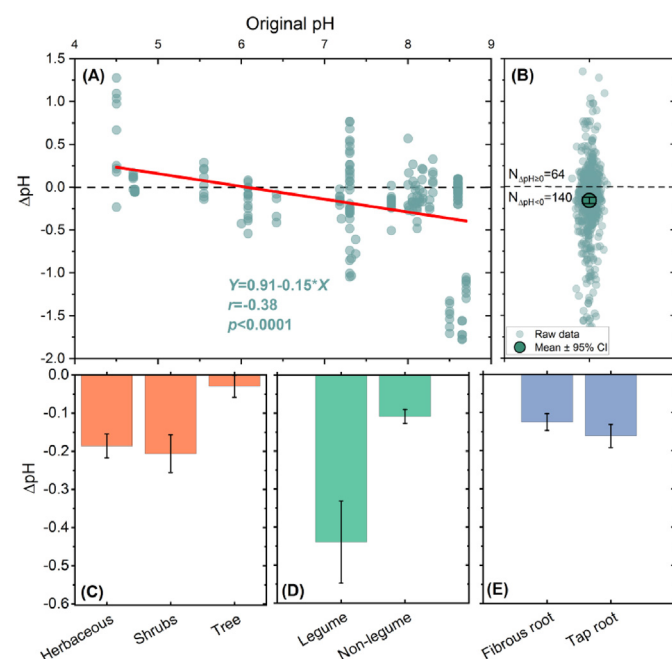


Fig. 7. Relationships between ΔpH and original pH (A), average ΔpH (B), and influence of plant characteristics on ΔpH ((C), (D) and (E)). The ΔpH was calculated by subtracting the pH value of the rhizosphere from the value of the bulk soil: the negative values show acidification (more common in neutral and alkaline soils). Error bars represent standard errors. $N_{\Delta pH \geq 0}$ and $N_{\Delta pH < 0}$ represent the number of observations with ΔpH above (or equal to) and below 0, respectively.

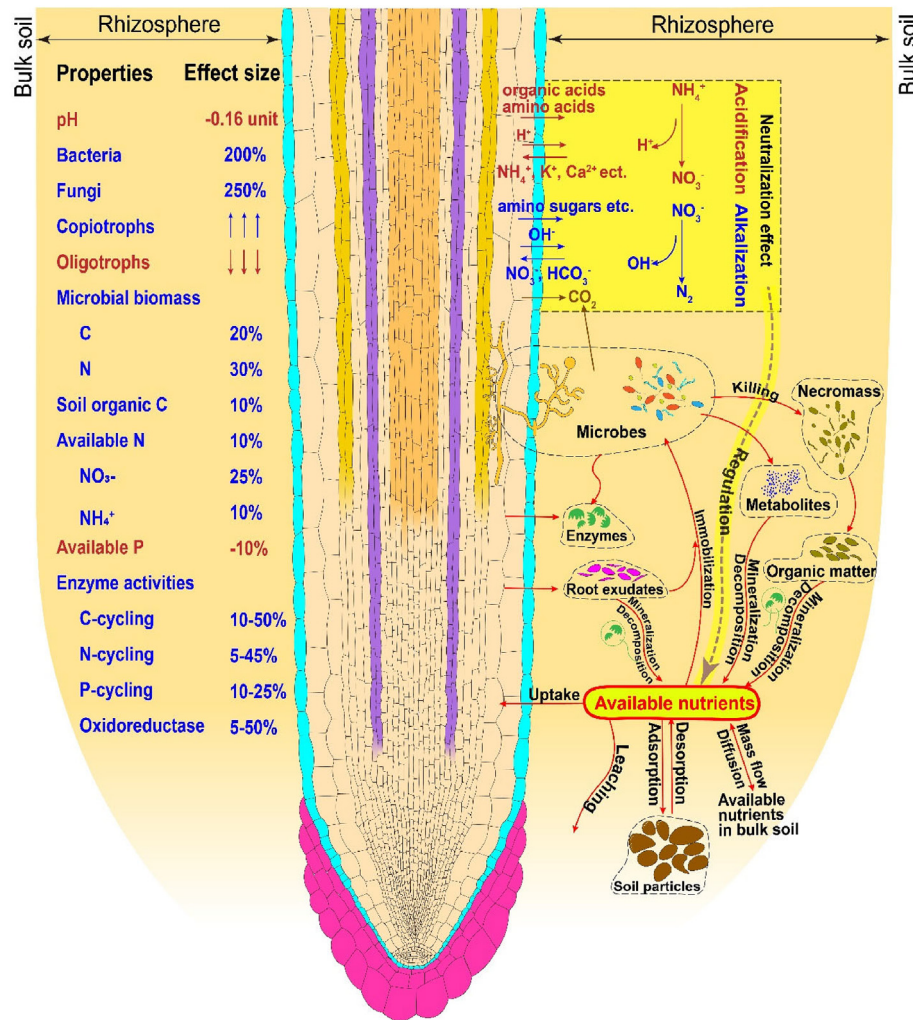


Fig. 8. Changes of soil biochemical properties in the rhizosphere compared to bulk soil (left), and nutrient depletion and accumulation processes (right). Note that the values in this conceptual figure are rounded up. Most soil properties (evaluated in this meta-analysis) increase in the rhizosphere as compared to the surrounding bulk soil. Exceptionally, soil pH decreases by 0.16 units. The available P decreased roughly by 10%, indicating extreme P demand for plants and microorganisms in the rhizosphere and slow diffusion from the surrounding soil. The relative abundance of oligotrophic microorganisms (K strategists) decreased in the rhizosphere with highly competitive copiotrophic microorganisms (r strategists) under greater C and nutrient availability. The available nutrients in the rhizosphere are mainly derived from the decomposition and mineralization of various organic compounds (organic matter, root exudates, metabolites, etc.) and microbial cells killed by phages and soil animals. Enzymes released by microorganisms and roots accelerate nutrient cycling. Mass flow, diffusion, and desorption from soil clay particles also contribute to nutrient accumulation in the rhizosphere. In contrast, root uptake, immobilization by microorganisms, leaching, and adsorption by soil particles lead to nutrient depletion in the rhizosphere. Acidity or alkalinity neutralization by roots and microorganisms regulates the nutrient availability in the rhizosphere.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.153908>.

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