Front. Agr. Sci. Eng. 2025, 12(1): 57–68 https://doi.org/10.15302/J-FASE-2024575

REVIEW

Soil–plant–microbe interactions in the rhizosphere: incremental amplification induced by localized fertilization

Liyang WANG[1,2], Dan LIAO[1,2], Zed RENGEL[3,4], Jianbo SHEN (✉)[2]

1 Inner Mongolia Key Laboratory of Soil Quality and Nutrient Resources, Key Laboratory of Agricultural Ecological Security and Green Development at Universities of Inner Mongolia Autonomous Region, College of Grassland, Resources and Environment, Inner Mongolia Agricultural University, Hohhot 010018, China.
2 State Key Laboratory of Nutrient Use and Management, Key Laboratory of Plant–Soil Interactions (Ministry of Education), Department of Plant Nutrition, College of Resources and Environmental Sciences, National Academy of Agriculture Green Development, China Agricultural University, Beijing 100193, China.
3 Soil Science & Plant Nutrition, UWA School of Agriculture and Environment, The University of Western Australia, Perth, WA 6009, Australia.
4 Institute for Adriatic Crops and Karst Reclamation, Split 21000, Croatia.

KEYWORDS

Incremental amplification, localized fertilization, root/rhizosphere engineering, high nutrient-use efficiency

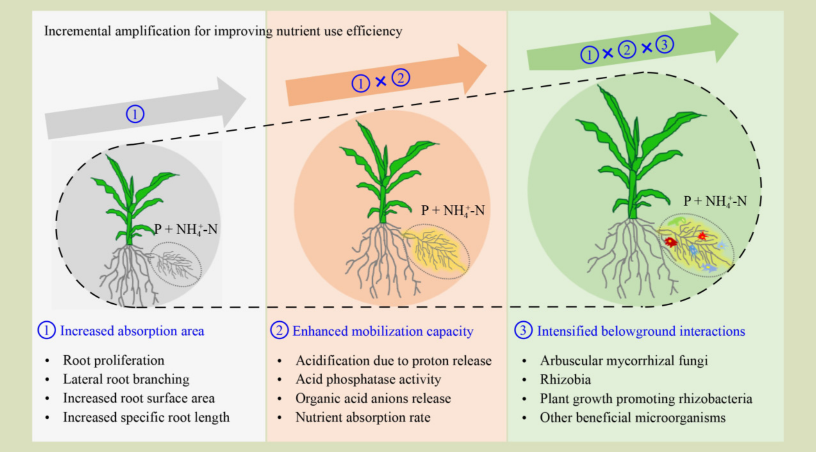
HIGHLIGHTS

- Plants can respond to heterogeneously distributed nutrient resources by enhancing root foraging capacity.
- Incremental amplification of root foraging for nutrients induced by localized fertilization was proposed.
- Incremental effects from the roots/rhizosphere to the plant-soil system conserve resources and reduce the environmental footprint of agricultural production.

Received April 26, 2024;
Accepted July 1, 2024.

Correspondence: jbshen@cau.edu.cn

GRAPHICAL ABSTRACT



ABSTRACT

Localized fertilization strategies (banding fertilizers) developed to minimize nutrient fixation by soil are used widely in intensive agricultural production. Localized fertilization encourages root foraging for heterogeneously distributed soil nutrients. This review focuses on the advances in root growth and nutrient acquisition of heterogeneously distributed soil resources. It is proposed that the incremental amplification of root foraging for nutrients induced by localized fertilization: (1) increased absorption area due to altered root morphology, (2) enhanced mobilization capacity underpinned by enhanced root physiological processes, and (3) intensified belowground interactions due to selective stimulation of soil microorganisms. The increase in root proliferation and the nutrient mobilization capacity as well as microbiome changes caused by localized fertilization can be amplified stepwise to synergistically enhance root foraging capacity, nutrient use efficiency and improve crop productivity. Engineering the roots/rhizosphere through localized, tailored nutrient application to stimulate nature-based root foraging for heterogeneously distributed soil nutrients, and scaling up of the root foraging capacity and nutrient acquisition efficiency from the rhizosphere to the field offers a potential pathway for green and sustainable intensification of agriculture.

1 Heterogeneous distribution of nutrients in soil

An intrinsic feature shared by agroecosystems and natural ecosystems is the spatial and temporal heterogeneity in distribution of soil nutrients (Fig. 1(a,b))[1–3]. Heterogeneity in the distribution of resources in natural ecosystems is mainly due to organic inputs that vary widely in their nature and origin (e.g., leaf litter, dead roots, animal carcasses, and dead microorganisms) and their subsequent microbial decomposition (Fig. 1(a))[2]. In agroecosystems, heterogeneous nutrient distribution is principally caused by fertilization and various management practices (Fig. 1(b)), including irrigation, crop rotation, straw incorporation, and tillage[4,5]. Collectively, the variation in heterogenous or patchy distribution of nutrient resources can be considerable in both natural ecosystems and agroecosystems, with the nutrient concentrations in the substrate differing by as much as several orders of magnitude between locations occupied by different roots of the same plant. For example, there can be as much variation in nutrient availability in the rooting zone of a single sagebrush (*Artemisia tridentata* ssp. *vaseyana*) as within an entire 120-m^2 plot[6]. Even at a small scale of 20 cm in a deciduous woodland, nitrate (NO_3^-) and ammonium (NH_4^+) concentrations in the soil solution showed 2- to 5-fold differences[7]. Similarly, in farmland soils, NO_3^- and NH_4^+ concentrations varied by more than two orders of magnitude when the sampling positions were located only 4 m apart[8]. In addition, there is a large variability in nutrient resources down the farmland soil profile, with the concentration of available phosphorus (Olsen-P) in the surface soil several or even dozens of times greater than in the subsoil[9].

Uneven distribution of organic matter and variable microbial activity are important reasons for the formation of soil nutrient patches. Unevenly distributed soil habitats with contrasting properties support a range of different soil microbial communities[10]. Microbial decomposition of organic matter releases inorganic nutrients that plants may capture. Importantly, the temporal and spatial variability in the release of inorganic nutrients due to microbial decomposition of organic matter is more complex than simply applying inorganic nutrients in a localized manner. For example, the concentration of plant-available iron would be significantly elevated in microsites with high organic matter deposition and low oxygen levels due to intense microbial activity[2]. Plant roots release a range of compounds (such as mucilage, enzymes, and organic anions) that provide nutrients to the microbiome and shape the structure and function of the rhizosphere microbial community[11]. Agricultural practices such as fertilization and irrigation drive changes in the root-associated microbiomes by affecting the release of organic exudates from roots[12,13]. The variation in nutrient availability caused by the interactions among root exudates and soil microorganisms adds further complexity to the spatially and temporally heterogeneous distribution of soil nutrients.

Differences in nutrient mobility determined by a degree of interactions of different ions with the charged surfaces of clays and other soil particles and organic matter in soil also contribute to the heterogeneous distribution of available nutrients. NO_3^- dissolved in soil water has a diffusion coefficient of 10^{-10} $m^2 \cdot s^{-1}$ (close to that in free solution) and can move freely within the soil to reach the root surface through mass flow, dependent on nutrient concentrations in the soil solution and plant transpiration rates. In contrast, NH_4^+ and K^+ are easily adsorbed to clay minerals. Phosphorus tends to form insoluble complexes with Al^{3+}, Fe^{3+} and Ca^{2+}, thus the mobility of P ions is severely restricted (diffusion coefficient in soil of only 10^{-13}–10^{-15} $m^2 \cdot s^{-1}$)[14]. Increased uptake of poorly mobile nutrients (such as P) by roots induces depletion gradients in the rhizosphere, further exacerbating the heterogeneity of soil nutrient distribution[5]. To overcome the rhizosphere nutrient depletion, plants must adopt specific nutrient-foraging strategies, such as growing long and thin roots, enhancing root hair formation and/or strengthening interactions with arbuscular mycorrhizal (AM) fungi, to exploit P sources further away from the initial root surface.

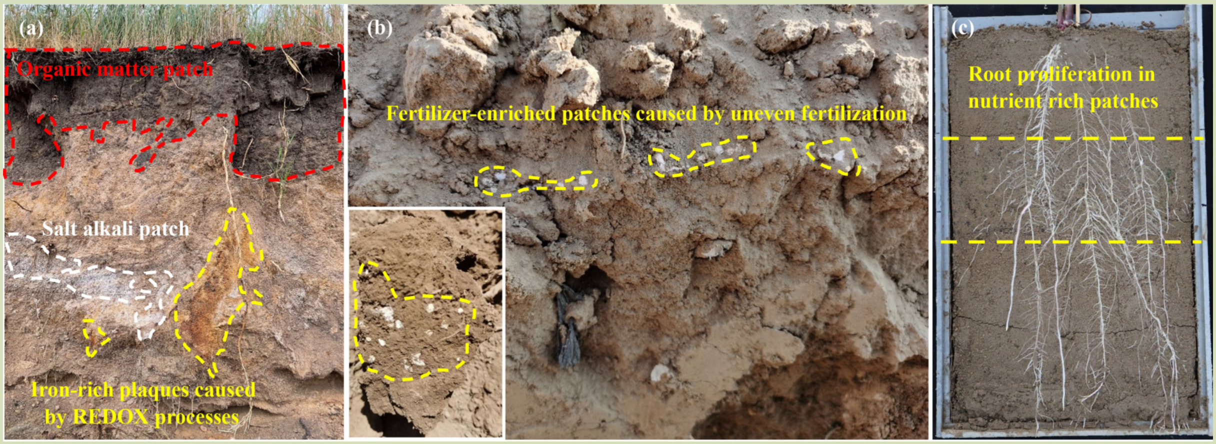


Fig. 1 Heterogeneous soil environment and root responses. (a) Heterogeneous soil structure and nutrient distribution in natural ecosystem. (b) Fertilizer-enriched patches created by localized fertilization in cropland ecosystems. (c) Root proliferation in nutrient-enriched middle section in a rhizobox.

2 Root plastic response to heterogeneously distributed soil nutrients

Roots can forage for heterogeneously distributed nutrient resources, whereby they recognize nutrient hotspots and exhibit morphological and physiological responses to exploit these local resources[2,15–17]. Morphologically, root biomass and length density are generally higher in the nutrient-rich than in the nutrient-poor patches, a phenomenon that occurs frequently in both natural and agroecosystems[2,17–19]. Physiological responses, such as altered composition and quantity of root exudates for mobilizing water-insoluble nutrients, are decisive in root foraging[20–22]. In addition, soil microbial community composition and activity in nutrient-enriched patches may also undergo profound changes that would in turn alter plant–soil interactions and affect root nutrient uptake. These root-dominated multipronged changes in nutrient patches may also lead to changes in the surrounding soil structure (e.g., aeration, moisture gradients and aggregation) to form a more favorable rooting environment[4,23].

2.1 Root morphological responses

Root proliferation in nutrient-rich patches is a common phenomenon (Fig. 1(c)), and includes enhanced rate of root elongation[24–26], increase in total root length[2,27], and intensification of lateral root branching[7]. Drew's barley experiment in 1975[28] is the seminal study of altered root morphology in response to heterogeneously supplied ammonium, nitrate and P, but not K. The strong root growth in the nutrient-enriched patches is often accompanied by decreased root growth in other areas (a compensatory effect) lacking the nutrient resources[29]. For example, study on two lupin species revealed that increased root proliferation in a high-nitrate zone was accompanied by decreased root growth in a low-nitrate zone, giving approximately the same total growth as in the uniform low-nitrate treatment[30].

Lateral root elongation occurred mainly in the topsoil layer in soils with uniform nutrient distribution, and in nutrient-enriched patches when present[17,19,31]. Such root plastic responses to heterogeneously distributed nutrients are essential for designing agricultural management schemes and selecting root traits to enhance plant performance in specific environments. For example, under the rainfall patterns in Western Australia characteristic of the Mediterranean climate, the optimal root structure for reducing the environmental footprint of nitrate features a rapid production of high root density in the topsoil early in the season, and a vigorous taproot growth into deeper soil layers that is likely to maximize nitrate capture from sandy soils later in the season after significant rainfall[32].

Despite root proliferation in nutrient-rich patches being a common occurrence, lateral root development in different species responds differently to heterogeneous nutrient supplies. In white lupin (*Lupinus albus*), heterogeneous supply of P or organic matter significantly promoted cluster root formation[33–35]. In maize (*Zea mays*), the second-order lateral root density was 3-fold greater in plants exposed to heterogeneous compared with uniform P supply[36]. Under heterogeneous P supply, the first- and second-order lateral root densities increased greatly in wheat (*Triticum aestivum*)[37], but not at all in faba bean (*Vicia faba*)[38]. In *Arabidopsis*, heterogeneous P supply resulted in greater lateral root length in the P-rich zones, whereas lateral root density was unaffected[31] or was even lower than in plants exposed to uniform P supply[39]. Although both formation and elongation of lateral roots can lengthen the total root system, lateral root formation is more responsive to nutrient patches[2].

Attempting to explain plant responses to heterogeneously distributed soil nutrients, de Kroon et al.[40] developed a modular concept of plant foraging behavior based on the interplay between local responses and systemic control. Generally, plant foraging for resources in heterogeneous environments must include (1) plastic responses of individual modules to local environmental signals and (2) the possibility to modify these responses either through signals received from the connected modules that may be exposed to different conditions or through signals reflecting the overall resource status of the plant. A series of studies have confirmed this conceptual model. For example, the heterogeneous distribution of nitrate in the rhizosphere generates a series of signals to facilitate root foraging for nutrients[41], including (1) local sensing and uptake of nitrate by the plasma membrane transceptor NRT1.1 in the root epidermis[42–44]; (2) long-distance signaling through the root C terminus encoded peptides indicating local nitrogen depletion in the rhizosphere[45]; (3) integration of local and systemic signals promoting root foraging for nitrate in the N-rich patches[46]; and (4) the relationship coordinating root proliferation and shoot N supply [47]. This process is also accompanied by the regulation of hormonal signals, such as the NRT1.1 transceptor affecting auxin transport during root development[48], and nitrate supply reducing auxin transport to roots in the N-rich patches, thereby promoting lateral root elongation[49]. Similarly, the root morphology responses to the heterogeneous supply of P in the rhizosphere are also regulated by the local signals of P availability and by the systemic signals of plant P nutritional status, and are mediated by auxin redistribution[36].

2.2 Root physiological responses

Root physiological responses are an important for plant foraging in nutrient patches. Higher concentrations of nutrients in nutrient patches increase plant nutrient uptake, possibly due to increased absorptive capacity of roots or favorable chemical equilibria[2]. When localized nutrient supply is applied to plants under nutrient stress, nutrient uptake per unit root may increase by 2- to 3-fold or even more than 5-fold[29,50]. This response is often quick, leading to an assumption that the physiological response precedes the morphological response[2,29,50]. Increased rate of ion uptake may also be a signal for plants to locate nutrient patches and trigger proliferation of their roots[2]. The physiological response, as a prelude to the morphological response, may be important in the short-term, but the morphological changes enable roots to acquire nutrients more efficiently in the nutrient patch area in the long-term[2]. However, Fransen and de Kroon[51] reported that, compared with morphological responses, the physiological responses of *Festuca rubra* and *Anthoxanthum odoratum* to heterogeneously supplied nutrients were advantageous, providing long-term competitiveness, potentially because physiological changes are less carbon-costly than root proliferation. The model study showed that when nitrate supply varied in space and time, the roots with sparse branches had higher nitrate-uptake efficiency, which was influenced only by the capacity to elevate the uptake kinetics locally; in contrast, the efficiency of roots with numerous branches decreased and was influenced only by the root proliferation capacity in the nitrate patch[52]. These findings indicate the root architecture and the plastic variation in root morphology and physiological function jointly determine the capacity of plants to acquire nutrients from soils containing heterogeneously distributed nutrients.

In nutrient-rich patches, changes in root morphology are often accompanied by changes in physiological plasticity. The root morphological response tends to be dominated by the formation of numerous thin roots with a relatively large root surface area, but also a high ion uptake rate. In sugar maple (*Acer saccharum*), the respiration rate of thin roots (diameter less than 0.5 mm) was 2- to 3-fold higher than that of thick roots[53]. The higher rate of respiration of thin roots in nutrient-rich patches may indicate higher rate of ion uptake, as shown for N and P uptake by a range of species[54,55]. Among lupin species, *Lupinus angustifolius* has the capacity to increase its nitrate-uptake rate for portions of the roots supplied locally with high nitrate (physiological response) whereas *Lupinus pilosus* does not, but the latter has robust root morphological response and may solely use increased root growth to exploit nitrate patches[56].

The acid phosphatase (APase) secretion and the ammonium transporter gene expression in maize roots were increased significantly in the nutrient patches containing ammonium nitrogen, and ammonium-induced acidification of the rhizosphere increased activity of APase[17,57]. The localized supply of P also altered the amount and rate of citrate and proton release from white lupin[33], and the composition and release of root exudates were affected by the abundance and form of P in the growth medium[34,58]. These response mechanisms and their interactions are extremely complex, which requires comprehensive analysis of the experimental data and the theoretical/modeled scenarios to quantify the root responses in heterogeneous soil environment to underpin the rhizosphere engineering design for sustainable use of nutrient resources.

2.3 Root-microbe interactions

Heterogeneous soil habitats can generate a wide range of soil fauna and microbial communities[10], making root-microbial interactions in nutrient patches quite complex. An important case of root-microbe interactions influencing plant nutrient acquisition is mycorrhizal symbiosis, with more than 80% of terrestrial plant species capable of forming such relationships with specific fungi. Similarly to roots, mycorrhizal fungi can proliferate hyphae in nutrient hotspots[59,60], often at the expense of growth in other areas[2]. Given that root proliferation usually occurs slowly and is dominated by fine roots that have fast turnover, it has been suggested that root proliferation in the nutrient patches becomes derelict when roots are colonized by mycorrhizal fungi[61].

Some recent reports have demonstrated the contribution of mycorrhizal fungi to root foraging under heterogeneous nutrient supply, especially in Karst plants. For example, AM fungi can regulate the root morphological development of *Bidens pilosa* in Karst soil with high spatial and substrate heterogeneity[62]. Consequently, mycorrhizal fungi and roots can be considered as complementary in foraging for nutrients in the nutrient patches[63]. In 13 sympatric temperate tree species, thin roots exploited nutrient patches in two distinct ways; AM trees produced more roots whereas ectomycorrhizal trees supported proliferation of mycorrhizal hyphae[64]. An experiment with heterogeneous N supply showed that the AM fungal colonization, root biomass and relative growth rate of *Albizia odoratissima* and pigeon pea (*Cajanus cajan*) were higher in heterogeneous than in homogeneous soil environments[65]. Further studies on the interaction between AM fungi and roots under heterogeneous nutrient conditions in farmland ecosystems are warranted.

In addition to mycorrhizal fungi, other soil microorganisms also affect root growth and development as well as govern biogeochemical cycling of soil nutrients. It is well-established that root-associated microorganisms serve crucial roles in nutrient acquisition and stress tolerance[66]. Plant growth-promoting rhizobacteria can regulate the synthesis and activity of plant hormones, such as ethylene, cytokinin and auxin, thus affecting root growth and development[67]. They are also directly involved in signaling pathways that regulate plant responses to nutrient stress (such as P) and immunity[68]. Therefore, the root-associated microbiome has a large impact on root foraging and plant growth. However, the interaction between roots and microorganisms in nutrient patches remains obscure. In complex organic patches, roots are unlikely to be competitive with microorganisms for released nutrient resources until microbial decay occurs[69]. It is unclear what other root-microbe interactions (beyond nutrient competition) may exist in nutrient patches. Uncovering the mechanisms of plant-microbe interactions in nutrient patches is crucial for developing strategies to generate an appropriate rhizosphere microbial community for sustainable agricultural production.

3 Incremental amplification effect driven by localized fertilization

3.1 Localized fertilization strategy

Localized fertilization (banding fertilizers) based on root responses to heterogeneously distributed soil nutrients is an important strategy of root/rhizosphere management that can minimize the fixation of nutrients (such as P, Zn, Fe, and other sparingly soluble nutrients) by soil particles. Localized fertilization increases the spatial heterogeneity of soil nutrients, and expands the total rhizosphere volume and the distribution of active roots down the soil profile by adjusting the root morphology and architecture, and by promoting the efficient capture of soil nutrients by roots[4,70,71].

Importantly, mineral elements are not just nutrients necessary for plant growth but can also be signal substances regulating root development[72]. Root physiological processes can be initiated and fostered by applying the appropriate fertilizers (such as ammonium N) to enhance the root capacity to mobilize sparingly soluble nutrients. For example, application of acidic P fertilizer (monoammonium phosphate, urea phosphate, or ammonium polyphosphate) to calcareous soil decreased rhizosphere pH compared with diammonium phosphate, thereby enhancing soil P availability[57]. Thus, modifying the root/rhizosphere processes by changing the rate and composition of the localized nutrient supply in the field represents a way to improve nutrient use efficiency and plant growth. In the intensive agricultural systems of the North China Plain, localized fertilization (superphosphate and ammonium sulfate) increased maize yield by 5% to 15% and resulted in significant input savings by reducing mineral N application by 40% to 50% and superphosphate application by 33% because localized fertilizer supply greatly increased soluble nutrient concentrations in the localized nutrient bands[17,70,73].

3.2 Incremental amplification of nutrient acquisition induced by localized fertilization

The incremental amplification induced by localized fertilization is similar to the domino effect, inducing a sequence of events among the huge rhizosphere continuum (if a whole field is considered) with root zones overlaying each other. Localized fertilization promotes nutrient uptake by plants mainly through three interconnected processes: (1) increased absorption area because of altered root morphology, (2) improved mobilization capacity due to enhanced root physiological processes, and (3) intensified belowground interactions via stimulating specific microbiota. The nutrients in local patches act as signal substances to induce a series of responses in roots, including promoting root growth (increased root length, lateral root branching, and the proportion of thin roots), enhancing root nutrient absorption rate, accelerating exudation of protons, organic acid anions and phosphatases, and intensifying the interactions between roots and microorganisms, to achieve incremental amplification of nutrient acquisition (Fig. 2).

A series of field and pot studies have shown that localized application of P and NH_4^+-N can stimulate maize root proliferation, promote proton secretion to induce rhizosphere acidification and enhance phosphatase activity[17,19,25]. By using the priming effect of a small amount of P in the rhizosphere of AM fungal-colonized plants, the mycelium secretion signals can be regulated to promote the synergistic interactions between phosphate-solubilizing bacteria and mycorrhizal fungi, and the nutrient use efficiency can be increased by 30%[74,75]. Therefore, the judicious choice of nutrient form and the precise supply in the crop root zone through localized fertilization strategy can effectively couple roots, rhizosphere, biological interactions, and other processes in the incremental amplification to boost nutrient uptake and achieve high nutrient use efficiency.

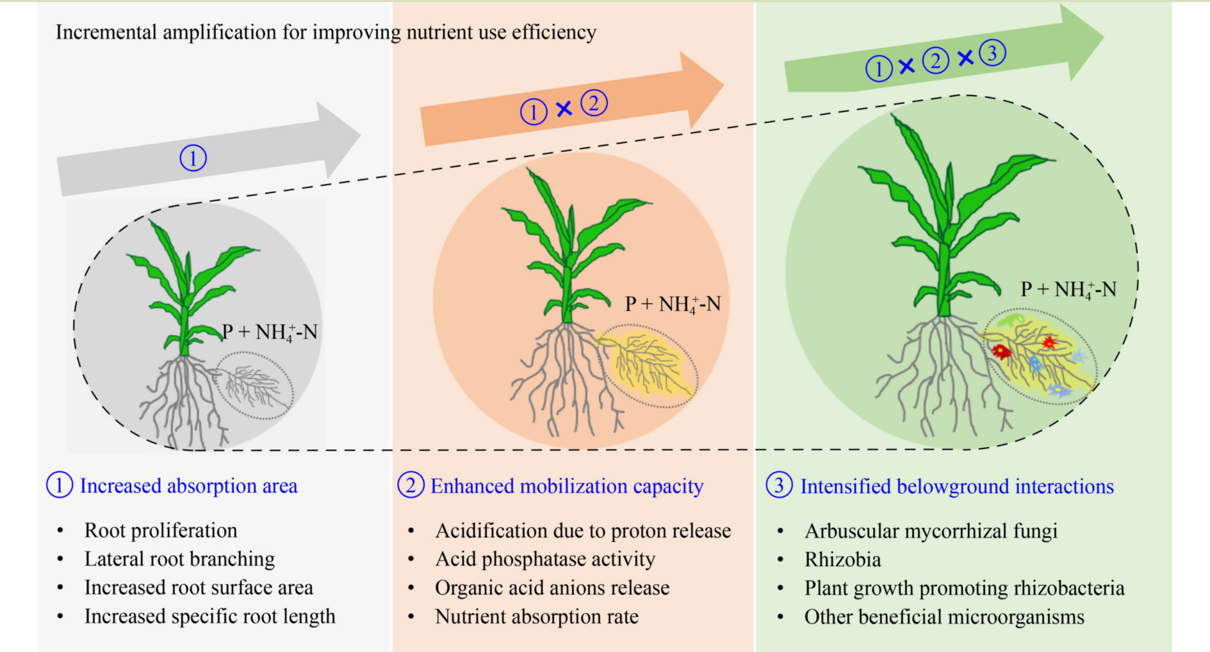


Fig. 2 Incremental amplification effect induced by localized fertilization for improving nutrient use efficiency. Localized fertilization promotes nutrient acquisition by plants mainly through the three inter-related processes: (1) increased absorption area as a consequence of altered root morphology, (2) enhanced mobilization capacity due to enhanced root physiological processes, and (3) intensified belowground interactions by stimulating microbiota. The increase in root proliferation and nutrient mobilization capacity as well as changes in the soil microbial community caused by localized fertilization can be incrementally amplified to synergistically enhance root foraging capacity and nutrient use efficiency, and thus improve crop productivity. The area of intensified rhizosphere processes and interactions is indicated in yellow.

First step: increased nutrient absorption area by altering root morphology

Inducing root proliferation is the first important step in the incremental amplification effect induced by localized fertilization (Fig. 2). As mentioned above, plant roots show high plasticity to changes in the soil environment and may respond to heterogeneous nutrient patches in the soil profile, which has been demonstrated in many crops, including maize, wheat, barley, and white lupin. Nutrient use efficiency is strongly affected by root length density in the soil and root-soil interactions. The root proliferation induced by localized fertilization can significantly increase the root length density and the proportion of thin roots in the nutrient patch to enhance the root-soil interactions[17,76]. Root length density exceeding 2 cm·cm^{-3} soil resulted in a 4-fold increase in the proportion of soil volume delivering P (from 5% to 20%) and K to roots (from 12% to 50%)[77].

In the case of localized application of P and NH_4^+-N, the application of P near the root zone can saturate the soil with P in a relatively small soil volume, thus increasing P availability and effectively stimulating root proliferation. This is crucial for fertilization management in areas with low temperature or drought in early spring because low temperature and limited water supply reduce soil nutrient availability. Therefore, banded application of P or P + N fertilizers near seeds at sowing is considered as an effective strategy to stimulate root development and establish optimal root structure for increasing crop yield[4,5,70,78]. In addition, better root growth (high root length density) is also needed to improve the spatial availability of soil nutrients due to the rapid depletion in the rhizosphere of mineral nutrients supplied mainly via diffusion (e.g., P, K, and micronutrients). Therefore, adjusting root morphology through localized fertilization strategy to foster root-soil interactions provides a feasible way to improve nutrient use efficiency.

Second step: enhanced mobilization capacity by enhancing root physiological processes

In nutrient-enriched patches, root proliferation is accompanied by a series of root physiological responses as another key link in the incremental amplification effect induced by localized fertilization (Fig. 2). First, the rate of nutrient uptake (e.g., N and P by roots[57,79]) may increase in the nutrient patches. The form of N supplied largely governs the uptake ratio of cations and anions, thus affecting the pH in the root apoplast and the rhizosphere[80]. In calcareous soils, localized application of ammonium sulfate with superphosphate can significantly promote P uptake by maize because ammonium absorption promotes proton release by roots, and the corresponding rhizosphere acidification results in improved phosphate availability[17,19]. In addition, the expression of ammonium transporter genes was increased in roots situated in the ammonium-containing patches[17]. In the fertilizer patches, the activity of alkaline phosphatase in the rhizosphere soil also increased, which facilitated the acquisition of soil organic P by roots[17]. All these processes cooperatively promote root nutrient foraging. Therefore, localized fertilization not only induces changes in root morphology and architecture, but also strengthens the root physiological processes (such as exudation), synergistically promoting crop growth and nutrient uptake.

Third step: intensified belowground interactions by stimulating microbiota

Localized fertilization can also intensify belowground interactions by activating the soil microbiota (Fig. 2), although this may occur later than the root morphological and physiological responses. There are relatively few reports on soil microbiota activation, especially for field crops. The regulation of plant ethylene signaling by introducing rhizosphere microorganisms such as *Variovorax paradoxus* strain 5C-2 containing the 1-aminocyclopropane-1-carboxylate deaminase in localized fertilization is a typical case[81]. Banding fertilizers increased maize root ethylene production by 54% compared with broadcast fertilization whereas *V. paradoxus* 5C-2 inoculation inhibited the increase in root ethylene. Reduction of ethylene production in maize roots by *V. paradoxus* 5C-2 inoculation was highly and positively correlated with a greater proportion of thin root length, resulting in a 12% increase in shoot biomass and a 50% increase in root length density[81]. However, little research in the farmland has been done on soil microbial community composition and functions in the fertilization strips. It is urgent to understand how banding fertilizers influences soil microbial communities, especially in nutrient-rich patches where soil properties are significantly different from those in the adjacent areas.

4 Implementation status and challenges of localized fertilization

The typical case of implementing localized fertilization strategy is starter fertilizer, a very common practice in American maize production[82]. At planting, subsurface starter fertilizers containing single nutrients or nutrient combinations (e.g., N, P, and K) are usually applied in bands close to the crop seed furrow to improve early-season nutrient uptake and plant growth under cool and dry soil conditions[82–84]. A series of studies have shown that nutrient placement close to seed reduces nutrient loss, improves nutrient use efficiency, increases early-season dry matter yield[19,83,85] and plant height[17,19,86], shortens the time between planting and silking[87], and reduces grain moisture at harvest[83]. The application of starter fertilizer to legumes can help the crop absorb more nutrients before the N_2 fixation system is fully established[88].

The crop yield responses to starter fertilizer are influenced by crop variety[84], management practices (e.g., tillage system[82,89], planting date[83], starter nutrient composition and placement[86,90], nutrient rates[91], plant density[92]), and environmental factors including soil moisture [83,86], soil temperature[83], and soil texture[89]. Nonetheless, the meta-analysis results showed that starter fertilizers increased maize yield by 5.2% on average in the USA, and this response was consistent across many agronomic and environmental conditions[82].

In the recent years, with the increased understanding and the promotion of machinery for planting seeds and locally applying starter fertilizer containing nutrients via deep banding, the implementation of localized fertilizer in China has gradually expanded, especially in Heilongjiang, Jilin, and Hebei Provinces. Importantly, this technology was listed as one of the main agricultural extension technologies by Ministry of Agriculture and Rural Affairs of the People’s Republic of China in 2024.

The proper implementation of localized fertilization strategy in intensive agriculture must consider fertilizer concentration and forms. High nutrient concentration or inappropriate nutrient form in the fertilizer band often leads to salt injury and ammonium toxicity[93]. Such fertilizer toxicity often occurs during seed germination and extends to seedling growth and development[94]. The salt injury caused by the repeated inappropriate localized fertilization may change the soil structure, affect the activity and diversity of soil microorganisms, thus deteriorating soil fertility and crop growth environment[94].

The inherent soil fertility affects the incremental amplification induced by localized fertilization because the yield benefits of localized fertilization decreased with increasing soil test P and K levels[25,82]. This also suggests that in low-input agriculture where resources are scarce (e.g., in some African countries), the incremental amplification benefits of implementing localized fertilization strategies may be greater. In countries with high-input, high-yield agriculture (e.g., China), the current fertilization strategy should be changed, and the incremental amplification principle should be implemented to reduce fertilizer input without a yield penalty. In addition, the selection of suitable fertilizer and the tailored fertilization management warrant further research to systematically manipulate key root-soil interfaces and maximize the incremental effects of localized fertilization.

We propose that the application of incremental amplification in intensive agricultural systems is an effective strategy to solve the problem of low nutrient use efficiency caused by excessive fertilizer input, while still matching the nutrient demand of high-yielding crops. To achieve these goals, a deeper understanding of how localized fertilization affects key rhizosphere interfaces, how nutrient composition and types influence incremental amplification, and how interactions between rhizosphere interfaces increase nutrient acquisition and improve plant growth and health is paramount. This knowledge can significantly contribute to the manipulation of soil-plant-microbe interactions aimed at mitigating impacts of intensive agriculture.

5 Concluding remarks and perspectives

In this review, we proposed the concept of incremental amplification in root foraging for nutrients induced by localized fertilization. Engineering soil–plant–microbe interactions through localized and tailored nutrient application to simulate natural root foraging for heterogeneously distributed soil nutrients initiates the incremental scaling up of root foraging capacity and nutrient-acquisition efficiency. These effects compound and amplify from the root-rhizosphere to the plant–soil system, conserving resources and reducing the environmental footprint of agricultural production while guaranteeing food security, thus providing a potential pathway for green and sustainable development of intensive agriculture.

Acknowledgements

This work was financially supported by the National Key Research and Development Program of China (2023YFD1901500/2023YFD1901503), the National Natural Science Foundation of China (32302669, 32202594, 32130094), the Natural Science Foundation of Inner Mongolia Autonomous Region of China (2023QN03002, 2024MS03004), the High-Level/Excellent Doctoral Talent Research Initiation Project of Inner Mongolia Agricultural University (NDYB2021-5, NDYB2022-20), and the Inner Mongolia Agricultural University Basic Research Project (BR22-13-04).

Compliance with ethics guidelines

Liyang Wang, Dan Liao, Zed Rengel, and Jianbo Shen declare that they have no financial or other conflicts of interest to disclose. This article does not contain any studies with human or animal subjects.

REFERENCES

1. García-Palacios P, Maestre F T, Bardgett R D, de Kroon H. Plant responses to soil heterogeneity and global environmental change. *Journal of Ecology*, 2012, **100**(6): 1303–1314
2. Hodge A. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist*, 2004, **162**(1): 9–24
3. Giehl R F, von Wiren N. Root nutrient foraging. *Plant Physiology*, 2014, **166**(2): 509–517
4. Wang L, Rengel Z, Zhang K, Jin K, Lyu Y, Zhang L, Cheng L, Zhang F, Shen J. Ensuring future food security and resource sustainability: insights into the rhizosphere. *iScience*, 2022, **25**(4): 104168
5. Wang X, Whalley W R, Miller A J, White P J, Zhang F, Shen J. Sustainable cropping requires adaptation to a heterogeneous rhizosphere. *Trends in Plant Science*, 2020, **25**(12): 1194–1202
6. Jackson R, Caldwell M. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology*, 1993, **81**(4): 683–692
7. Farley R, Fitter A. Temporal and spatial variation in soil resources in a deciduous woodland. *Journal of Ecology*, 1999, **87**(4): 688–696
8. Lark R, Milne A, Addiscott T, Goulding K, Webster C, O' flaherty S. Scale-and location-dependent correlation of nitrous oxide emissions with soil properties: an analysis using wavelets. *European Journal of Soil Science*, 2004, **55**(3): 611–627
9. Khan A, Lu G, Zhang H, Wang R, Lv F, Xu J, Yang X, Zhang S. Land use changes impact distribution of phosphorus in deep soil profile. *Journal of Soil Science and Plant Nutrition*, 2019, **19**(3): 565–573
10. Fierer N. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nature Reviews. Microbiology*, 2017, **15**(10): 579–590
11. Sasse J, Martinoia E, Northen T. Feed your friends: do plant exudates shape the root microbiome. *Trends in Plant Science*, 2018, **23**(1): 25–41
12. Chen S, Waghmode T R, Sun R, Kuramae E E, Hu C, Liu B. Root-associated microbiomes of wheat under the combined effect of plant development and nitrogen fertilization. *Microbiome*, 2019, **7**(1): 136
13. Dai Z, Liu G, Chen H, Chen C, Wang J, Ai S, Wei D, Li D, Ma B, Tang C, Brookes P C, Xu J. Long-term nutrient inputs shift soil microbial functional profiles of phosphorus cycling in diverse agroecosystems. *ISME Journal*, 2020, **14**(3): 757–770
14. Tinker P B, Nye P H. Solute Movement in the Rhizosphere. *Oxford University Press*, 2000
15. McNickle G G, Clair C C S, Cahill J F. Focusing the metaphor: plant root foraging behaviour. *Trends in Ecology & Evolution*, 2009, **24**(8): 419–426
16. de Kroon H, Hendriks M, van Ruijven J, Ravenek J, Padilla F M, Jongejans E, Visser E J W, Mommer L. Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. *Journal of Ecology*, 2012, **100**(1): 6–15
17. Jing J, Gao W, Cheng L, Wang X, Duan F, Yuan L, Rengel Z, Zhang F, Li H, Cahill J F Jr, Shen J. Harnessing root-foraging capacity to improve nutrient-use efficiency for sustainable maize production. *Field Crops Research*, 2022, **279**: 108462
18. Wang P, Mou P, Hu L, Hu S. Effects of nutrient heterogeneity on root foraging and plant growth at the individual and community level. *Journal of Experimental Botany*, 2022, **73**(22): 7503–7515
19. Jing J, Rui Y, Zhang F, Rengel Z, Shen J. Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification. *Field Crops Research*, 2010, **119**(2–3): 355–364
20. Fransen B, Blijjenberg J, de Kroon H. Root morphological and physiological plasticity of perennial grass species and the exploitation of spatial and temporal heterogeneous nutrient patches. *Plant and Soil*, 1999, **211**(2): 179–189
21. Jansen C, Van Kempen M, Bögemann G, Bouma T, de Kroon H. Limited costs of wrong root placement in *Rumex palustris* in heterogeneous soils. *New Phytologist*, 2006, **171**(1): 117–126
22. García-Palacios P, Maestre F T, Gallardo A. Soil nutrient heterogeneity modulates ecosystem responses to changes in the

identity and richness of plant functional groups. *Journal of Ecology*, 2011, **99**(2): 551–562

23. Jin K, White P J, Whalley W R, Shen J, Shi L. Shaping an optimal soil by root-soil interaction. *Trends in Plant Science*, 2017, **22**(10): 823–829
24. Zhang H, Forde B G. An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root architecture. *Science*, 1998, **279**(5349): 407–409
25. Wang L, Li X, Mang M, Ludewig U, Shen J. Heterogeneous nutrient supply promotes maize growth and phosphorus acquisition: additive and compensatory effects of lateral roots and root hairs. *Annals of Botany*, 2021, **128**(4): 431–440
26. Li H B, Zhang F S, Shen J B. Contribution of root proliferation in nutrient-rich soil patches to nutrient uptake and growth of maize. *Pedosphere*, 2012, **22**(6): 776–784
27. Hodge A, Robinson D, Griffiths B S, Fitter A H. Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. *Plant, Cell & Environment*, 1999, **22**(7): 811–820
28. Drew M C. Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. *New Phytologist*, 1975, **75**(3): 479–490
29. Robinson D. The responses of plants to non-uniform supplies of nutrients. *New Phytologist*, 1994, **127**(4): 635–674
30. Dunbabin V, Rengel Z, Diggle A. The root growth response to heterogeneous nitrate supply differs for *Lupinus angustifolius* and *Lupinus pilosus*. *Australian Journal of Agricultural Research*, 2001, **52**(4): 495–503
31. Linkohr B I, Williamson L C, Fitter A H, Leyser H O. Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*. *Plant Journal*, 2002, **29**(6): 751–760
32. Dunbabin V, Diggle A, Rengel Z. Is there an optimal root architecture for nitrate capture in leaching environments. *Plant, Cell & Environment*, 2003, **26**(6): 835–844
33. Shen J, Li H, Neumann G, Zhang F. Nutrient uptake, cluster root formation and exudation of protons and citrate in Lupinus albus as affected by localized supply of phosphorus in a split-root system. *Plant Science*, 2005, **168**(3): 837–845
34. Shu L, Shen J, Rengel Z, Tang C, Zhang F, Cawthray G R. Formation of cluster roots and citrate exudation by Lupinus albus in response to localized application of different phosphorus sources. *Plant Science*, 2007, **172**(5): 1017–1024
35. Li H G, Shen J B, Zhang F S, Lambers H. Localized application of soil organic matter shifts distribution of cluster roots of white lupin in the soil profile due to localized release of phosphorus. *Annals of Botany*, 2010, **105**(4): 585–593
36. Wang X, Feng J P J W, Shen J, Cheng L. Heterogeneous phosphate supply influences maize lateral root proliferation by regulating auxin redistribution. *Annals of Botany*, 2020, **125**(1): 119–130
37. Sun H, Zhang F, Li L, Tang C. The morphological changes of wheat genotypes as affected by the levels of localized phosphate supply. *Plant and Soil*, 2002, **245**(2): 233–238
38. Li H B, Ma Q H, Li H G, Zhang F S, Rengel Z, Shen J B. Root morphological responses to localized nutrient supply differ among crop species with contrasting root traits. *Plant and Soil*, 2014, **376**(1-2): 151–163
39. Liu Q, Zhou G, Xu F, Yan X, Liao H, Wang J. The involvement of auxin in root architecture plasticity in *Arabidopsis* induced by heterogeneous phosphorus availability. *Biologia Plantarum*, 2013, **57**(4): 739–748
40. de Kroon H, Visser E J, Huber H, Mommer L, Hutchings M J. A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. *Plant, Cell & Environment*, 2009, **32**(6): 704–712
41. Oldroyd G E, Leyser O. A plant's diet, surviving in a variable nutrient environment. *Science*, 2020, **368**(6486): eaba0196
42. Parker J L, Newstead S. Molecular basis of nitrate uptake by the plant nitrate transporter NRT1. 1. *Nature*, 2014, **507**(7490): 68–72
43. Krouk G, Crawford N M, Coruzzi G M, Tsay Y F. Nitrate signaling: adaptation to fluctuating environments. *Current Opinion in Plant Biology*, 2010, **13**(3): 265–272
44. Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K, Zazimalova E, Benkova E, Nacry P, Gojon A. Nitrate-regulated auxin transport by NRT1. 1 defines a mechanism for nutrient sensing in plants. *Developmental Cell*, 2010, **18**(6): 927–937
45. Tabata R, Sumida K, Yoshii T, Ohyama K, Shinohara H, Matsubayashi Y. Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. *Science*, 2014, **346**(6207): 343–346
46. Ohkubo Y, Tanaka M, Tabata R, Ogawa-Ohnishi M, Matsubayashi Y. Shoot-to-root mobile polypeptides involved in systemic regulation of nitrogen acquisition. *Nature Plants*, 2017, **3**(4): 17029
47. Zhang H, Jennings A, Barlow P W, Forde B G. Dual pathways for regulation of root branching by nitrate. *Proceedings of the National Academy of Sciences of the United States of America*, 1999, **96**(11): 6529–6534
48. Maghiaoui A, Bouguyon E, Cuesta C, Perrine-Walker F, Alcon C, Krouk G, Benková E, Nacry P, Gojon A, Bach L. The *Arabidopsis* NRT1. 1 transceptor coordinately controls auxin biosynthesis and transport to regulate root branching in response to nitrate. *Journal of Experimental Botany*, 2020, **71**(15): 4480–4494
49. Liu J, An X, Cheng L, Chen F, Bao J, Yuan L, Zhang F, Mi G. Auxin transport in maize roots in response to localized nitrate supply. *Annals of Botany*, 2010, **106**(6): 1019–1026
50. Drew M, Saker L. Nutrient supply and the growth of the seminal root system in barley: III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. *Journal of Experimental Botany*, 1978, **29**(2): 435–451
51. Fransen B, de Kroon H. Long-term disadvantages of selective root placement: root proliferation and shoot biomass of two

perennial grass species in a 2-year experiment. *Journal of Ecology*, 2001, **89**(5): 711–722

52. Dunbabin V, Rengel Z, Diggle A. Simulating form and function of root systems: efficiency of nitrate uptake is dependent on root system architecture and the spatial and temporal variability of nitrate supply. *Functional Ecology*, 2004, **18**(2): 204–211
53. Pregitzer K S, Laskowski M J, Burton A J, Lessard V C, Zak D R. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology*, 1998, **18**(10): 665–670
54. Tjoelker M, Craine J M, Wedin D, Reich P B, Tilman D. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist*, 2005, **167**(2): 493–508
55. Volder A, Smart D R, Bloom A J, Eissenstat D M. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytologist*, 2005, **165**(2): 493–502
56. Dunbabin V, Rengel Z, Diggle A. *Lupinus angustifolius* has a plastic uptake response to heterogeneously supplied nitrate while *Lupinus pilosus* does not. *Australian Journal of Agricultural Research*, 2001, **52**(4): 505–512
57. Wang L, Rengel Z, Cheng L, Shen J. Coupling phosphate type and placement promotes maize growth and phosphorus uptake by altering root properties and rhizosphere processes. *Field Crops Research*, 2024, **306**: 109225
58. Shu L Z, Shen J B, Rengel Z, Tang C X, Zhang F S. Growth medium and phosphorus supply affect cluster root formation and citrate exudation by *Lupinus albus* grown in a sand/solution split-root system. *Plant and Soil*, 2005, **276**(1–2): 85–94
59. Hodge A, Campbell C D, Fitter A H. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature*, 2001, **413**(6853): 297–299
60. Ritz K, Millar S M, Crawford J W. Detailed visualisation of hyphal distribution in fungal mycelia growing in heterogeneous nutritional environments. *Journal of Microbiological Methods*, 1996, **25**(1): 23–28
61. Tibbett M. Roots, foraging and the exploitation of soil nutrient patches: the role of mycorrhizal symbiosis. *Functional Ecology*, 2000, **14**(3): 397–399
62. Li Q, Umer M, Guo Y, Shen K, Xia T, Xu X, Han X, Ren W, Sun Y, Wu B, Liu X, He Y. Karst soil patch heterogeneity with gravels promotes plant root development and nutrient utilization associated with arbuscular mycorrhizal fungi. *Agronomy*, 2022, **12**(5): 1063
63. Cheng L, Chen W, Adams T S, Wei X, Li L, McCormack M L, DeForest J L, Koide R T, Eissenstat D M. Mycorrhizal fungi and roots are complementary in foraging within nutrient patches. *Ecology*, 2016, **97**(10): 2815–2823
64. Chen W, Koide R T, Adams T S, DeForest J L, Cheng L, Eissenstat D M. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences of the United States of America*, 2016, **113**(31): 8741–8746
65. Liang Y, Pan F, Jiang Z, Li Q, Pu J, Liu K. Accumulation in nutrient acquisition strategies of arbuscular mycorrhizal fungi and plant roots in poor and heterogeneous soils of karst shrub ecosystems. *BMC Plant Biology*, 2022, **22**(1): 188
66. Timmusk S, Behers L, Muthoni J, Muraya A, Aronsson A C. Perspectives and challenges of microbial application for crop improvement. *Frontiers in Plant Science*, 2017, **8**: 49
67. Verbon E H, Liberman L M. Beneficial microbes affect endogenous mechanisms controlling root development. *Trends in Plant Science*, 2016, **21**(3): 218–229
68. Castrillo G, Teixeira P J P L, Paredes S H, Law T F, De Lorenzo L, Feltcher M E, Finkel O M, Breakfield N W, Mieczkowski P, Jones C D, Paz-Ares J, Dangl J L. Root microbiota drive direct integration of phosphate stress and immunity. *Nature*, 2017, **543**(7646): 513–518
69. Hodge A. Root decisions. *Plant, Cell & Environment*, 2009, **32**(6): 628–640
70. Zhang F S, Shen J B, Zhang J L, Zuo Y M, Li L, Chen X P. Rhizosphere processes and management for improving nutrient use efficiency and crop productivity: implications for China. *Advances in Agronomy*, 2010, **107**: 1–32
71. Shen J, Wang L, Wang X, Jin K, Xiong C. Interplay between root structure and function in enhancing efficiency of nitrogen and phosphorus acquisition. In: Rengel Z, Djalovic I, eds. The Root Systems in Sustainable Agricultural Intensification, *John Wiley & Sons Ltd.*, 2021, 121–157
72. Vance C P, Uhde-Stone C, Allan D L. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytologist*, 2003, **157**(3): 423–447
73. Jiao X, Lyu Y, Wu X, Li H, Cheng L, Zhang C, Yuan L, Jiang R, Jiang B, Rengel Z, Zhang F, Davies W J, Shen J. Grain production versus resource and environmental costs: towards increasing sustainability of nutrient use in China. *Journal of Experimental Botany*, 2016, **67**(17): 4935–4949
74. Zhang L, Xu M, Liu Y, Zhang F, Hodge A, Feng G. Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. *New Phytologist*, 2016, **210**(3): 1022–1032
75. Zhang L, Zhou J, George T S, Limpens E, Feng G. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends in Plant Science*, 2022, **27**(4): 402–411
76. Wu X, Li H, Rengel Z, Whalley W R, Li H, Zhang F, Shen J, Jin K. Localized nutrient supply can facilitate root proliferation and increase nitrogen-use efficiency in compacted soil. *Soil and Tillage Research*, 2022, **215**: 105198
77. Fusseder A, Kraus M. Individual root competition and exploitation of the immobile macronutrients in the root space of maize. 1986, **178**(1): 11–18
78. Zhang K, Rengel Z, Zhang F, White P J, Shen J. Rhizosphere engineering for sustainable crop production: entropy-based insights. *Trends in Plant Science*, 2023, **28**(4): 390–398
79. Ma Q, Tang H, Rengel Z, Shen J. Banding phosphorus and

ammonium enhances nutrient uptake by maize via modifying root spatial distribution. *Crop & Pasture Science*, 2013, **64**(10): 965–975

80. Rengel Z, Cakmak I, White P J. Marschner's Mineral Nutrition of Plants. *Elsevier Ltd*., 2023
81. Jin K, Li H, Li X, Li H, Dodd I C, Belimov A A, Davies W J, Shen J. Rhizosphere bacteria containing ACC deaminase decrease root ethylene emission and improve maize root growth with localized nutrient supply. *Food and Energy Security*, 2021, **10**(2): 275–284
82. Quinn D J, Lee C D, Poffenbarger H J. Corn yield response to sub-surface banded starter fertilizer in the US: a meta-analysis. *Field Crops Research*, 2020, **254**: 107834
83. Kaiser D E, Coulter J A, Vetsch J A. Corn hybrid response to in-furrow starter fertilizer as affected by planting date. *Agronomy Journal*, 2016, **108**(6): 2493–2501
84. Gordon W, Pierzynski G. Corn hybrid response to starter fertilizer combinations. *Journal of Plant Nutrition*, 2006, **29**(7): 1287–1299
85. Kim K I, Kaiser D E, Lamb J. Corn response to starter fertilizer and broadcast sulfur evaluated using strip trials. *Agronomy Journal*, 2013, **105**(2): 401–411
86. Rutan J, Steinke K. Pre-plant and in-season nitrogen combinations for the Northern Corn Belt. *Agronomy Journal*, 2018, **110**(5): 2059–2069
87. Cromley S M, Wiebold W J, Scharf P C, Conley S P. Hybrid and planting date effects on corn response to starter fertilizer. *Crop Management*, 2006, **5**(1): 1–7
88. Galpottage Dona W H, Schoenau J J, King T. Effect of starter fertilizer in seed-row on emergence, biomass and nutrient uptake by six pulse crops grown under controlled environment conditions. *Journal of Plant Nutrition*, 2020, **43**(6): 879–895
89. Kaiser D E, Rubin J C. Corn nutrient uptake as affected by in-furrow starter fertilizer for three soils. *Agronomy Journal*, 2013, **105**(4): 1199–1210
90. Roth G W, Beegle D B, Heinbaugh S M, Antle M E. Starter fertilizers for corn on soils testing high in phosphorus in the northeastern USA. *Agronomy Journal*, 2006, **98**(4): 1121–1127
91. Rehm G W, Lamb J A. Corn response to fluid fertilizers placed near the seed at planting. *Soil Science Society of America Journal*, 2009, **73**(4): 1427–1434
92. Li H, Wang X, Brooker R W, Rengel Z, Zhang F, Davies W J, Shen J. Root competition resulting from spatial variation in nutrient distribution elicits decreasing maize yield at high planting density. *Plant and Soil*, 2019, **439**(1-2): 219–232
93. Pan W L, Madsen I J, Bolton R P, Graves L, Sistrunk T. Ammonia/ammonium toxicity root symptoms induced by inorganic and organic fertilizers and placement. *Agronomy Journal*, 2016, **108**(6): 2485–2492
94. Makaza W, Khiari L. Too salty or toxic for use: a tale of starter fertilizers in agronomic cropping systems. *Agronomy*, 2023, **13**(11): 2690