Soil Biology and Biochemistry 135 (2019) 343–360

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Review Paper

Rhizosphere size and shape: Temporal dynamics and spatial stationarity

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ARTICLE INFO

Keywords:
Rhizosphere processes
Biogeochemical gradients
Rhizodeposits
Microbial hotspots
Accumulation and depletion of nutrients
Enzyme distribution and localization

ABSTRACT

The soil volume affected by roots – the rhizosphere – is one of the most important microbial hotspots determining the processes, dynamics and cycling of carbon (C), nutrients and water in terrestrial ecosystems. Rhizosphere visualization is necessary to understand, localize and quantify the ongoing processes and functions, but quantitative conclusions are very uncertain because of: 1) the continuum of the parameters between the root surface and root-free soil, i.e., there are no sharp borders, 2) differences in the distributions of various parameters (C, nutrients, pH, enzyme and microbial activities, gases, water etc.) across and along roots, 3) temporal changes of the parameters and processes with root growth as well as with water and C flows.

In situ techniques: planar optodes, zymography, sensitive gels, ^{14}C and neutron imaging as well as destructive approaches (thin layer slicing) have been used to analyze the rhizosphere extent and the gradients of various physico-chemical and biological characteristics: pH, CO_2, O_2, redox potential, enzyme activities, content of water, nutrients and excess elements, and organic compounds. A literature analysis allows the conclusion that: i) the rhizosphere extent for most of the parameters assessed by non-destructive visualization techniques is 0.5–4 mm but exceeds 4 mm for gases, nitrate, water and redox potential. ii) The rhizosphere extent of nutrients (N, P) is decoupled from the extent of the corresponding enzyme activities. iii) The imbalance between element flows to and uptake by roots may lead to accumulation of excess elements and formation of root carapaces (e.g. $CaCO_3$ rhizoliths, Fe plaque) ranging up to a few cm. iv) All destructive approaches show a much (3–5 times) larger rhizosphere extent compared to visualization techniques. These conclusions are crucial for a mechanistic understanding of rhizosphere properties and functioning, estimation of the nutrient stocks available to roots, and for rhizosphere modelling considering root growth and architecture.

Overall, roots function as ecosystem engineers and build their environment, serving as the main factors shaping rhizosphere extent. Sharp gradients are formed within a few days for nutrients and enzymes, but more time is necessary for the establishment of specific microbial communities. Despite the very strong dynamics of most parameters, their stationarity is reached within a few days because the release of C and enzymes or nutrient uptake are very quickly compensated by utilization by surrounding microorganisms or/and sorption and diffusion processes. We conclude that despite the dynamic nature of each property, the rhizosphere gradients, their extent and shape are quasi-stationary because of the opposite directions of their formation processes.

1. Introduction

1.1. Why rhizosphere?

The rhizosphere is the soil volume around the root that is strongly affected by root functioning (Hiltner, 1904). This classical definition describes the rhizosphere as a four-dimensional (4D) object: 3D for volume, and time for functioning. Do we need, and can we achieve, a 4D picture for this object – the rhizosphere? We need an image, if only because humans obtain ~90% of their information visually and any visualization simplifies and accelerates the reception, preservation, localization, understanding and exchange of information. This is especially valid for the rhizosphere because (Kuzyakov and Razavi, 2016, 2017): 1) it is in the soil – hidden from view, 2) most sampling methods destroy the rhizosphere – the spatial and functional connections between solid, liquid, gaseous and living matter are lost, 3) rhizosphere boundaries are not sharp – this makes their extent and shape very elusive, 4) diverse soil parameters may change in varied and partly divergent ways, and 5) the rhizosphere is very dynamic – the object changes over time and it is difficult (but very intriguing) to imagine its

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https://doi.org/10.1016/j.soilbio.2019.05.011
Received 31 December 2018; Received in revised form 10 May 2019; Accepted 14 May 2019
Available online 18 May 2019
0038-0717/

"stable", stationary state. We therefore have only a nebulous picture of what the rhizosphere looks like, and talking about "*the rhizosphere*" at conferences and in papers may conjure up different pictures for various colleagues, depending on the specific parameters they study, plant and root features, the equipment and methods used, and last but not least the imagination of individual researchers.

The present overview was prompted not only by the hidden nature of the rhizosphere, but also because it is the most important hotspot in the soil (Kuzyakov and Blagodatskaya, 2015) and probably in terrestrial ecosystems in general (Hinsinger et al., 2003). Consequently, most processes measured along soil profiles and at larger scales are actually taking place in a very small soil volume – in hotspots – and will be simply 'diluted' by the huge surrounding soil volume. This makes it even more important to obtain an image of the dynamic locations at which the processes are ongoing at much faster rates. Based on these premises, this review presents a comprehensive attempt to visualize the extent and shape of the rhizosphere. Thus, we take up the challenge of illustrating a 4D object on 2D paper.

1.2. Processes affecting substance fluxes and gradients in the rhizosphere

The first step is to define the processes contributing to the extent, shape and dynamics of a broad range of parameters in the rhizosphere. Biotic and abiotic processes affect the concentration, movement and thus the distribution of substances around the roots (Table S1). The processes are bidirectional: from root to soil and from soil to the root, and are connected with 1) uptake of water and nutrients by roots (inflow); 2) active and passive release of various groups of rhizodeposits (secretions, mucilage, exudates, sloughed-off cells, enzymes; for definitions and processes, see Nguyen, 2003) by roots (outflow); 3) uptake of these organics and nutrients by microorganisms; 4) uptake and release of O_2 and CO_2 by both roots and microorganisms; and 5) physicochemical processes of sorption, desorption, precipitation and dissolution. The rates of all these processes decrease with increasing distance from the roots (or occur solely at the root surface, e.g. root exudation). Accordingly, concentration gradients are established from the roots to the bulk soil and reverse (Fig. S1). The importance of individual biotic and abiotic processes for establishing gradients differs for various substances. This review therefore presents and evaluates the common gradients for most substances and, based on these gradients, draws conclusions about the extent of the rhizosphere, its temporal dynamics and spatial stationarity, ultimately revealing rhizosphere shape.

Various models have simulated individual and interconnected processes in the rhizosphere, including water uptake (Roose and Schnepf, 2008; Carminati, 2012), nutrient uptake (Roose and Schnepf, 2008; Barber et al., 1963; Jungk and Claassen, 1997), and exudate release (Farrar and Jones, 2000), and have thus visualized the rhizosphere (Jungk, 2001). For most simulated parameters, however, the modeling results are difficult to validate experimentally because the spatial and temporal resolution of experiments is considerably lower than that of the models. This review therefore focuses solely on experimental results that illuminate rhizosphere parameters related to functions.

2. Material and methods

2.1. Principles of data collection

To evaluate gradients in the rhizosphere, we collected literature data based on destructive and non-destructive approaches (Kuzyakov and Razavi, 2016, 2017). 1) The destructive approaches include: i) growth of plants in pots with zonation by gauzes with small mesh size: 0.2–40 μm (Helal and Sauerbeck, 1981); ii) slicing of soil with increasing distance to the root surface (Tarafdar and Jungk, 1987; Kuchenbuch and Jungk, 1982; Begg et al., 1994; Zoysa et al., 1997; Kandeler et al., 1999; Kandeler et al., 2002; Sauer et al., 2006; Hafner et al., 2014; zu Schweinsberg-Mickan et al., 2010) and iii) compartment rhizoboxes (Youssef and Chino, 1987, 1988, 1989).

2) The non-destructive approaches (reviewed by Oburger and Schmidt, 2016) include: i) planar optodes for CO_2, pH, O_2 (Blossfeld et al., 2011; Schreiber et al., 2012; Rudolph-Mohr et al., 2014; Larsen et al., 2015; Koop-Jakobsen and Wenzhöfer, 2015); ii) gels sensitive for pH (Römheld, 1986) of for the exudation of aluminum complexing ligands or Fe(III) reducing agents (Engels et al., 2000; Neumann, 2007); iii) zymography for enzyme activities (Spohn and Kuzyakov, 2013; Razavi et al., 2016); iv) DGT (diffusive gradients in thin films) gel for elements (Fresno et al., 2017); v) imaging of radioactive isotopes: ^{14}C (Holz et al., 2018a), ^{32}P, ^{33}P, ^{40}Ca for nutrients; vi) neutron imaging and X-ray synchrotron for water and rhizosphere porosity (Carminati, 2012; Zarebanadkouki et al., 2013; Helliwell et al., 2017); vii) microelectrodes for Eh (Fischer and Schaller, 1980) or pCO_2 (Gollany et al., 1993). We do not describe these approaches here and refer to the original papers and reviews (Oburger and Schmidt, 2016) for further methodological details. The full description of collected data and parameters, data standardization for assessing lateral gradients, and standardization of parameters along the roots are presented in detail in Supplementary Materials: Methods.

3. Rhizosphere shape and extent

To simplify the first step of evaluating rhizosphere extent, we

Table 1
Biotic and abiotic process groups directly[a] affecting the fluxes of substances from and to the roots and thus establishing the rhizosphere gradients.

Processes[b]		From the root ⟛→	To the root ⟛←	To/from soil matrix ↓↑
Biotic	Root	Release (active) of: secretes, mucilage, enzymes, H^+, (OH^-) etc. Root CO_2 release	Uptake of nutrients O_2 uptake Uptake of organic and inorganic toxicants	Precipitation of excess elements Oxidation: $Fe^{2+} \rightarrow Fe^{3+}$, $Mn^{2+} \rightarrow Mn^{4+}$ $CaCO_3$ precipitation SiO_2 precipitation
	Microbes	Uptake of organics Microbial CO_2 release	Nutrient transport by mycorrhiza	Release of enzymes Uptake of nutrients Nutrient mobilization Depolymerization of enzymes
Abiotic[c]		Release of exudates (passive) Ion diffusion	Water uptake	Sorption, Desorption Precipitation, Dissolution Nutrient exchange with H^+ Organics decomposition by exoenzymes

[a] Various *indirect* processes may affect the matter and energy fluxes in the rhizosphere, e.g. release of signaling molecules. *Indirect* processes are omitted in Table 1.
[b] Certain processes cannot be defined distinctly as biotic or abiotic (e.g. passive release of root exudates, water uptake, etc.). Such processes may be abiotic by nature, but strongly controlled by roots.
[c] Diffusion is not mentioned here as an abiotic process because it is driven by the emerging gradients and proceeds in both directions: from and to the root, depending on the gradient.

organized the results according to the processes mentioned in Table 1: Gradients induced by *biotic* (roots and microorganisms) and by *abiotic* drivers, and specified them for: *from the roots* and *to the roots*.

Fluxes from root to bulk soil.

3.1. Release of H^+ and OH^- ions

The release of H^+ by roots into slightly acidic, neutral and alkaline soils (without N fertilization) is one of the dominant mechanisms of plants to mobilize nutrients and maintain the electrochemical potential on the root surface (Marschner, 2012). The common distance of root-induced pH changes is about 2–3 mm (Fig. 1). The high buffer capacity of soil (CEC, aluminosilicate hydrolysis, Al^{3+} and Fe^{3+} release, $CaCO_3$, etc.) neutralizes the common difference of 0.5–1 pH units between root surface and bulk soil (Begg et al., 1994; Hinsinger et al., 2009). Even the largest reported changes of 2.5 pH units (Rao et al., 2002a,b) (350–400 fold difference in H^+ concentration) are completely neutralized within ~5 mm (Blossfeld et al., 2011). Depending on the neutralization agents and the intensity of H^+ release by roots, two changes are common with increasing pH of the bulk soil: i) pH decrease at the root surface (compare Fig. 1) and ii) decrease of the rhizosphere pH extent. Consequently, the pH gradient between root surface and surrounding soil increases with increasing soil pH.

Three key factors strongly affect the pH changes and gradients: i) soil pH, ii) N fertilization and iii) plant species. The effect of the initial soil pH is much larger than that of N nutrition (Fig. 1), despite the fact that N form (NH_4^+ or NO_3^-) is a major determinant of the overall cation–anion balance for root uptake. Although most plant species acidify the rhizosphere, some plants (e.g. most cereals) release OH^- ions. Plant species affect the rhizosphere pH depending on the initial soil pH (Fig. 1). Specifically, the roots increase or decrease the rhizosphere pH by H^+ or OH^- release and changing the equilibrium between cations and anions at the root-soil interface (Youssef et al., 1989). The pH increased by about 2 units for barley roots grown in clay loamy soil with a bulk pH of 5, whereas rhizosphere pH was reduced by 1.5 units if the initial bulk pH was 7 (Fig. 1). Consequently, roots compensate the extreme (too low or too high) pH values of the soil and thereby alleviate the associated constraints such as Al^{3+} or Fe^{3+} toxicity at acidic pH or Fe or Mn deficiency at alkaline pH.

Legumes strongly acidify the rhizosphere by two main mechanisms: i) proton release following excess uptake of cations over anions during N_2 fixation (Israel and Jackson, 1978; Haynes, 1983; Bolan et al., 1991); ii) photosynthetic activity (light-induced acidification) altering the cation-anion uptake ratio (Rao et al., 2002a,b). NO_3^- fertilization (especially in acidic soils) strongly contributes to OH^- release (to maintain root cell electro-neutrality). The pH changes and gradients have a very similar trend (Fig. 1) but in reverse directions (Heckman and E Strick, 1996; Li et al., 2007; Zhou et al., 2009): the uptake of NH_4^+ promotes H^+ efflux and reduces the rhizosphere pH, whereas NO_3^- uptake promotes OH^- efflux and raises the rhizosphere pH (Marschner et al., 1982). Exceptionally, legumes acidify their rhizosphere even when fed with nitrate (Marschner and Römheld, 1983).

Root type and water content can alter rhizosphere pH. For instance, pH as a function of radial distance from crown and lateral maize roots under wet conditions ($\Theta = 0.24\ cm^3\ cm^{-3}$) showed no acidification (Rudolph-Mohr et al., 2017). In contrast, under dry conditions ($\Theta = 0.12\ cm^3\ cm^{-3}$) lateral roots acidified their rhizosphere by 0.25 pH units, and crown roots even acidified their rhizosphere by up to 1.0 pH unit compared to bulk soil (Rudolph-Mohr et al., 2017).

The pH buffering agents ($CaCO_3$ for H^+; organic acids for OH^-) reduced the rhizosphere extent (Fig. 1, $CaCO_3$ effect), which agrees with the neutralization theory. The extension of root-mediated pH changes in the rhizosphere of peanuts was larger (2.8 mm) in a poorly buffered soil with an initial pH of 5.5 than in more buffered alkaline and acidic soils (1.4 mm) (Schaller, 1987; Nye, 1981). Thus, the greater the pH buffering capacity, the smaller the plant-induced pH changes (Schubert et al., 1990; Hinsinger et al., 2009).

3.2. Release of organic substances

The next group of rhizosphere parameters involves the release of various organic substances by roots – the rhizodeposits.[1] Rhizodeposits include the continuously and passively released exudates, and the dynamically and actively released mucilage, secretions and enzymes from various root zones (Jones et al., 2004, 2009; Nguyen, 2003). All these substances have 1–3 orders of magnitude slower diffusion than H^+. Two main mechanisms decrease the concentration of organic compounds in soil solution (Table 1): i) microbial uptake and utilization (Fischer et al., 2010; Jones et al., 2005; Oburger et al., 2009), and ii) sorption on surfaces of minerals or organic matter (Kalbitz et al., 2005; Kaiser and Guggenberger, 2003). The diffusivity in soil depends strongly on the water content, roughly as the square of the water content (Olesen et al., 2000). With distance and time, the organic compounds are progressively metabolized to CO_2 or into recalcitrant C compounds (Hartmann et al., 2009). For exudates (passively released soluble low molecular weight organic compounds), microbial uptake is very fast – minutes (Jones et al., 2005; Fischer et al., 2010; Dippold et al., 2014; Gunina and Kuzyakov, 2015). This causes microbial uptake and mineralization to dominate over sorption (Fischer et al., 2010; Oburger et al., 2009). For secretions and mucilage, however, microbial uptake is much slower because they are high molecular weight substances – mainly polysaccharides – present in soil solution as gels (Carminati et al., 2017a; Saez-Aguayo et al., 2017). This makes them less available for microorganisms, requiring splitting by exoenzymes. Their gelled and sticky properties promote attachment to the surface of soil minerals (Benard et al., 2018) and additionally retard the decomposition.

Root development changes the zonation and composition of released exudates. Young root hairs and the cortical cells around emerging branches of legume roots release flavonoids to trigger nodules in only those specific regions (Mathesius et al., 2000). Sucrose is released mostly from the apical region of the primary root, while efflux of the amino acid tryptophan is associated with branch roots (Jaeger et al., 1999).

The distribution of rhizodeposits is commonly measured by ^{14}C and/or ^{13}C (and ^{15}N) (rarely with $^{11}CO_2$) labeling of plants and subsequent tracing i) by autoradiography (for ^{14}C, Fig. 2) (Holz et al., 2018a; Rovira, 1973) (or with a positron emitting tracer imaging system PETIS, for ^{11}C; Fujikake et al., 2003; Suzuki et al., 2008; G. Bonito, personal communication) as non-destructive approaches or ii) destructive slicing of soil from the root surface and ^{14}C or $\delta^{13}C$ (or $\delta^{15}N$) analysis (Fig. 2). ^{14}C (and ^{11}C) imaging over a very short period (few hours) after labeling mainly reflects the distribution of root exudates because the high molecular weight compounds (secretions, mucilage) are released later (Oburger et al., 2018). The rhizosphere extent measured by ^{14}C imaging of exudates is usually only 2–3 mm (Fig. 2) (Holz et al., 2018a). Destructive slicing, however, reveals much larger extents: up to 10–12 mm (Sauer et al., 2006; Kuzyakov et al., 2003; Helal and Sauerbeck, 1981; zu Schweinsberg-Mickan et al., 2010). Increasing the time after labeling reflects the distribution of more high molecular weight organics – secretions, mucilage, and sloughed-off cells (Dennis et al., 2010; Holz et al., 2018a). The secretions and mucilage have never been visualized in soil. Their physico-chemical parameters (charge, molecular weight, functional groups; Saez-Aguayo et al., 2017) allow

[1] Rhizodeposits also include the sloughed-off root cells, broken root hairs etc. We do not describe these groups because they do not move in soil. We are aware, however, that even insoluble organic root debris may strongly affect enzyme activities and affect the content, composition and activity of microorganisms in the rhizosphere.

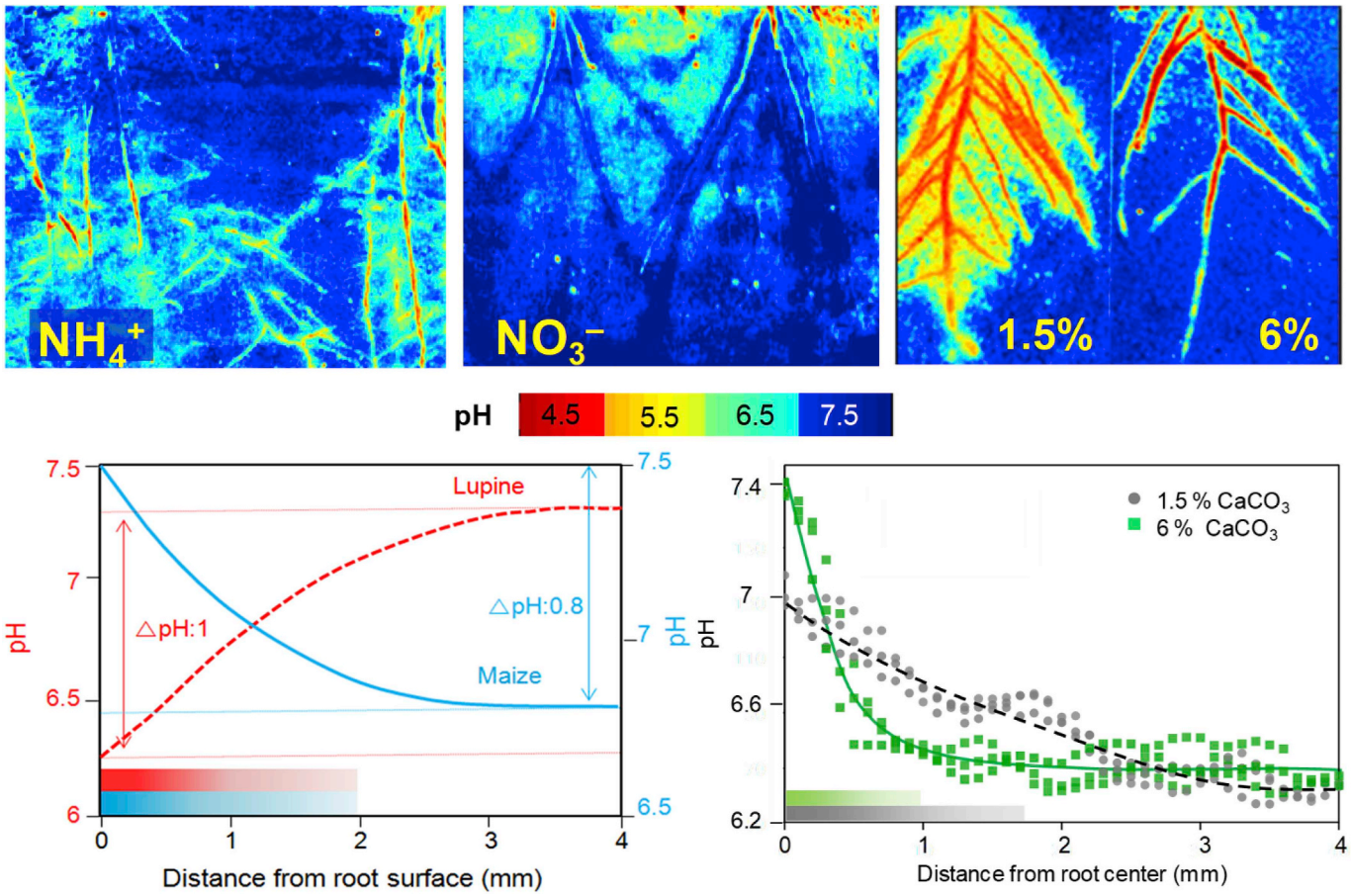

Fig. 1. pH gradients in the rhizosphere depending on N sources (top left and middle): NH_4^+ and NO_3^-, and soil buffering capacity (top right). NH_4^+ and NO_3^- were added combined with nitrification inhibitor under ryegrass (modified, Heckman and Strick, 1996). The generalized pH changes (ΔpH) from root surface to the bulk soil are presented depending on the initial soil pH (bottom left): barley roots increased the initial bulk pH of 4.8 (red line) to 7.1 and reduced pH of 7.1 to 5.5 (blue line) in the clay loam soil. Vertical arrows show maximum ΔpH. Effect of soil buffering capacity (bottom right) is presented based on the example of $CaCO_3$ content in soil (1.5% and 6% of soil d.w.) under chickpea (*Cicer arietinum* L.). The extension of root-induced rhizosphere acidification strongly increases with the decrease of the buffering capacity: color bars at the bottom of the left figure show the rhizosphere extents. Data for NH_4^+ and NO_3^- fertilization are extracted from Rudolph et al. (2013); Youssef et al., 1989 and for $CaCO_3$ buffering from Römheld (1986); Luster et al., 2009, modified. Color gradients at the bottom of the graphs show the rhizosphere extents. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the assumption that their gradients in the rhizosphere will be similar to those of enzymes (Holz et al., 2018b).

3.3. Enzyme gradients

Although enzymes belong to the organic substances released by roots into the rhizosphere and could have been described in the previous section, we devote a separate section to them because: 1) Enzyme gradients are characterized by activity and not by concentration. 2) The molecular weight of enzymes (~12–500 kD) is generally much higher than that of other organic substances released by roots. As diffusion strongly decreases with molecular weight, the gradients may differ from other organics with lower molecular weight. 3) Enzymes have various functions and reflect processes, not pools. 4) Various enzymes directly and strongly affect the gradients of other soil properties: nutrient (N, P, S) contents, available C, microbial biomass and activity, etc. 5) Enzymes are released not only by roots but also by microorganisms, whose activities directly depend on root functions, mainly organic C release. 6) A broad range of visualization studies is available on the spatial distribution of enzymes, allowing conclusions about the rhizosphere extent for individual enzyme groups.

Enzyme activities in the rhizosphere are commonly much higher than in bulk soil (Fig. 3). The distribution of enzyme activity can be visualized by soil zymography (Spohn et al., 2013; Razavi et al., 2016; Liu et al., 2017) or by measurements involving destructive approaches (Tarafdar and Jungk, 1987; Kandeler et al., 1999; Marschner et al., 2012). The rhizosphere extent for most enzymes is 1–3 mm (Fig. 3) and activity decreases with distance from the root surface. Enzyme activity in the rhizosphere is 1.3–2 times higher than in the bulk soil (Fig. 3) and typically demonstrates a sigmoidal curve.

Nutrient deficiency widens the rhizosphere. For instance, P starvation of roots due to infection by nematodes (*Meloidogyne incognita*) enlarged the rhizosphere 1 mm more than in uninfected plants (Razavi et al., 2017). Similarly, cellulose addition enlarges the rhizosphere with regard to acid and alkaline phosphatases (Wei et al., 2019b), which actively compensates for the increased C/P stoichiometric ratio by P mineralization from SOM. Correspondingly, P fertilization decreases the rhizosphere extent.

Generally, independent of soil nutrient content, the maximal rhizosphere extent is shown by the enzymes of the P cycle (up to 5 mm), followed by those of N and C cycles (Ge et al., 2017; Ma et al., 2018) (Fig. 3). This reflects the intensity of limitation for plants (P > N > C) and the lesser P mobility in soils and solution compared to N. Plants must therefore acquire the most strongly limiting nutrient (P > N) that can be enzymatically mobilized from soil organic matter, plant residues and microbial necromass.

The duration of root occupation of a soil volume affects the maximal activity: with time, enzyme activities at the root surface can increase by

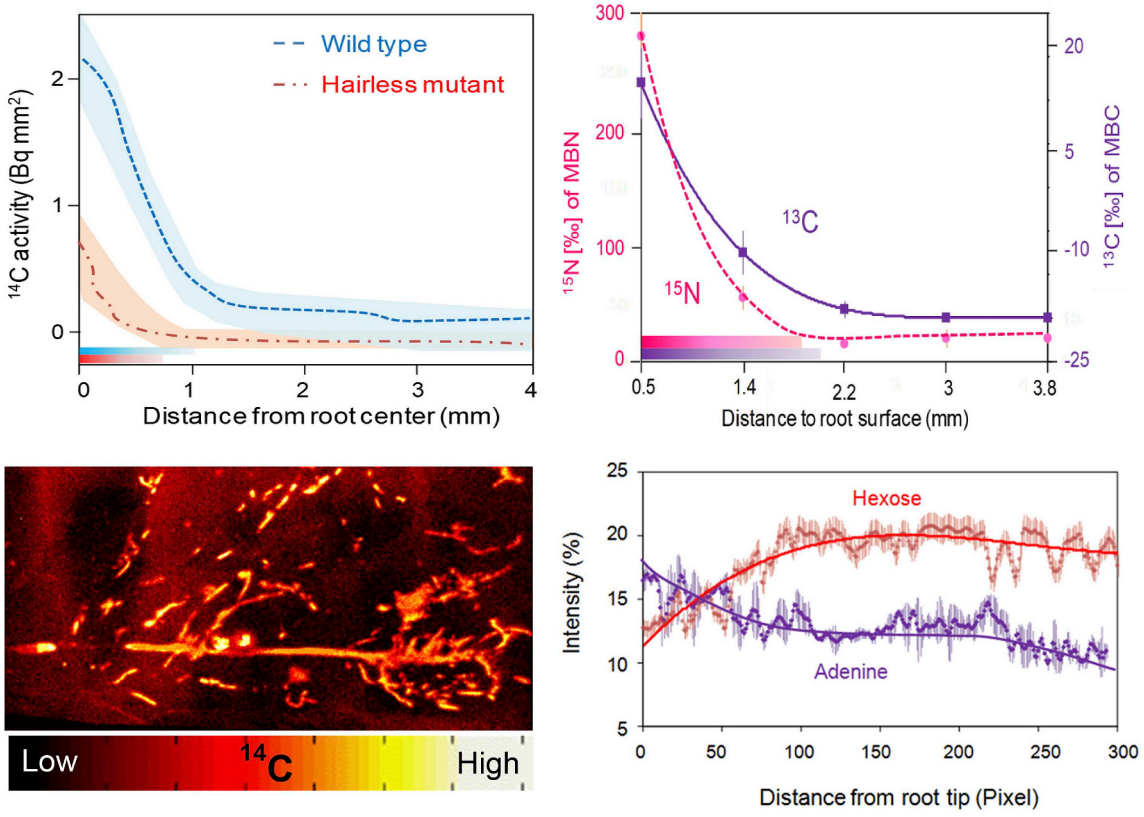

Fig. 2. Gradients of root exudates. Top left: ^{14}C profiles reflecting the exudate release by barley roots: Wild type with root hairs (blue dashed line) vs. hairless mutant (red dash-dotted line). Shading demonstrates ± SE between replicates (data from Holz et al., 2018c, modified). Bottom left: ^{14}C image of lupine roots reflecting photoassimilate allocation (after $^{14}CO_2$ labeling). The arrows show the high intensity of the light color corresponding to high ^{14}C activity (high C allocation) in nodules (from Razavi unpublished). Top right: Incorporation of ^{13}C- and ^{15}N-labeled rhizodeposits into microbial biomass in the rhizosphere depending on increasing distance to the root surface of *Lolium perenne* (after $^{14}CO_2$ labeling and ^{15}N leaf labeling). Bottom right: Distribution of adenine and hexose as a function of distance along the root (data extracted from Vetterlein and Doussan, 2016). The Y axis reflects the relative concentration measured as the mass-to-charge (m/z) ratio measured on GC-MS. The X axis is presented in pixels because no scale was provided in the original paper. According to our rough estimation, 100 pixels correspond to 1 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

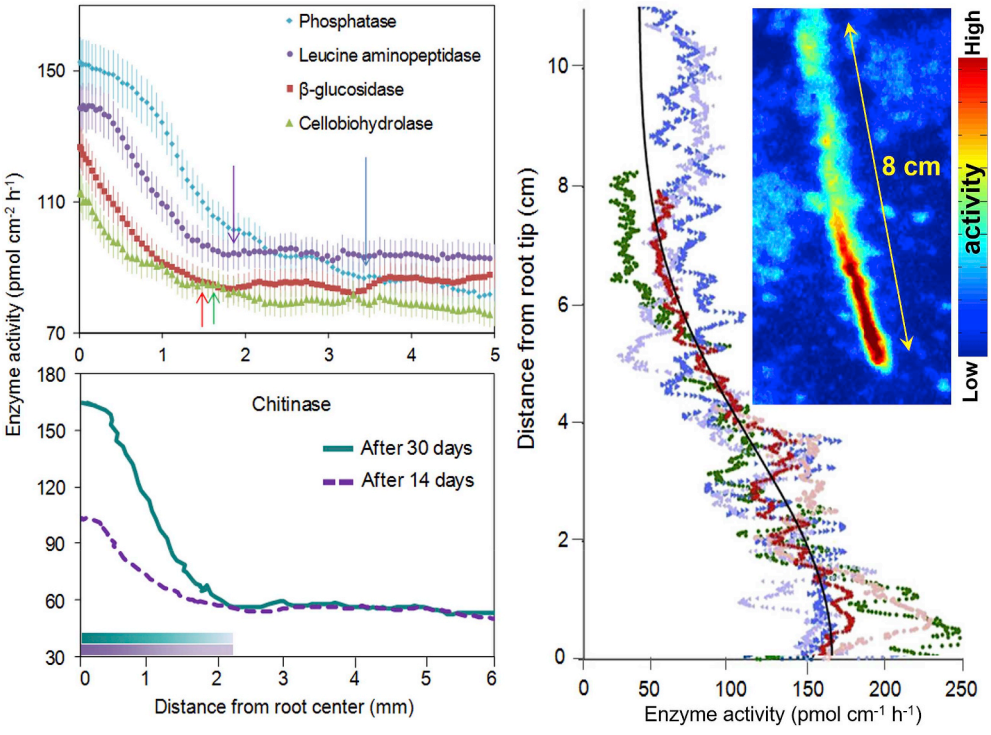

Fig. 3. Enzyme gradients. Top left: Activity gradients of 4 enzymes *across* roots in the maize rhizosphere. Bottom left: Effects of root occupation period (14 and 30 days) of soil on the chitinase activity gradients in rice rhizosphere. Each line represents one root (data from Razavi et al., 2016 and Ge et al., 2017). Right: *β*-glucosidase activity *along* the maize root. Each dotted line represents one root (example of a zymogram is presented in the inset). The continuous black line reflects the average. Although maximal activity at the root tip is 2–4-fold larger than 6–8 cm from it, the enzyme activity along the whole root is 2–3-fold larger than in the root-free soil (data from Razavi et al., 2016).

10–30% (Fig. 3), but the rhizosphere extent remains stable (Ge et al., 2017). The rhizosphere boundaries for chitinase and phosphatase remained constant in response to temperature (Ge et al., 2017) or heavy metal pollution (Duan et al., 2018). The spatial stability of the rhizosphere extent reflects the equilibrium between the input – release from roots and diffusion – and the output – microbial decomposition and other enzyme inactivation (Schimel et al., 2017). This stable pattern is an excellent strategy for plants to efficiently acquire nutrients in a narrow root zone independent of root age (Ge et al., 2017; Vetterlein and Doussan, 2016). Root hairs can expand the rhizosphere extent by about 2–7 times, whereas the root radius merely increases enzyme activity per root area (Ma et al., 2018). The high exudate release in the presence of root hairs (Fig. 2) (Holz et al., 2018c) stimulates microbial activity (Pausch et al., 2016) and thus enzyme production by microorganisms (Ma et al., 2018).

Although the diffusivity of high molecular weight enzymes is much slower (actually negligible, Siddiqui and Cavicchioli, 2006) than that of the low molecular weight compounds forming root exudates (see previous section and Kuzyakov et al., 2003; Zhang et al., 2019), the rhizosphere range is similar: 1–3 mm (compare Figs. 2 and 3). We explain this phenomenon by two mechanisms: 1) enzymes are released not only by roots, but also by microorganisms. As microbial activity strongly increases in the presence of root exudates, more enzymes will be microbially produced compared to the bulk soil; and 2) much longer stability of enzymes in soil (weeks, Schimel et al., 2017) compared to low molecular weight organic compounds (minutes to hours Jones et al., 2005). Enzyme stability reflects their rapid sorption to the soil (within 10 min), and protection from microbial consumption and/or thermal denaturation (George et al., 2005). Consequently, the longer half-lives of enzymes may contribute to their wider dissemination from roots. Comparing these two process groups, we conclude that only the enzyme activities on the rhizoplane (root surface) or associated with root hairs originate directly from roots. Because the diffusion of enzymes is very limited (Guber et al., 2018), the direct enzyme release by roots is relevant only for the rhizoplane, and most of the rhizosphere enzymes are produced by microorganisms (which are stimulated by root exudates). This conclusion calls for simultaneously analyzing the spatial distribution of root exudates (e.g. by ^{14}C imaging), enzyme activities (Spohn and Kuzyakov, 2013; Bilyera et al., 2019) and omics analysis to identify enzyme origins in the rhizosphere.

3.4. Gradients of CO_2 and O_2 concentrations and of the redox potential

Roots and root endophytes utilize photoassimilates, consume O_2 and release CO_2 into the soil. The CO_2 production rates by roots vary from around 20 mg C g^{-1} root d^{-1} (for maintenance) up to 600 mg C g^{-1} root d^{-1} (for young, growing roots) (Eissenstat and Yanai, 1997; Eissenstat et al., 2000). Because CO_2 is distributed mainly in the gaseous phase, its rhizosphere extent is much larger compared to the substances dissolved in water. The rhizosphere range for CO_2 is extremely difficult to assess because the very high temporal and spatial variation of the CO_2 concentration in bulk soil hinders calculating a distinct SD (see Fig. 4). Furthermore, the CO_2 concentration strongly increases with depth: from < 1000 ppm in the upper 3–5 cm to > 20,000 ppm in subsoil (Gaudinski et al., 2000; Pausch and Kuzyakov, 2012). This reflects the longer diffusion path from the production site to the soil surface and atmosphere (not higher specific respiratory activity of roots or microorganisms in deep soil).

The increase in root and microbial respiration with temperature reduces the O_2 concentration (Blossfeld, 2008). O_2 limitation may be bypassed by O_2 supply from the rhizosphere of other nearby plant species. Thus, even if the O_2 supply of one species is comparatively sensitive to temperature increase, other plant species can sustain the rhizospheric O_2 concentration within the dense inter-specific root network (Blossfeld, 2008).

CO_2-sensitive sensors help overcome some of the measurement difficulties and reveal a CO_2 rhizosphere range of 1.5–1.8 mm (Fig. 4) (Blossfeld, 2013; Uteau et al., 2015). Optodes showed an O_2 depletion range of a few millimeters (Koop-Jakobsen and Wenzhöfer, 2015; Larsen et al., 2015), which is very similar but reverse to that of CO_2 (Fig. 4). The O_2 and CO_2 ranges decrease very strongly with soil moisture (Moldrup at al., 2000). In lowland conditions, the concentration and gradients of CO_2 and O_2 decrease over time around the root, but the rhizosphere extent increases (Larsen et al., 2015). Conversely, in upland plants (e.g. maize) both the O_2 gradient and range decrease over time (Rudolph-Mohr et al., 2017).

Closely associated with O_2 concentration, the redox potential may have sharp gradients around the roots, especially under water-saturated conditions (Fig. 4, rice roots photo). According to the Nernst equation, pH decreases lead to Eh increases. Thus, any Eh changes are affected by H^+ release by roots (Fischer et al., 1989). Redox potential variations in the rhizosphere are caused by several processes: 1) Oxygen consumption combined with CO_2 release by living roots. 2) Growing roots release exudates containing phenolic compounds, which reduce Fe^{3+} and Mn^{4+} oxides (Brown and Ambler, 1973; Marschner et al., 1982). The respective electron transfer reactions are rapid and are active mainly on the root tip. Thus, these Eh effects are restricted to a short period and restricted rhizosphere volume. 3) Even if root exudates themselves have no reducing properties, the redox potential is lowered by microbial utilization of exudates and consumption of O_2 or other electron acceptors. Except for the second group (release of phenolic compounds), these processes influence a relatively large soil volume because O_2 (determining Eh) has a high diffusion rate in soils compared to that of root exudates. The rhizosphere-oxidized area is not controlled by plant growth stage, cultivars or yield parameters directly. Among the parameters, only root biomass strongly correlated with the rhizosphere-oxidized area (Atulba et al., 2015).

Fluxes from bulk soil to the root.

3.5. Nutrient gradients

The most important gradients formed by the fluxes from the bulk soil to the roots involve nutrients. The nutrient rhizosphere volume is crucial for plant nutrition because it defines the total amount of each nutrient potentially available to the plant. The nutrient gradients are well known, especially for P and for both mineral N forms: NH_4^+ and NO_3^-. Nutrients move towards the root by diffusion and mass flow (the movement of nutrients with water) (Barber et al., 1963). The effective diffusion rate of a nutrient depends on the concentration gradient, the charge between particle surfaces and the nutrient, and saturation with water and other nutrient concentrations. The nutrient diffusion that depends strongly on soil particles is limited, and the depletion zones will be narrow (few mm). Very strong depletion zones (e.g. 1–2 cm) are created when the uptake of a nutrient exceeds mass flow to the root (Barber et al., 1963). According to solubility and affinity, the shortest gradients are common for phosphate (2–3 mm), then for NH_4^+ and K^+ (3–5 mm) and longer for NO_3^- (5–20 mm) (Fig. 5) (Bray, 1954; Barber et al., 1963). Note however, that these large rhizosphere extents for P, N and K were obtained by destructive approaches and may be not supported by the visualization techniques. Within this range, depletion can be so strong that the concentration of the soluble nutrients falls close to 0 at the root surface (Fig. 5) (Gahoonia and Nielsen, 1991). The gradients have a diffusion shape similar to that of pH and ^{14}C labeled exudates (Figs. 2 and 5).

Such nutrient gradients become established within a few days – faster for low-mobility nutrients such as P and K (Jungk and Claassen, 1997). The gradient within the root hair cylinder is established within just one day, and the concentration gradient to the bulk soil evolves within 3–4 days (Jungk, 2001). Generally, the gradients are steeper for nutrients with low diffusivity and higher affinity to clays, sesquioxides, carbonates and organic matter (Barber et al., 1963) (Fig. 5). If,

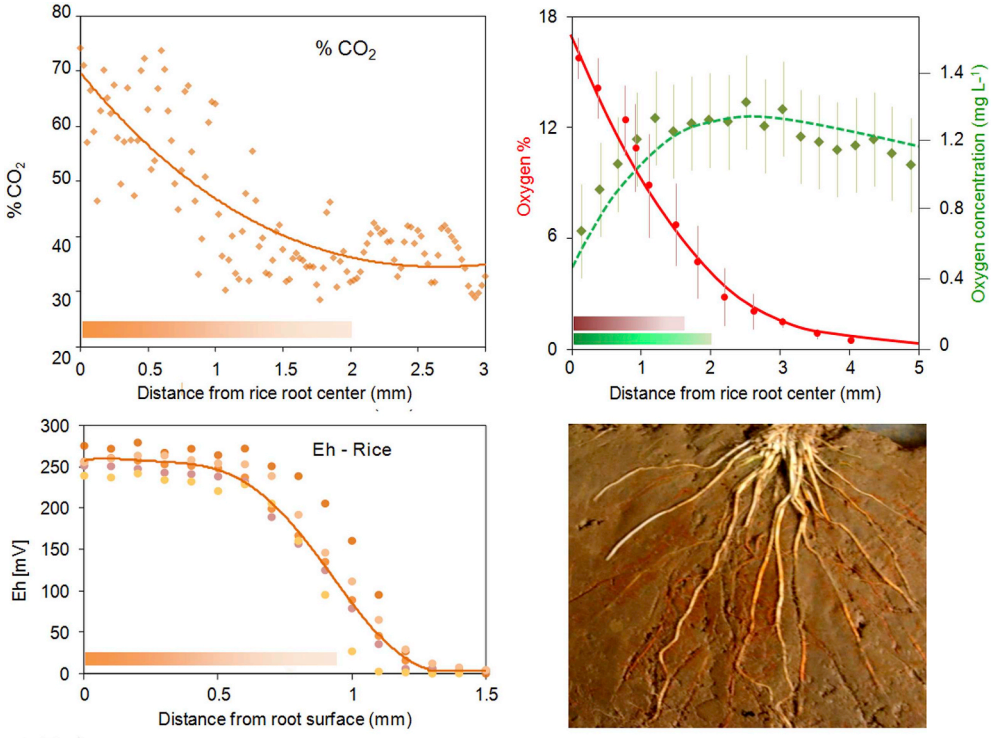

Fig. 4. Concentration gradients of gases and redox potential around the roots. Top left: CO_2 gradients around the roots of *V. juncea* (extracted from Blossfeld, 2013); Top right: O_2 gradients around the roots of maize (extracted from Rudolph-Mohr et al., 2014) and rice (extracted from Uteau et al., 2015). Bottom: Redox potential around rice root (extracted from Schmidt et al., 2011; Atulba et al., 2015) and the respective distribution of oxidized areas in rice rhizosphere (red, true color) (Courtesy of Xiaomeng Wei). The color gradient bars at the bottom show the rhizosphere extents. Note the opposite O_2 gradients to and from the roots by maize and rice. Eh values were measured by redox electrodes and recalculated by digital image analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

however, the uptake of chemicals moving to the root surface does not exceed the supply from mass flow, then those chemicals increase in concentration surrounding the root and create accumulation zones (Barber and Ozanne, 1970; York et al., 2016). For instance, because the Ca and Mg contents in many soils of arid and semiarid climates are in huge excess compared to plant demand, these elements take on a role both as nutrients and as excess or ballast elements.

3.6. Excess elements

Various excess elements (present in soil as ions: Na^+, $H_2SiO_4^{2-}$, HCO_3^-, Al^{3+}) and those nutrients that are present in the soil in excess (in arid and semiarid environments: Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}; or under anoxic conditions: Fe^{2+} and Mn^{2+}) are moved with water to the roots and precipitate in the rhizosphere. Because their uptake is lower than the mass flow, they accumulate at the root surface and build up gradients opposite to those of nutrient depletion (Fig. 5). Accordingly, the composition and concentration of excess ions is typically much higher in the rhizosphere than the bulk soil (Hinsinger et al., 2003).

Extremely high accumulations of excess elements in the rhizosphere may lead to specific phenomena such as calcified roots – rhizoliths (Fig. 5) – common in semiarid climates (Zamanian et al., 2016) or Fe^{3+} precipitation and formation of plaque around the roots in reduced environments or under changing redox conditions (Melton et al., 2014; Khan et al., 2016; Kölbl et al., 2017). Both the rhizoliths and the Fe^{3+} plaques can grow up to a few cm in diameter, leading to the formation of new pedogenic features (Fig. 5) that remain in the soil as relict rhizospheres over centuries and millennia (Zamanian et al., 2016).

3.7. Bidirectional water gradients

One of the most important functions of roots is water uptake from soil. If soil is wet and the water pressure deficit in the air is high, then water continuously flows to the root, creating gradients of water pressure and sometimes of water content (Carminati, 2012; Zarebanadkouki et al., 2012, 2013, 2014): In wet soil, the rhizosphere is drier than the surrounding soil (Fig. 6). In contrast, the rhizosphere in dry soil is wetter. This is especially pronounced during changes of water content (by drying or rewetting) and is related to the hydrophobic and hydrophilic properties of mucilage (Carminati, 2012; Zarebanadkouki et al., 2018; Ahmed et al., 2017; Young, 1995; Carminati et al., 2010; Moradi et al., 2011). Decreased porosity (Fig. S2) (and increased soil density, see below) at the root surface (rhizoplane) also increases the water content near the root surface at negative water potentials (Aravena et al., 2014). In contrast, the presence of surfactants in the mucilage can decrease the water content in the rhizosphere relative to the bulk soil (Read et al., 2003; Dunbabin et al., 2006).

The water content in the rhizosphere increases during soil drying toward the roots within 0.5–2 mm. The reverse process – rewetting – however, produces stronger gradients with a similar extent. This indirectly reflects the zone penetrated by mucilage – mainly polysaccharides (~95%) and proteins (~5%) (Bacic et al., 1986; Read et al., 2003) – released by roots into the soil to lubricate root growth and maintain the water content in the rhizosphere. Therefore, although the rhizosphere extent varies from 0.5 to 2 mm, it may increase during periods of soil moisture changes (Carminati, 2012; Carminati et al., 2010; Moradi et al., 2011; Ahmed et al., 2017; Benard et al., 2018).

The water gradients in the rhizosphere are very dynamic (Carminati, 2012). Therefore, the timing of changed conditions is crucial for best estimating the rhizosphere extent for water (Fig. 6), whether this be drying or rewetting or day/night cycles. For instance, root water uptake decreases in the evening to avoid excessive dehydration of the rhizosphere (Caldeira et al., 2014). Also, the root morphology (e.g. root hairs) or root type (e.g. seminal, crown and lateral roots) extend the water depletion zone (Segal et al., 2008; Carminati et al., 2017b; Holz et al., 2018; Ahmadi et al., 2018).

3.8. Life gradients: microbial distribution in the rhizosphere

The distribution of life in the rhizosphere is a very interesting and intriguing aspect, but the respective data are nearly absent. The previous sections and figures clearly show that microhabitat properties change across and along the roots (Schmidt et al., 2018). Accordingly, these microhabitats are occupied by microorganisms specialized for

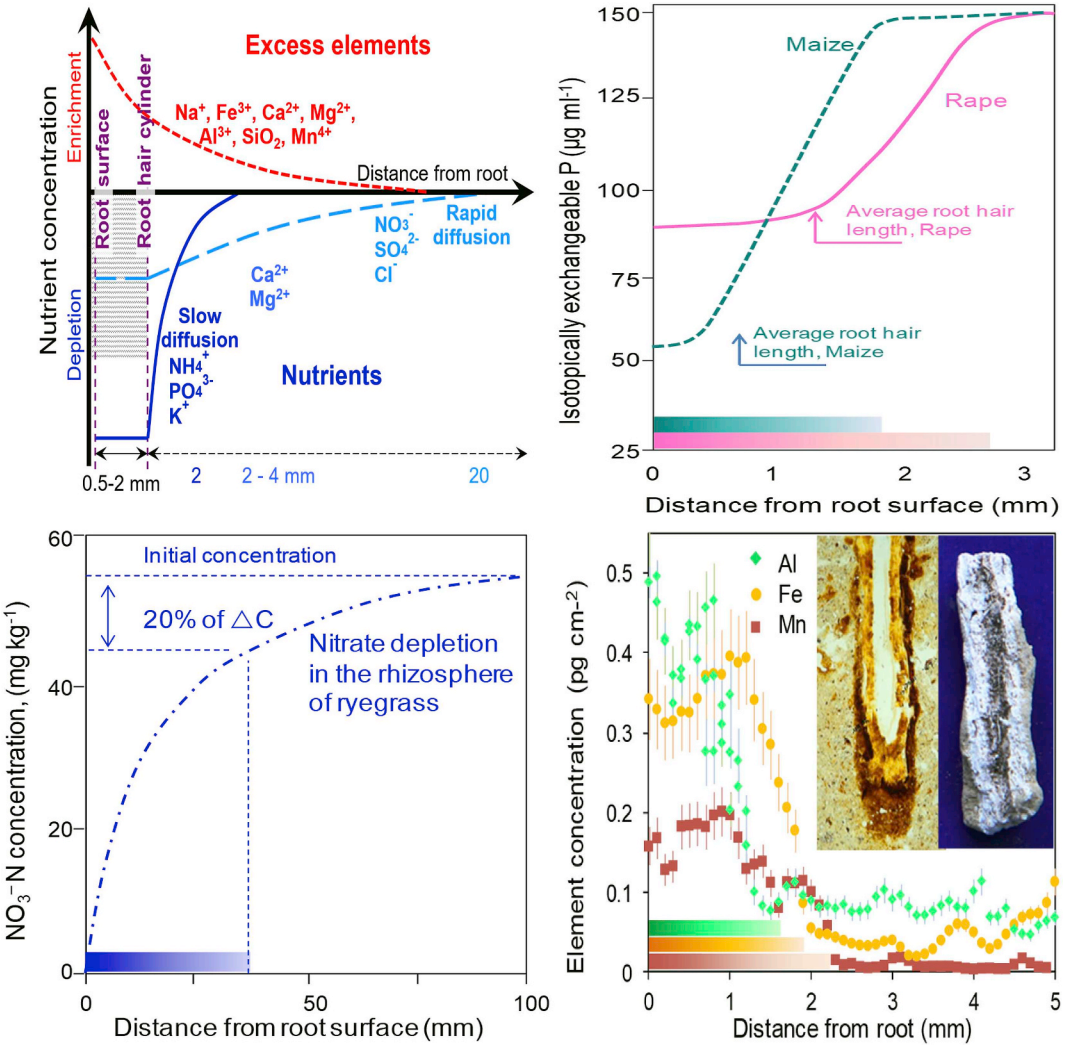

Fig. 5. Gradients of nutrients and excess elements in the rhizosphere. Top left: Generalized gradients and extents of nutrients (below the X axis, blue lines) with rapid (3–5 mm) and slow diffusion (0.5–2 mm) and of excess elements (above the X axis, red lines) from soil to root. The depletion and accumulation are presented relative to the concentration of nutrients or excess elements in the bulk soil. The periods of nutrient depletion within the root hair cylinder and in the rhizosphere correspond to ~1 and 3–4 days, respectively. The duration of excess element accumulation at the root surface strongly depends on their concentration in solution and cannot be generalized. Top right: Depletion of the isotopically exchangeable phosphate in the rhizosphere of maize and rape grown in a sandy soil. The data were obtained from scanning autoradiographs of 5-day-old root segments with a micro-densitometer (modified from Hendriks and Jungk, 1981).
Bottom left: Nitrate depletion in the rhizosphere of ryegrass grown in a sandy soil. The soil was separated from roots by a fine-meshed screen to provide for a planar soil-root interface. Only soil solution and root hairs could penetrate the screen, but not the root cylinders. After ten days, the soil was frozen, divided into thin layers parallel to the screen, and the layers separately analyzed for nitrate (modified, from Claassen and Steingrobe, 1999). The 20% of concentration difference (ΔC) are presented as an example for significant difference to the initial NO_3^- concentration in root unaffected soil to show the rhizosphere size.
Bottom right: Gradients of excess elements: Al, Fe and Mn in the rhizosphere of metal-accumulating willow and rice (data extracted from Hoefer et al., 2017; Williams et al., 2014). Although Fe and Mn are plant nutrients, their mass flow (as Fe^{2+} or Mn^{2+}) with water is frequently much higher than the root uptake. Consequently, they accumulate in excess in the rhizosphere compared to the bulk soil and form gradients. The extremely high accumulation of excess elements on the root surface (because their mass flow with water is much larger than the root uptake) is presented in the inset below. Inset left: Thin-section photography of Fe_2O_3 plaque accumulation by mass flow of Fe^{2+} with water and oxidation to Fe^{3+} and precipitation at the root surface (courtesy Dr. Otto Ehrmann, Bildarchiv Boden – Landwirtschaft – Umwelt: http://www.bildarchiv-boden.de); Inset right: Photo of rhizolith – $CaCO_3$ accumulation around the root and its calcification (courtesy of Dr. Kazem Zamanian, see also Zamanian et al., 2016). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

various niches, defined mainly by pH (Fig. 1), amounts and composition of organics (Fig. 2), as well as direct mutualistic interactions with the roots. The time for the development of microbial communities specific for individual root zones is decisive (Watt et al., 2006; Dupuy and Silk, 2015). This combination of properties and time leads to gradients of microbial groups from the root endodermis to the bulk soil (Figs. 7 and 8): endophytes/nodules – arbuscular mycorrhiza – ectomycorrhiza/rhizoplane bacteria – rhizosphere bacteria – mycorrhizal hyphae – bulk soil bacteria/fungi (Watt et al., 2006).

This life distribution (Fig. 7) is typically visualized statically – it does not reflect the niche development and occupation over time. The niches are associated with various microbial communities common for root zones because they reflect various substrate inputs and development periods. To evaluate such niche formation and their occupation, microbial growth rates must be seen in light of the root growth rates (Dupuy and Silk, 2015). The main difficulty here is that root growth (~20 mm day^{-1} corresponding to ~ 1 mm h^{-1} Watt et al., 2006) is linear, but microbial growth (averaging 0.01–0.1 h^{-1}, van Bodegom, 2007) reflects the local biomass increase. Accordingly, to establish the biogeochemical niches in the rhizosphere, the longitudinal root growth

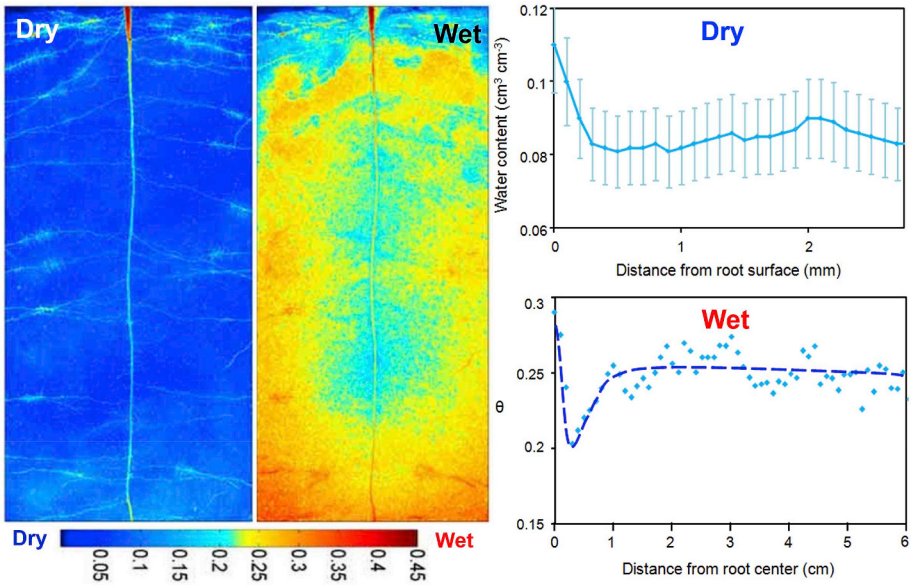

Fig. 6. Gradients of water content in soil and rhizosphere: Water content around lupine roots when soil is dry, but rhizosphere is still wet (color left) – shortly before irrigation; and shortly after irrigation when the soil is wet, but the rhizosphere still has low water content (right). The color scale reflects the volumetric water content ($cm^3\ cm^{-3}$) (courtesy Prof. Carminati; from Carminati, 2012). Note the clear hotspots of high water content (white patches) around some roots in the left color subfigure and the same hotspots with low water content in the right subfigure.
The subfigures on the left represent the water gradients from the roots calculated from the left and right color figures under dry and wet conditions, respectively. The water gradients under drought increase to the root, 2) under wet conditions – decrease to the root (from Carminati, 2012 and Rudolph-Mohr et al., 2017). The rhizosphere extent after drying is ~10 mm, but after rewetting ~0.3 mm. Note that the scales at the top subfigure are in mm and at the bottom in cm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

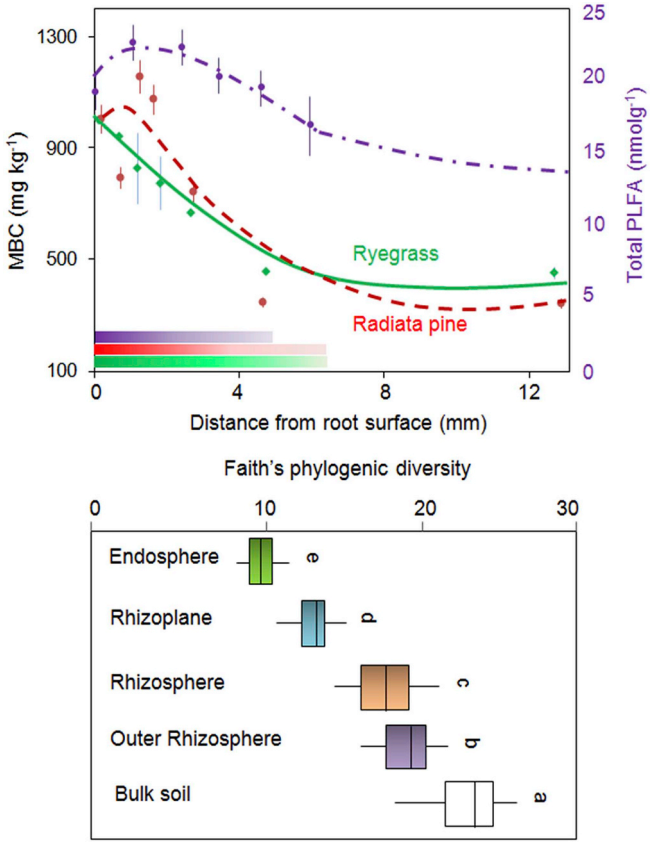

Fig. 7. Gradients of life in the rhizosphere: Top: Microbial biomass content (MBC, from Chen et al., 2002). Gradient of total PLFA in rhizosphere of *Lolium perenne* L. (from He et al., 2009, modified). Bottom: Abundances of Proteobacteria in the rhizosphere, rhizoplane, and endosphere fractions (Chen et al., 2016, modified).

must correspond to the local increase of microbial biomass in the soil volume. Bacteria may adhere to roots, and certain populations may therefore be very temporary at a given position on a root and may wash easily from that location (Silk et al., 1989; Huang et al., 1994; Watt et al., 2006).

The root development stage affects rhizosphere life as well: young root regions covered by epidermal cells have more abundant *Pseudomonas* and *Cytophaga*, whereas the older regions with abscised sheaths and cortices have much more abundant actinomyces. Root development, however, does not always change bacterial populations, and e.g. *oligotrophic* and *copiotrophic* bacteria frequently coexist in various root branches (Semenov et al., 1999). The gradients in the diversity and abundance of microbiomes have opposite trends (Fig. 8): while abundance and activity decrease from roots to the bulk soil, the diversity from roots to the bulk soil increases (Figs. 7 and 8) (Chen et al., 2016; Poole, 2017; Semenov et al., 2019). In both wheat and rice, for example, alpha diversity of the bacterial community was lowest in the root compartment (Wang et al., 2018).

Mobility of "life" in the rhizosphere is crucial for gradient formation. Some bacteria swim quickly in aqueous media. *Pseudomonas fluorescence* swims at between 1.7 and 6.0 $m\ d^{-1}$ in water (Arora and Gupta, 1993), two orders of magnitude faster than the root growth, and three orders of magnitude faster than hyphal extension (1.5–4 $mm\ d^{-1}$). Certain bacteria therefore move rapidly through water-filled spaces in the rhizosphere. Nonetheless, the motility and the true expansion rates of bacteria in the soil environment (liquid-solid interfaces) remain unknown.

The evaluation of rhizosphere size and shape are more complicated for signaling compounds, secondary metabolites and other chemo-attractants because most of them are volatile and not strongly absorbed by soil minerals. Consequently, the travel distances and concentration gradients of signaling compounds and secondary metabolites are very dynamic and depend on soil properties (e.g. organic matter content) and moisture, root release (pathogen infections) and root development (reviewed in Bowen and Rovira, 1999). Accordingly, the distance from which microorganisms are stimulated and grow or move towards a root indicates the solutes' and exudates' diffusion ranges (Huisman, 1982). These distances are determined by the densities of a fungal inoculum in the soil and on infection densities on the root. The response distances for most microorganisms are within 1 mm from the root, but *Rhizoctonia solani* can respond at 5 mm, *Gaemannomyces gramminis* at 12 mm, and VAM up to 16 mm away from the root (Huisman, 1982). *Pseudomonas putida* cells in tomato rhizosphere have a maximum communication distance of ~80 μm that is defined by the concentration of N-acyl homoserine lactone as chemoattractant (Gantner et al., 2006). Despite the crucial importance of signaling compounds for understanding root-microbial interactions in the rhizosphere, only very few studies have investigated these topics experimentally, with most of

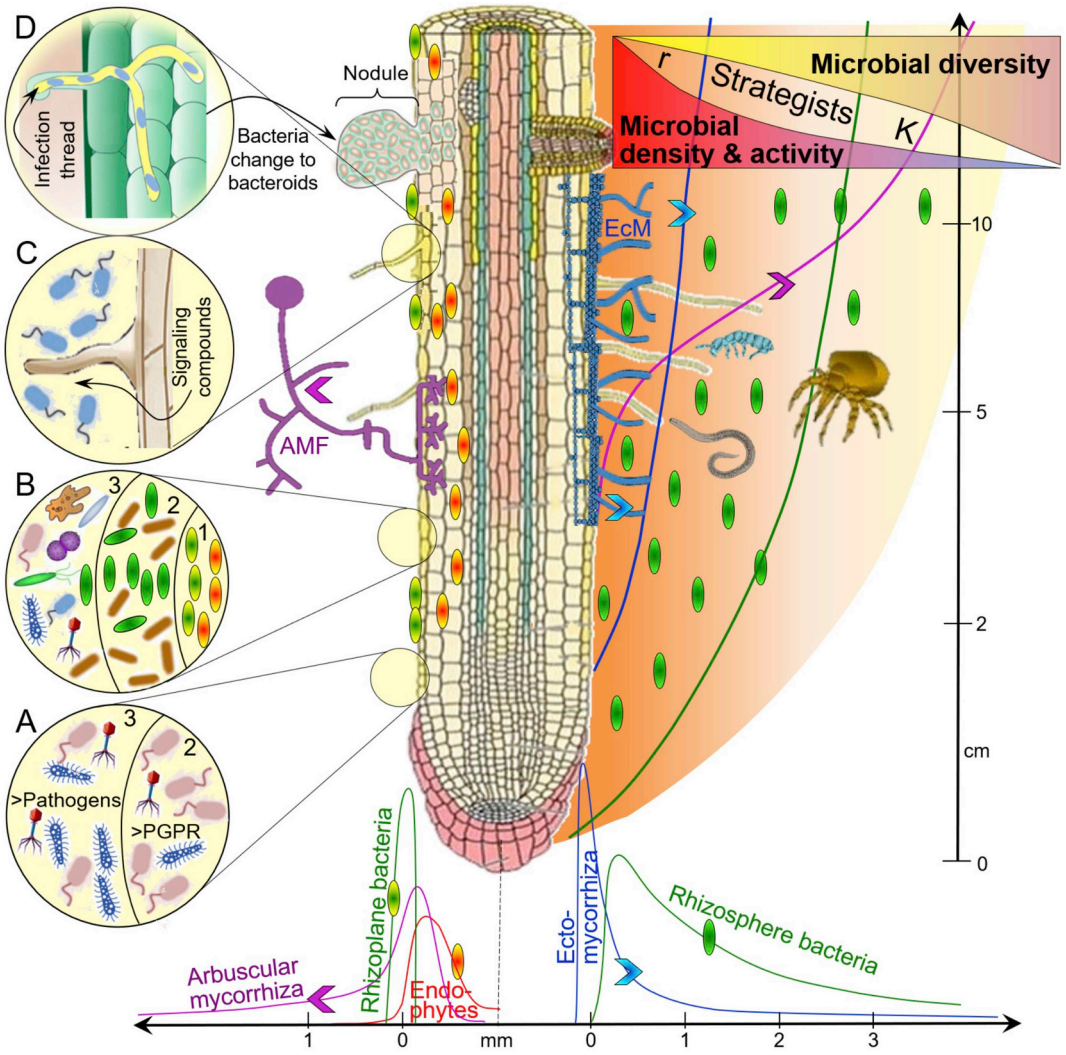

Fig. 8. Distribution of life in the rhizosphere. The abundance of various microbial groups across (X axis at the bottom, in mm from the root surface) and along (Y axis at the right, in cm, not proportional) the young root is presented by continuous color curves. Microbial groups include: Arbuscular mycorrhiza (violet, AMF) and Ectomycorrhiza (blue, EcM); Endophytic, Rhizoplane and Rhizosphere bacteria (green). The gradients of microbial density, activity and diversity, as well as the dominance of r and K strategists are presented at the top right.
The loupes magnify various processes and microbial distribution: A: higher density of plant growth promoting rhizobacteria (PGPR) compared to pathogens in 2) the rhizosphere and 3) reverse in bulk soil; B: abundance of various microbial groups 1) on rhizoplane, 2) in the rhizosphere, 3) in bulk soil; C: release of signaling compounds and attraction of rhizobia and other PGPR; D: infection of root hairs by rhizobia and formation of nodules. The numbers in the loupes reflect: 1) rhizoplane, 2) the rhizosphere, 3) bulk soil. The schematic presentation of the abundance of individual microbial groups to the left or right of the root is made solely to avoid much overlapping of the curves. The overall life density is presented with orange shading on the right. Note that the size of (micro)organisms is not proportional to their real size. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

them focused on i) bacterial cell-to-cell communication and ii) root-pathogen interactions. Compared with our understanding of the role of rhizodeposits in the communication between symbionts and plants, information on exudates that activate and attract soil born pathogens is more scarce and fragmented (Weston et al., 2012). Hence, expanding our analytical skills for rhizodeposits chemistry, their spatiotemporal production and distribution pattern, termed 'ecometabolomics' (Weston et al., 2012), will resolve the dialogues between pathogens and roots.

Similarly, only few studies have attempted to connect root zones or the distance from the root surface (i.e. the 3D picture) with microbial community structures (Silk et al., 1989; Huang et al., 1994; He et al., 2007, 2009; Chen et al., 2016; Wang et al., 2018). We found no studies on the stationarity of microbial communities in the root zones (except one in which OTU richness remained stable in the rice rhizosphere during 1.5 months of flooding, Wei et al., 2019). The data on gradients of microfauna (protozoans, nematodes), microarthropods (mites, collembolans), and macroarthropods in the rhizosphere are much rarer than those on microorganisms.

3.9. Factors affecting rhizosphere extent and shape

The distributions of the parameters described above are not fixed, and various plant, root, soil, environmental and management factors affect the rhizosphere extent, the gradients and the time necessary to reach the quasi-stationary state. Although this review is not aimed at an exhaustive analysis of these factors, they need to be mentioned (Table 2). The following conclusions on the key factors are warranted: 1) Time: The duration of root occupation of a soil volume makes all gradients steeper – from and to the root (Fig. 3). Importantly, these steeper gradients pertain to mainly the maximum or minimum values at the root surface, but the rhizosphere extent remains nearly constant (Fig. 3). 2) Root morphology: All root morphological properties – root

Table 2
Effects of soil, plant and environmental factors (columns) on rhizosphere extent for main parameters (rows)[a].

Factor[b]/Parameter[c]	pH	Exudates	Secretes	CO_2/O_2	NO_3^-	NH_4^+, K^+	P	Ca^{2+}, Mg^{2+}	Life	Enzymes	Mechanisms[d]
Soil											
- Moisture	↑	↑	↑	↓↓	↑↑	↑	↑	↑↑	↑	↑	Diffusion ↑
- Fe^{3+}, Al^{3+}	↓	↑↑			↓		↓↓↓	↓	↓		Sorption ↑
- SOM	↓	↑	↑	↓	↑	↑	↓	↓	↑	↑	Sorption ↑, Diffusion ↓
- Clay	↓	↓	↓	↓	↓	↓↓↓	↓↓	↓↓	↓		Diffusion ↓, Sorption ↑
- pH	↓	↑	↑	↓	↓	↑	↑	↑↑	↓	↓	Neutralization
- Salinity	↓	↑	↑	↓↓	↓	↓	↓↓↓	↓	↓↓	↓↓	Ion competition ↑, Osmosis ↑
- Density/Compaction	↓	↓	↓	↓↓	↓	↓	↓	↓	↓↓	↓↓	Ion competition ↑, Osmosis ↑
Plant/Root											
- Root age	↓↓	↓	↓	↑	↑	↑	↑		↑↑↑	↑↑	Process duration
- Proteolytic Roots	↓↓↓	↓↓↓	↓↓	↑↑↑	↑↑	↑↑	↑↑↑	↑	↑↑	↑↑	Process intensity
- Mycorrhiza	↓	↑	↑	↑	↑↑	↑↑	↑↑↑		↑↑↑	↑↑	
Environment[e]											
- WPD					↑	↑					Uptake ↑
- Light	↑↑	↑↑	↑	↑↑	↑↑	↑↑	↑	↑	↑↑	↑↑	Rhizodeposition ↑
- *Elevated CO_2*	↑	↑↑	↑	↑↑	↑↑	↑↑	↑↑		↑	↑↑	Rhizodeposition ↑
- *Temperature*		↓		↑	↓		↓	↓↓	↑	↑	Rhizodeposition ↓
- *N deposition*	↑↑↑	↓	↓		↓	↓	↑	↑↑	↑	↑↑	Rhizodeposition ↓

The environmental factors affecting the gradients of all parameters in the rhizosphere in the same direction: decreasing (soil porosity, etc.) or increasing (clay content) are not mentioned in the Table.

[a] Note that the Table presents the changes of the rhizosphere extents from or to the root, not the changes of processes.

[b] To correctly read the Table: Factors always increase, and the extents may ↑ increase, ↓ decrease, or ≈ remain nearly unchanged.

[c] Note that the arrows show extents changes.

[d] Only the main mechanisms are mentioned here.

[e] The factors mentioned in *italic* in Environment corresponds to the global change components.

hairs (Fig. 2), fine roots, mycorrhiza, etc. – leading to a higher release of exudates also increase the rhizosphere extent for organics, enzymes and consequently for other microbial parameters. The root hairs enlarge the rhizosphere extent (Ma et al., 2018) and, together with fine roots, increase the maximum of each property close to the root (Fig. 2). Mycorrhiza also increase the rhizosphere extent. The specific root zones crucially influence rhizosphere size and shape. Most visualization approaches clearly show that certain processes are especially intensive at the root tip (e.g. exudation: Fig. 2, enzyme activities: Fig. 3), whereas others dominate in the elongation and root hair zones (e.g. pH: Fig. 1, redox: Fig. 4, water uptake: Fig. 6). 3) Soil factors increasing sorption (contents of Fe^{3+}, Al^{3+}, SOM, clays, biochar) or uptake (microbial biomass) of organics decrease the rhizosphere extent, causing steeper gradients. 4) Soil moisture: Increasing soil moisture increases the rhizosphere extent of all parameters (except gases), mainly because of faster diffusion from/to the root surface. 5) Environmental parameters: All environmental parameters (light, elevated CO_2, temperature, etc.) that intensify rhizodeposition and especially exudation increase the rhizosphere extent for organics, enzymes and nutrients. Light promotes photosynthesis and may affect pH changes of more than 2.5 units even during a single day, leading to a diurnal acidity pattern (Rao et al., 2002a). 6) Temperature stimulates microbial activity and membrane permeability of root cells, accelerating exudation and enlarging the rhizosphere for CO_2 and enzyme activities (Razavi et al., 2019). Despite the effects of root/plants, soil and environmental factors on various processes, we conclude that most of them make the gradients steeper, but the rhizosphere extent remains nearly constant. Beyond the abiotic factors affecting such gradients (see above) (Whalley et al., 2005; Daly et al., 2015; Naveed et al., 2018), the roots themselves structure the environment. Plants modify the local soil environment in the rhizosphere very early during root growth (Helliwell et al., 2019) and influence the pore structure at the root–soil interface by root hairs (Koebernick et al., 2014, 2019). Thus, roots structure not only the entire range of biotic and chemical parameters, but also the physical environment. This is clearly demonstrated by the increased soil porosity around roots (Fig. S2). Decreased porosity (Fig. S2) and increased soil density (see below) directly at the root surface (rhizoplane) also increase the water content near the root surface at negative water potentials (Aravena et al., 2014). Growing roots increase the soil density in the rhizoplane to improve water uptake and decrease porosity in the rhizosphere for better water flow. Soils with contrasting textures are variously deformed by roots, depending on the initial bulk density and plant species. X-ray microtomography of loam sandy and clay loamy soils showed an increase in porosity adjacent to the roots of pea, tomato and wheat, but this increase was independent of root diameter (Helliwell et al., 2019). A porosity increase by 5–15% of the soil volume leads to a much faster diffusion of gases as well as of water with dissolved nutrients and exudates. This broadens the rhizosphere extent.

4. Synthesis

4.1. Comparison of destructive and non-destructive approaches

The rhizosphere extent depends not only on the specific parameters, but also on the resolution of the methods. This calls for comparing the two major groups of approaches: i) destructive approaches – mainly soil slicing, and ii) non-destructive approaches – mainly *in situ* visualization. Destructive methods (Helal and Sauerbeck, 1981; Tarafdar and Jungk, 1987; Youssef and Chino, 1987, 1988, 1989; Sauer et al., 2006; Marschner et al., 2012; Kuzyakov et al., 2003; zu Schweinsberg-Mickan et al., 2010) showed a (much) larger rhizosphere extent for all parameters compared to *in situ* visualizations (Römheld, 1986; Gahoonia and Nielsen, 1991; Fischer and Schaller, 1980; Blossfeld et al., 2011; Carminati, 2012; Zarebanadkouki et al., 2012; Schreiber et al., 2012; Rudolph et al., 2013; Razavi et al., 2016, 2017; Fresno et al., 2017). This was opposite to our own expectation that *in situ* methods would show at least similar and probably larger rhizosphere extents. We have only one straightforward explanation for this phenomenon: the experimental pots used for most destructive approaches produce a large root mat (Sauer et al., 2006; Hafner et al., 2014). Consequently, fluxes from and to the root mat are ongoing in parallel and are actually one-dimensional. In contrast, the fluxes from individual roots (common for

all *in situ* visualization approaches) are radial, i.e., two-dimensional. This means that the flux from (or to) an individual root will be diluted according to the distance to the power of two (or power of three at the root tip) by surrounding soil, making it negligible already after a few mm. This confirms that *in situ* visualization approaches reflect the real rhizosphere state and processes more correctly than the destructive approaches.

In contrast to the rhizosphere extent, the relative increase of maxima measured by destructive approaches is less than that by *in situ* visualization. This is because the latter reflects the ongoing processes, whereas the former stops most processes that maintain the gradients. Accordingly, the subsequent analyses measure gradients that are already partly dampened by ongoing diffusion, microbial C utilization, H^+ neutralization, etc.

The difference between destructive and non-destructive approaches increases as the maximal rhizosphere extent is reduced. This means that differences between the approaches are greatest for the parameters with the narrowest rhizosphere. Consequently, *in situ* visualization methods are especially important for revealing the localized soil parameters very close to the root surface. Based on these methodological differences, we recommend estimating rhizosphere extent and shape by non-destructive visualization approaches where possible.

4.2. Grouping of parameters based on their rhizosphere extent and shape

All the gradients, rhizosphere extents and shapes of the parameters described above can be summarized into a few groups according to: 1) direction of the flow: to or from the root (Table 1), 2) increase or decrease toward the root, corresponding to the accumulation or depletion in the rhizosphere, respectively, and 3) the shape of the curve: diffusion (D) curve or sigmoidal (S) curve. Figs. 9 and 10 summarize these properties for most of the main parameters and macronutrients (Fig. 9, left), and separately for micronutrients and toxic elements (Fig. 9, top right), and enzymes (Fig. 9, bottom right).

Even though the reviewed studies applied a broad range of approaches (only the results of non-destructive approaches were considered here) and involved various soils and plants, all parameters can be subdivided into three groups according to the rhizosphere extent (Fig. 10): 1) The minimal extents are common for micronutrients and heavy metals, i.e., typically 0.5 mm and not exceeding 1.0 mm (Fig. 9 top right). The fluxes are directed to the root and lead to depletion of the element concentration according D or S curves. 2) Most of the parameters exhibit a rhizosphere extent between 2 and 4 mm (Fig. 9). Most enzymes also belong to this group despite negligible diffusion (Fig. 9). 3) Only very few parameters have rhizosphere extents > 4 mm. This group encompasses: gases (Figs. 9 and 10), electrical conductivity,

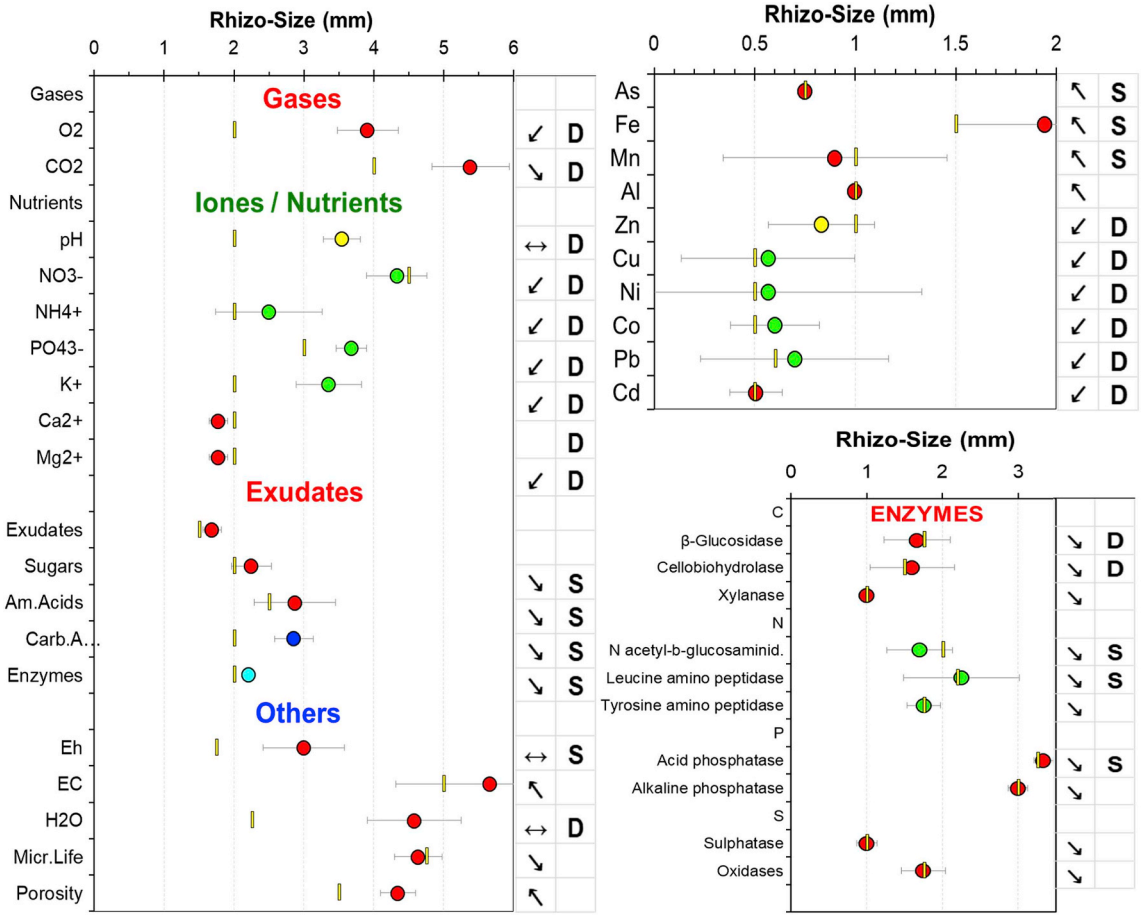

Fig. 9. Summary of rhizosphere extents and gradients for the most frequently investigated parameters. Left: Main parameters: Gases (O_2, CO_2), Ions and Nutrients (H^+, NH_4^+, NO_3^-, PO_4^{3-}, K^+, Ca^{2+}, Mg^{2+}), Root exudates (sugars, amino acids, carboxylic acids and enzymes), and other parameters (Eh, Electrical conductivity, H_2O content, Microbial life, Soil porosity). Top right: Micronutrients, excess elements (Fe^{3+}, Mn^{4+}, Al^{3+}) and heavy metals. Bottom right: Activities of enzymes responsible for C, N, P and S cycles. Circles and whiskers reflect the mean ± SE. Vertical dashes indicate the median. The closer the median is to the mean, the higher the probability that the distribution is normal. All parameters were calculated based on at least 3 measurements. The points, whiskers and dashes for an individual group of parameters were calculated based on all values of all parameters belonging to that group. Arrows on right of each Figure reflect the direction of flux: ↗: flux from the root with increasing concentration (or activity), ↘: from the root decreasing concentration, ↖: flux to the root with increasing concentration, ↙: to the root with decreasing concentration. **D** or **S** reflects the shape of the gradient curve: **D**iffusion curve or **S**igmoidal curve, respectively. Note that the presented summary does not reflect the whole complex of processes leading to gradient establishment.

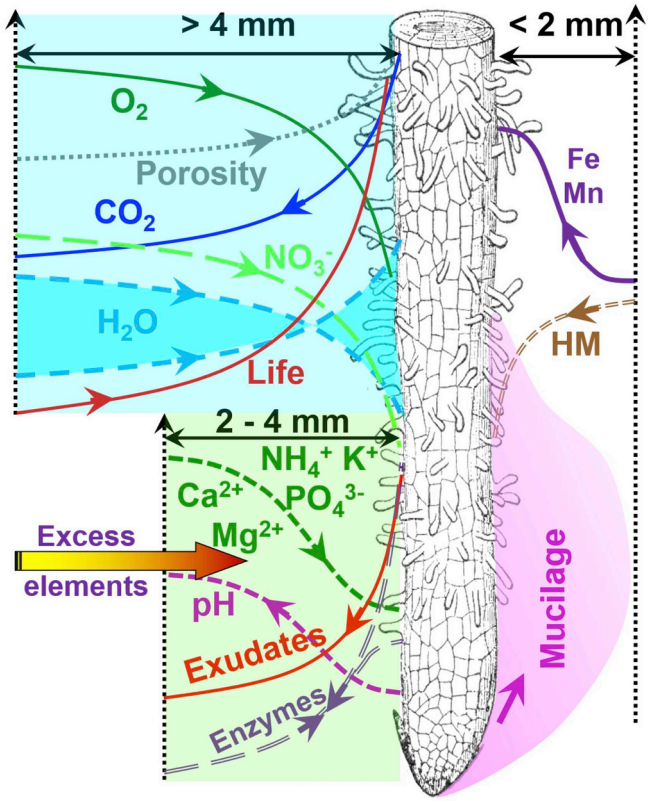

Fig. 10. Generalization of rhizosphere extents and gradient types for the most investigated parameters: Gases, Root exudates, Nutrients and Excess elements, pH and Eh, Enzyme activities and microorganisms (Life). Three groups of rhizosphere extents were typical: 0.5–2 mm (right), 2–4 mm (left bottom), and > 4 mm (left top). The shapes of the curves reflect the "diffusion" (D) or "sigmoidal" (S) gradients (compare Fig. 9). Despite the dynamic nature of each parameter, these gradients are quasi-stationary because of opposite directions of their formation processes. HM: heavy metals (Zn, Cu, Ni, Co, Pb, Cd, As).

Eh (Fig. 9), water content (Fig. 9), and the gradients of microorganisms (Fig. 9). Importantly, the rhizosphere extent of microorganisms exceeds the distance of root exudates by nearly two times. Thus, the rhizosphere effect on microorganisms is larger than the measured distance of exudate concentration, enabling some organic compounds to reach up to 4–5 mm before they are trapped by microbial cells.

4.3. Stationarity of the rhizosphere

In comparing the data from many studies focused on the same parameters, we were surprised about the agreement in the rhizosphere ranges (Fig. 10) and in the shape of the gradient curves, which were nearly independent of plant species or soil conditions. This allows an important conclusion: Despite the very high dynamics of root growth, of water fluxes with nutrients and exudates, of microbial growth etc., *the shape of individual parameters in the rhizosphere is stable – it is quasi-stationary*. Despite a broad number of factors affecting the gradients (Table 2), most of them affect the concentration maximum or minimum at the root surface, but not the rhizosphere extent and not its shape. This reflects the outcome of competitive processes: release by roots, diffusion, root uptake, microbial uptake, sorption/desorption, precipitation (Table 3). The dominance of these processes can be easily recognized based on the nature of each property and the diffusion or sigmoidal curve. We conclude that, despite the dynamic nature of each parameter, these gradients are quasi-stationary because of opposing formation processes. In most cases, only 2 main processes determine the rhizosphere extent and the shape for individual parameters.

More precisely estimating the process parameters for specific soil conditions and root characteristics will be a research topic in the future and is expected to provide important inputs for modeling. Should this quasi-stationary state be confirmed in further – more detailed – studies, the rhizosphere extent can be clearly defined for various parameters and can be used in further applications, e.g. extrapolations considering root architecture (Downie et al., 2015), modeling, assessment of the soil volume occupied by roots, stocks of nutrients potentially available for plants, etc.

4.4. Future research directions

The future experimental research directions are multi-facetted, and include developing new and optimizing existing methods, analyzing new rhizosphere properties, coupling various parameters, site-specific sampling, effects of various new factors crucial for root development and rhizosphere properties, and finally assessing the ecological relevance. Despite the broad range of available *in situ* visualization approaches (Oburger and Schmidt, 2016), many of them have significant limitations in sensitivity, spatial and temporal resolution, and applicability. Importantly, nearly all visualization approaches started to be developed just a few years ago (except imaging of radioisotopes – autoradiography, which has already been applied for > 40 years for rhizosphere research, Claassen et al., 1981). A key prerequisite for the future development of all visualization approaches is that their spatial resolution should be at least 3–5 times (preferably one order of magnitude) smaller that the gradients to be investigated. Assuming a rhizosphere extent of 2 mm (Figs. 8 and 9), visualization methods having a resolution of < 0.2 mm across a total image size of at least a few cm (the size of small roots) are desirable. Most of the methodologies presented in this review do not have this resolution (> 100:1).

The development of visualization methods that are especially focused on rhizodeposition components is very desirable. Despite significant progress in the analysis of exudates, secretions, mucilage, sloughed-off cells, etc., no suitable approaches allow them to be visualized at the rhizosphere level. Even ^{14}C imaging, well suited to localizing organic substances, enables only hypothetical separation based on the very weak assumption that individual groups of rhizosphere compounds will be subsequently released with increasing time after ^{14}C allocation into the roots (Oburger et al., 2018). The major future challenge is to adapt and optimize the methods for the broad range of soil conditions, especially for their physical structures. This challenge includes improving the resolution of all methods to accommodate the roughness of the soil surface on rhizotron windows and the contact between the sensor and the soil (Bais et al., 2006).

Another direction of future studies should focus on combining various properties characterizing the same roots. This will be a crucial step in understanding rhizosphere processes and determining how the micro-cycles of nutrients are coupled with C, water fluxes with nutrients, microbial community structure with rhizodeposition and enzyme activities, as well as rhizodeposition release with its decomposition (O_2 consumption and CO_2 production).

The switch from pure 2D mapping to 3D visualization and localization, and even tracing the dynamics (4D) of properties (Downie et al., 2015) will become a crucial and fascinating step in understanding of rhizosphere processes, their sequence and interactions (Baveye et al., 2018). Methods need to be developed to produce 3D maps of soil properties based on spatial sequences of 2D maps, e.g. based on the regression trees and ordinary kriging (Hapca et al., 2015) or other spatial correlation approaches (Kravchenko et al., 2019).

The most limiting (nearly absent) data are the life gradients: microbial community structure and functions across and along the roots. Most studies sampling the rhizosphere and root-free (bulk) soil do not capture microbial successions during root growth or community composition and functions at the level of microhabitats common in the rhizosphere. As the rhizosphere forms gradients of microbial communities to the root-free soil, we can expect that microbial predators and

Table 3
Main mechanisms responsible for the distribution and gradients of various parameters in the rhizosphere.

Property	R[a] release	R uptake	Diffusion	Mass flow	Micr uptake	Sorption	Desorption	Precipitation	Other
Gases									
- O_2		+ + +	+ + +		+ + +				
- CO_2	+ + +		+ + +						
pH (H^+)	+ + +	+	+ + +						Neutralization
Redox	+		+			+			e^- acceptors
EC/ions		+ +	+ +	+ + +					
H_2O		+ + +	+	+ + +					
Exudates	+ + +	+	+ + +	+ +	+ + +	+	+	+	Mineralization
Enzymes	+ + +		+		+ +	+ +			Mineralization
Nutrients		+ + +	+ +	+ +			+ +		
- NO_3^-		+ + +	+	+ + +	+ +				
- NH_4^+		+ + +	+ +	+	+ +	+ +			
- PO_4^{3-}		+ + +	+ + +	+	+	+ + +	+	+ + +	
- K^+		+ +	+ +	+		+ +			
- Ca^{2+}		+	+	+ +		+		+ + +	
- Mg^{2+}		+ +	+ +	+ +		+		+	
- SO_4^{2-}		+ +	+ +	+		+		+	
MicroNutr.		+ + +	+ + +	+		+ +			
Ballast elements		+	+	+ + +					
- Ca^{2+}		+		+ + +				+ + +	
- $Fe^{2+/3+}$				+ + +		+ +		+ +	Oxidation
- Si		+	+	+ +				+ +	
- Al^{3+}				+				+	
- $Mn^{2+/4+}$				+					Oxidation
Microorganisms				+					Growth, (motility)

The number of + corresponds to the relative importance of individual processes for specific properties.
[a] R means root.

other enemies (e.g. viruses) follow these gradients. The above-mentioned site-specific sampling would shed first light on this aspect of life in the rhizosphere.

Process visualization in the rhizosphere goes beyond providing satisfying images, to achieve a better understanding of ongoing interactions. It should also be used in site-specific micro-sampling to enable much more detailed analyses with destructive methods. This would allow the application of physico-chemical and molecular biology approaches to identify the properties, functions and interactions in hotspots.

This review focused solely on the rhizosphere. Roots, however, also grow to or in other hotspots, e.g. into the detritusphere (due to the abundant nutrients released by litter decomposition) or biopores (because of the much lower impedance and fast transfer of available water and nutrients from the subsoil, Athmann et al., 2017). The mechanisms and consequences of such hotspot interactions are completely unknown and their effects on gradients need to be investigated.

Currently, the effects of factors affecting the rhizosphere extent (Table 2) are qualitative and mainly based on educated guesses. Future studies should specify and quantify these effects and identify which of these effects are more important in developing rhizosphere management strategies.

Among the important applied questions that can be addressed based on rhizosphere size and shape is the amount of available nutrients. Another key aspect is assessing when and how the rhizospheres of two (or more) roots start to overlap (Jungk, 2001). Despite the many studies on root architecture and nutrient gradients, these two issues have been very seldom linked to predict the resource (nutrients, water) stocks available for roots (Ahmed et al., 2015). For instance, recent development of root growth visualization by using Synchrotron Radiation X-ray Tomographic Microscopy (SRXTM) uncovered the three-dimensional interactions of root hairs (Keyes et al., 2013). Methods for imaging nutrient uptake by root hairs growing in real soils are absent (Keyes et al., 2013). Linking root architecture and rhizosphere gradients would be a step forward in helping plant breeders to develop varieties exhibiting expanded rhizospheres with a branched architecture.

5. Conclusions and relevance

Based on a critical evaluation of studies analyzing the effects of growing roots on the characteristics and functions in the surrounding soil, we calculated the extent of the rhizosphere and presented the shape and gradients of the key parameters: gases, water, macro- and micro-nutrients, organic substances, enzymes, redox potential, and microbial life (Figs. 9 and 10). All gradients were formed by two (seldom more) main oppositely directed processes (Tables 1 and 3): release or uptake by roots, and utilization by microorganisms or precipitation and sorption on clay minerals and sesquioxides (Bray, 1954; Barber et al., 1963). All curve shapes are either diffusion (D) or sigmoid (S) types, but more than one process is always responsible for the gradients of all parameters in the rhizosphere (Table 3).

Generalizing, the spatial stationarity of each property gradient is reached at least after a few days and sometimes within hours – despite the high temporal dynamics of the parameters in the rhizosphere related to root growth and aging, and despite the interactions of various processes (Hinsinger et al., 2003; Watt et al., 2006; York et al., 2016). This means that, after occupying a new soil volume, roots immediately structure the local microenvironment, which then remains stable (*quasi steady state*). Roots can therefore be interpreted as ecosystem engineers that optimize their habitat for better growth under specific soil conditions.

The stability of the gradients in the rhizosphere is fundamentally relevant.

1) Roots structure the environment to optimize their functioning (water and nutrient uptake), to establish habitats for

microorganisms and their activities, e.g. for nutrient mobilization, to attract and stimulate root-growth-promoting bacteria and mycorrhiza, to protect against pathogens, and probably to mediate kin recognition and cooperation with neighboring roots and plants to reduce wasteful competition (Semchenko et al., 2014). For instance, exudates transport information about plant identity (kinship, species and community origin) and trigger behavior changes such as increased cooperation with relatives and competition with non-relatives. Such cooperation can be identified by roots showing less competitive traits like reduced branching or specific root length (Semchenko et al., 2014). 2) The rhizosphere size enables calculating the maximal root density in a soil layer at which the competition between individual roots is absent or minimal (Jungk, 2001). This helps optimize plant density, irrigation and fertilization by considering the belowground competition between individual roots and rhizosphere size.

3) Knowledge about the extent and shape of the rhizosphere simplifies calculating the soil volume of potentially available nutrients (and other parameters). Multiplying the root length by the integrated gradient of each nutrient (assuming the same gradient in all radial directions in soil) will yield the total amount of nutrients available for crops. This approach works well for nutrients with slow diffusion (P, K) (Fusseder and Kraus, 1986) and can be used when fertilizing with macro-nutrients to optimize the N, P, K, S, Ca, Mg stoichiometry of crops. Importantly, this effort will be based not on the nutrient amounts available in the total soil but those present in the rhizosphere.
4) Assuming similar (not identical) nutrient gradients of various plants (Jungk, 2001), the selection of crops with better nutrient uptake and acquisition should focus mainly on improving root architecture and the characteristics enlarging the rhizosphere: more roots, especially fine roots or roots with long hairs (Silk et al., 1989; Huang et al., 1994; Watt et al., 2003). Consequently, the efficiency of intercropping can be optimized if the rhizosphere extents do not overlap between two or more species and if maximal niche differentiation is attained.
5) Analysis of physical and chemical properties should be combined with simultaneous measurements of biological properties and functions, along with their dynamics. This will allow, for the first time, linking rhizosphere habitats with their occupation by microbial communities and their specific functioning as related to the recycling of C and nutrients between plants and microorganisms.
6) Determining the correspondence of the rhizosphere extent and shape for various parameters can help to understand their interactions. For example, the correspondence of the rhizosphere shape for enzymes with that of microorganisms reflects the proportion of enzymes produced microbially versus released by roots. Furthermore, the correspondence of rhizosphere shape for nutrients with that of the specific enzymes can reflect what portion of the nutrients will be mobilized from organic matter. Similarly, the overlapping of nutrients with pH reflects the area of nutrient acquisition from mineral forms.
7) The density gradients of life (e.g. bacteria, fungi) and of soil biochemical properties will help identify safe zones protecting from pathogen invasion. Microbial abundance on the rhizoplane and in the rhizosphere influence nutrient availability either i) through direct competition for nutrients between microorganisms and the root, or ii) via the microbial decomposition of nutrient-mobilizing exudates and enzymes.

These insights yield the first generally valid conclusions about the extent and shape of the most important hotspot in the soil – the rhizosphere.

Acknowledgements

We would like to acknowledge the work carried out by the researchers whose published data were included in this study. YK is very thankful for the long-term support by Deutsche Forschungsgemeinschaft (DFG) within various rhizosphere projects investigating belowground C allocation by plants, root–microbial interactions, rhizodeposition and microbial transformation of rhizodeposits. BR is thankful to her spiritual supporter: Ali Feizi and gratefully acknowledge the DFG for supporting the project: RA3062/3-1 within priority program 2089 and highlighted importance of imaging approach to overcome current knowledge gap between soil, microbiome and plant scientists. We thank two anonymous reviewers for their critical but very constructive comments, Dr. Søren O. Petersen for the final suggestions and improvements, and Dr. Kyle Mason-Jones for the improvement of language and writing style.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.05.011.

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