Tansley review

Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance

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Key words: carbon (C) and nitrogen (N) turnover, competition for nitrogen (N) and phosphorus (P), mutualism, niche differentiation, nutrient acquisition, plant–microbe interactions, priming effect, rhizosphere ecology.

Summary

Demand of all living organisms on the same nutrients forms the basis for interspecific competition between plants and microorganisms in soils. This competition is especially strong in the rhizosphere. To evaluate competitive and mutualistic interactions between plants and microorganisms and to analyse ecological consequences of these interactions, we analysed 424 data pairs from 41 ^{15}N-labelling studies that investigated ^{15}N redistribution between roots and microorganisms. Calculated Michaelis–Menten kinetics based on K_m (Michaelis constant) and V_{max} (maximum uptake capacity) values from 77 studies on the uptake of nitrate, ammonia, and amino acids by roots and microorganisms clearly showed that, shortly after nitrogen (N) mobilization from soil organic matter and litter, microorganisms take up most N. Lower K_m values of microorganisms suggest that they are especially efficient at low N concentrations, but can also acquire more N at higher N concentrations (V_{max}) compared with roots. Because of the unidirectional flow of nutrients from soil to roots, plants are the winners for N acquisition in the long run. Therefore, despite strong competition between roots and microorganisms for N, a temporal niche differentiation reflecting their generation times leads to mutualistic relationships in the rhizosphere. This temporal niche differentiation is highly relevant ecologically because it: protects ecosystems from N losses by leaching during periods of slow or no root uptake; continuously provides roots with available N according to plant demand; and contributes to the evolutionary development of mutualistic interactions between roots and microorganisms.

I. Introduction

All living organisms require nearly the same nutrients for their maintenance, growth, and reproduction. This forms the basis for interspecific competition between plants and microorganisms in nutrient-limited soils. This competition for available nutrients is particularly strong in the rhizosphere because of at least three factors.

First, plants and microorganisms in all soils (except soil types such as Phaeozems, Chernozems, and some Fluvisols) are limited by at least some nutrients, mainly nitrogen (N) and phosphorus (P) and certain other macro- and microelements. For soils in humid climates, this limitation is mainly ascribed to annual nutrient leaching (Lehmann & Schroth, 2003). Soils of semiarid and arid regions are not subjected to intensive chemical weathering, eliminating or reducing nutrient release from primary minerals. By contrast, in both tropical and wet subtropical soils that have very high weathering rates, only a few nutrients are present in the deeply weathered parent materials. Additionally, the remaining iron (Fe) and aluminium (Al) oxides bind nutrients occurring in anionic forms (e.g. P and molybdenum (Mo)) and render them unavailable for plants and microorganisms (Barber, 1996).

Secondly, continuous nutrient uptake by plants leads to the development of strong depletion zones around the roots (Fusseder & Kraus, 1986; cited after Jungk, 2001). Within 1–3 mm from the root surface, the concentration of nutrients that diffuse slowly, such as P, might decrease by *c.* 5–10 times compared with that in the nonrhizosphere soil (Tinker & Nye, 2000; Jones *et al.*, 2004). On the other hand, mobile nutrients in soil solution, such as NO_3^-, do not develop strong depletion zones around roots; however, their concentration decreases extremely rapidly as a result of root uptake (Tinker & Nye, 2000). By contrast, NH_4^+ develops strong depletion zones around roots because it is not very mobile (Orcutt & Nilsen, 2000).

A third factor contributing to an increased competition is the release of large amounts of easily available carbon (C) into the rhizosphere (Kuzyakov & Domanski, 2000; Nguyen, 2003). This available C leads to an increase in the abundance (Newman & Watson, 1977; Lynch, 1990; Kapoor & Mukerji, 2006; Saharan & Nehra, 2011), activity, and growth of microorganisms in the rhizosphere (Oger *et al.*, 2004; Blagodatskaya *et al.*, 2009, 2010), and consequently depletes the remaining available nutrients by microbial uptake and immobilization (Zak *et al.*, 2000).

Because of these three factors, particularly the last two, nutrient limitation for roots and microorganisms in the rhizosphere is far greater than that in the nonrhizosphere soil; this leads to strong competition between roots and microorganisms for nutrients.

II. General solution: trade of C for nutrients

Despite this competition, microorganisms and roots depend on each other and have developed various mechanisms for symbiotic coexistence. One of the most well known, and probably the best investigated, mechanisms is the fixation of atmospheric N_2 by rhizobia and *Frankia*, which occurs on the basis of the C and energy provided by the roots of legumes and nonlegumes (Newton *et al.*, 2008; Franche *et al.*, 2009). The other is the development of mycorrhizal fungi on the root surface (ectomycorrhizas) or within the roots (e.g. ericoid and arbuscular mycorrhizas) with highly proliferating hyphae that penetrate into small pores and develop an all-embracing network (Read & Perez-Moreno, 2003; Southworth *et al.*, 2005; Simard *et al.*, 2012). This allows intensive acquisition of nutrients from a considerably larger soil volume. Additionally, mycorrhizal fungi substantially enhance N acquisition by plants from organic sources (Hodge & Fitter, 2010; Talbot & Treseder, 2010; Whiteside *et al.*, 2012). The two above-mentioned examples (rhizobacteria and mycorrhizas), however, are based not on the competition between roots and microorganisms, but on the mutualism evolved over millions of years of co-evolution (Lambers *et al.*, 2009; Kiers *et al.*, 2010). Roots provide microorganisms with C, and in turn obtain nutrients, because these microorganisms efficiently acquire nutrients from sources that are chemically or spatially unavailable to plants.

Numerous microorganisms in the soil are growing because of the absence of easily available substrates. The easily available C released by roots stimulates microbial growth in the rhizosphere, leading to the mining of additional N from soil organic matter (SOM; Kuzyakov, 2002; Luo *et al.*, 2006), that is, the production of some extracellular enzymes and thus enhancement of subsequent SOM decomposition (German *et al.*, 2011). This increases the N content in microbial biomass, and often also in plants (Hu *et al.*, 2006). A similar situation has been observed in many studies under field (Hamilton & Frank, 2001; Finzi *et al.*, 2007) and controlled conditions (De Graaff *et al.*, 2010; Medina-Roldán & Bardgett, 2011). Therefore, three effects (i.e. mutualism, neutralism, and competition; Table 1) can be observed in the interactions between plants and microorganisms. However, thus far, it is unclear how roots and microorganisms coexist and benefit from each other, although they depend on the same nutrients and strongly compete for them, particularly in the rhizosphere.

We describe these interactions between plants and microorganisms (Table 1) and focus mainly on their mutualism and competition. As N is the main limiting element in many terrestrial ecosystems (LeBauer & Treseder, 2008) and most published studies deal with N, this review mainly describes the processes

Table 1 Interplay of positive (+), neutral (0) and negative (−) effects between plants and microorganisms (MO)

		Effects on plants		
		+	0	−
Effects on microorganisms	+	Mutualism	Commensalism	Parasitism on plant
	0	Commensalisms	Neutralism	Antagonism of plant
	−	Parasitism on MO	Antagonism of MO	Competition

related to N acquisition. Importantly, the mechanisms described for N might be similar for P and other nutrients. We hypothesize that N-cycling by microbes from SOM ultimately benefits plants, and that competitive and mutualistic interactions develop mainly on the basis of temporal and spatial niche differentiation for N acquisition when roots occupy new soil volume. To test this hypothesis, we conducted a survey of studies published since 1970, and here we suggested some of principles underlying the coexistence of roots and microorganisms in the rhizosphere.

III. Methods

Evaluating mutualisms between roots and microorganisms and their competition for nutrients requires consideration of the following three important aspects: the spatio-temporal dynamics of available nutrients in the rhizosphere; the temporal dynamics of nutrient partitioning between microorganisms and plants; and the dynamics of the fitness and competitive abilities of microorganisms and plants. These dynamics can vary markedly depending on the prevalence of competition or mutualisms (Schimel & Bennett, 2004), and depend on the time that has elapsed since the start of N uptake. Accordingly, the most valuable studies include repeated measures of N in roots and microorganisms as well as changes in N availability in soil.

1. Literature survey and data selection criteria

According to the three dynamics mentioned in the above paragraph, we selected the following parameters: Michaelis–Menten kinetics, that is, the maximal uptake rate (V_{max}) and substrate affinity (K_m) for N uptake by microorganisms and roots, as well as ^{15}N redistribution between plants and microorganisms. We searched data published since 1970 for this review in the *Web of Science*, *Google Scholar*, *CAB Abstracts*, and book series. The parameters obtained from these surveys were screened for explicit evaluation of the ecological significance of plant–microbe competition for N.

In all, we collected 118 articles for the meta-analysis reporting N uptake by both plant roots and microorganisms. Forty-two studies were screened for the V_{max} and K_m parameters of N uptake by microorganisms (Supporting Information Table S1). These parameters were differentiated on the basis of the uptake kinetics of NH_4^+, NO_3^-, and amino acids for microorganisms grown in culture or in soil. Another 35 studies were screened for the V_{max} and K_m parameters of N uptake by roots (Table S2). Furthermore, 41 ^{15}N-labelling studies were collected to analyse ^{15}N redistribution between plants and microorganisms (Table S3). Only those ^{15}N studies that simultaneously investigated ^{15}N uptake and partitioning between plants and microorganisms were included in this database.

2. Data assembly

The first database focused on microorganisms and contained 249 pairs of V_{max} and K_m values for N uptake from the 42 studies. The second database contained 436 pairs of V_{max} and K_m values for N uptake by roots from 35 studies. All plant species were classified into three functional groups: grasses, forbs, and trees (grasses are herbs, and forbs are herbs that are not grasses; Table S2). All V_{max} values from original studies were recalculated and expressed as $\mu mol\ g^{-1}\ DW\ h^{-1}$ (dry root weight used for plants and dry cell weight for microorganisms). When the values were presented for fresh weight, they were converted to dry weight using a coefficient of 0.2. All K_m values were presented in μM.

We used V_{max} and K_m parameters from the first two databases to predict the results of the competition between plants and microorganisms for N uptake. We assumed that the Michaelis–Menten functions evaluate competition outcome in a broad range of NO_3^-, NH_4^+, and amino acid concentrations, and possible chemical niche differentiation on the basis of microbial uptake of all three N forms in soil: reduced inorganic (ammonia), oxidized inorganic (nitrate), and reduced organic (amino acids). We evaluated V_{max} and K_m for microorganisms and plants and summarized them separately for the three N forms: ammonia (NH_4^+, including studies on urea); nitrate (NO_3^-); and amino-N, including mainly amino acids and also some amino sugar studies.

We assumed that these calculations overestimate the rate of plant N uptake under soil conditions because of the spatial distribution of roots in soil, as well as the considerably lower diffusion of nutrients in soil vs nutrient solution. However, to our knowledge, thus far, no approach has evaluated the extent of this overestimation.

3. ^{15}N-labelling approach

The third database was developed to evaluate ^{15}N partitioning between microorganisms and plants in order to represent their direct and ecologically relevant competition for N. This database contains 424 data pairs from 41 ^{15}N-labelling studies (Table S3) that investigated ^{15}N redistribution between plants and microorganisms across different ecosystem types (Table 2).

Adding very small amounts of ^{15}N label allows short-term evaluation of competition. Such short-term experiments reflect dynamic N uptake by roots and microorganisms, and therefore the competition in the rhizosphere over a specific growth period. Commonly, ^{15}N is added in mineral (NH_4^+ or NO_3^-) or organic (amino acids) forms. The amounts of added ^{15}N are usually very small (Biernath *et al.*, 2008; Xu *et al.*, 2011a) and, therefore, the equilibrium between the N forms remains unaffected and ^{15}N functions as a label rather than an N fertilizer. The ^{15}N label is added on the soil surface (Xu *et al.*, 2003; Littschwager *et al.*, 2010) or injected directly at a specific soil depth (Jackson *et al.*, 1989; Hart *et al.*, 1993; McKane *et al.*, 2002). This approach ensures that plants and microorganisms have equal access to the added ^{15}N.

We used the third database to evaluate the plant–microbial competition for N. This evaluation was made on the basis of the ratio of ^{15}N in microbial biomass (analysed by the extraction-fumigation approach) and in plants (including roots). Ratios of > 1 show that microorganisms outcompete roots. Additionally, the dynamics of the ^{15}N ratio in plants and microorganisms is important, because it shows the temporal changes in the acquisition of the limiting resource (Magyar *et al.*, 2007).

Most studies on root–microorganism competition have been conducted using this ^{15}N-labelling approach. We therefore

Table 2 Ecosystem types for the 41 ^{15}N-labelling studies used in this study

No.	Subtype	Vegetation	References
1	Alpine/subarctic	Shrub	Andresen *et al.* (2008)
2	*Calluna*/grasses/mosses	Heath	Andresen *et al.* (2009)
3	*Calluna*/grasses/mosses	Heath	Andresen *et al.* (2011)
4	*Acomastylis rossii*	Tundra	Ashton *et al.* (2008)
5	Temperate grassland	Grassland	Bardgett *et al.* (2003)
6	*Holcus lanatus*	Mesocoms	Barnard *et al.* (2006)
7	*Fraxinus excelsior* + *Dactylis glomerata*	Forest	Bloor *et al.* (2009)
8	*Quercus douglasii*	Forest	Cheng & Bledsoe (2004)
9	Blue oak (*Quercus douglasii*)	Forest	Cheng & Bledsoe (2005)
10	Shortgrass prairie	Grassland	Clark (1977)
11	Heath	Tundra	Clemmensen *et al.* (2008)
12	*Festuca rubra*	Grassland	Dunn *et al.* (2006)
13	Birch	Forest	Grogan & Jonasson (2003)
14	*Festuca*/*Agrostis*/*Gallium*	Grassland	Harrison *et al.* (2007)
15	Temperate grassland	Grassland	Harrison *et al.* (2008)
16	Annual grassland	Grassland	Hart *et al.* (1993)
17	*Puccinellia phryganodes*	Mash	Henry & Jefferies (2003a)
18	*Puccinellia phryganodes*	Mash	Henry & Jefferies (2003b)
19	*Lolium perenne*	Crop	Hodge *et al.* (2000b)
20	Barley	Crop	Inselsbacher *et al.* (2010)
21	Grassland	Grassland	Jackson *et al.* (1989)
22	Alpine moist meadow	Grassland	Jaeger *et al.* (1999)
23	*Atriplex parryi*	Shrub	James & Richards (2006)
24	*Carex*	Grassland	Kastovska & Santruckova (2011)
25	*Kobresia myosuroides*	Tundra	Lipson & Monson (1998)
26	Dry alpine meadow	Grassland	Lipson *et al.* (1999)
27	White spruce	Forest	McFarland *et al.* (2010)
28	*Calluna*/grasses/mosses	Heath	Miller *et al.* (2009)
29	Grass–legume	Crop	Nannipieri *et al.* (1985)
30	Acidic site	Tundra	Nordin *et al.* (2004)
31	Tussock	Tundra	Schimel & Chapin (1996)
32	Subalpine	Heath	Sorensen *et al.* (2008b)
33	Alpine/subarctic	Tundra	Sorensen *et al.* (2008a)
34	Tropical montane	Forest	Templer *et al.* (2008)
35	Pine clearcut	Shrub	Vitousek & Matson (1984)
36	Steppe	Grassland	Wu *et al.* (2011)
37	*Kobresia pygmaea*	Grassland	Xu *et al.* (2003)
38	*Kobresia pygmaea*	Grassland	Xu *et al.* (2004)
39	*Kobresia humilis*	Grassland	Xu *et al.* (2011b)
40	*Allium tricoccum*	Forest	Zak *et al.* (1990)
41	Northern hardwood forest	Forest	Zogg *et al.* (2000)

evaluated the following parameters of the competition: (1) ^{15}N allocation in plants vs ^{15}N allocation in microorganisms, and (2) the dynamics of ^{15}N distribution between plants and microorganisms over time.

IV. Interactions between roots and rhizosphere microorganisms

1. Sequence of processes for nutrient acquisition by occupation of new soil volume

The N uptake by roots is not even throughout the rooted soil volume and along the roots. The main uptake occurs in the root hair zone (Waisel *et al.*, 2002), *c.* 1–5 cm behind the root tip (Fig. 1). The zones behind the root hairs are responsible for only minimal nutrient uptake and are not considered here. Therefore, when a new soil volume is occupied, the duration of N uptake in the individual zones is limited by the passage in the root from the root tip to the root hair zone and just behind it (Clarkson, 1985; Ingestad & Ågren, 1988). The distance from the root tip to the end of the root hair zone is *c.* 1–5 cm, and roots grow from 0 to 2 cm d^{-1}. This limits the period of direct N uptake from newly occupied soil to a few days (Thaler & Pagès, 1998).

Generally, root hairs have a life span of a few days, although they may persist for longer periods, particularly in grasses (Mengel *et al.*, 2001; Gregory, 2006). During root growth, different root zones release rhizodeposits of different compositions (Fig. 1). Although roots might take up some of the released organics (mainly low-molecular-weight organics; Näsholm *et al.*, 1998, 2009; Kuzyakov & Jones, 2006; Biernath *et al.*, 2008; Hill *et al.*, 2012), a substantially greater release than uptake results in a net release. When root hairs die and lyse, this C also contributes to rhizodeposition. Most of the C released as rhizodeposition is readily available, and microorganisms use this C for growth. Microbial utilization of rhizodeposits is very fast and occurs within a few hours for exudates (Jones & Kielland, 2002; Jones *et al.*, 2005; Kuzyakov & Jones, 2006; Kemmitt *et al.*, 2008; Fischer & Kuzyakov, 2010; Fischer *et al.*, 2010) and a few days for sloughed-off cell walls and root hairs (Dormaar, 1992).

Considering these short utilization periods and the turnover time of rhizosphere microorganisms ranging from days to weeks (Staddon *et al.*, 2003; Schmidt *et al.*, 2007; Blagodatskaya *et al.*, 2011), we assume that the excess of easily available C is depleted within a few days via microbial uptake, utilization, and decomposition. This causes the microorganisms that were previously growing on the excess of substrate to starve. This absence of new C input and continuous consumption of C in the microorganisms leads to the release of N immobilized in microbial biomass into the soil. This process sequence results (Fig. 2) in the availability of N for plants.

As described in the sequence of processes involving the competition between plants and microorganisms for available N, the microorganisms stimulated by available C begin capturing N earlier than the roots (vertical arrow, right, in Fig. 2). This leads to a temporary decrease in the available N for the roots, and this N limitation in turn stimulates them to release additional C (Merckx *et al.*, 1987; Liljeroth *et al.*, 1990; Kuzyakov *et al.*, 2001). Although the mechanisms underlying the stimulation of C release by roots as a result of N limitation remain unclear, the increase in C is associated with the development of more abundant fine roots, and consequently higher rhizodeposition. Clarifying the C release by roots as a result of N limitation could significantly contribute to our understanding of mutualistic mechanisms, that is, whether they occur at the level of the root system or individual roots.

Following the uptake of root exudates, microorganisms use the C for growth and maintenance respiration. As N is limited even for microorganisms, they produce certain extracellular enzymes for the mineralization of poorly available C sources, such as SOM, to obtain N (Schimel & Weintraub, 2003; Manzoni *et al.*, 2012). These depolymerizing extracellular enzymes are glycosidases,

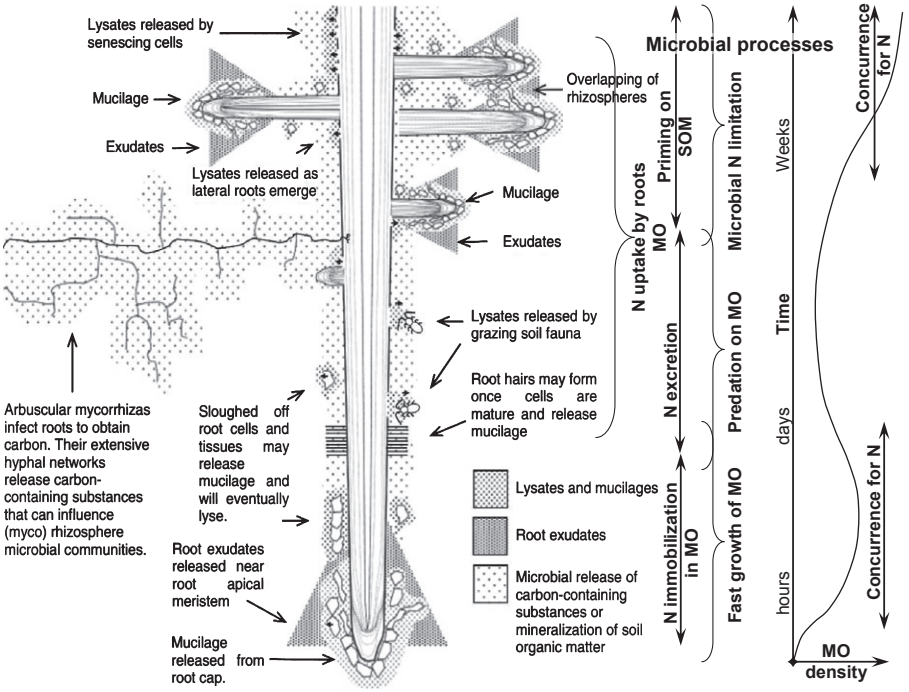

Fig. 1 Microbial processes along the growing root and released rhizodeposits. The competition for nitrogen (N) between roots and microorganisms peaks at periods of strong microbial growth. Strong root–microorganism competition for N as well as stimulation of microbial activity by easily available rhizodeposits accelerates the decomposition of soil organic matter (SOM) for additional N mineralization (real priming effect). The time line on the right represents the period after the root occupies new soil volume. The microorganism (MO) density is presented as changes compared with root-free soil. Compilation from Kuzyakov (2002) and Dennis *et al.* (2010).

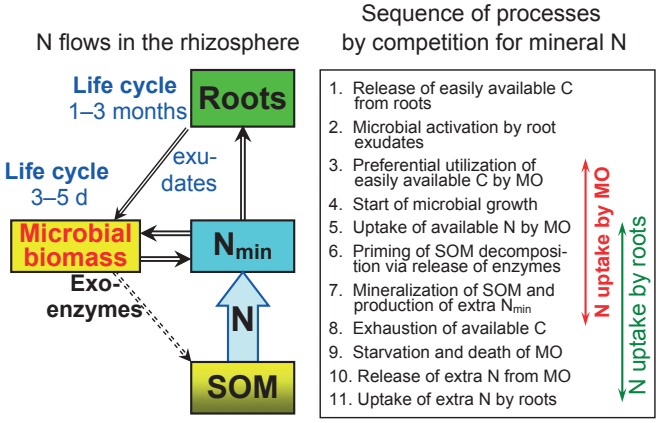

Fig. 2 Sequence of processes when ingrowing roots occupy new soil volume and during interactions between roots and microorganisms for carbon (C) and nitrogen (N) uptake. Despite the initial uptake of N mineralized from soil organic matter (SOM) by microorganisms (MO), their much shorter life cycle compared with that of plant roots leads to the release of acquired N back into the soil; this mineral N is then available for root uptake. N_{min}, mineralized N. See text for further explanation.

phenoloxidases, peroxidases, glucosaminidases, and peptidases (Blagodatskaya & Kuzyakov, 2008), which break down polymers and generate dimers and monomers that are soluble and available for microbial uptake (Hill *et al.*, 2012). Because microbial turnover in the rhizosphere is very rapid (a few days), the C losses by respiration are very high. Consequently, these microorganisms become energy-starved and obtain their energy from amino acids. Microorganisms strip off the N from the amino acids, thereby making the C skeletons available for the tricarboxylic acid (TCA) cycle for energy and growth. Finally, NH_4^+ is released as a metabolite in this process (ammonification). This form of N can be absorbed by roots. Importantly, the net N release from starving or dying microorganisms is higher than the initially available N content because of microbial mining for extra N from SOM during root growth. Clarholm (1985) suggested another mechanism of N release from microorganisms that involves microbial grazing by soil animals, and which is particularly important in the rhizosphere (described in detail by Bonkowski *et al.*, 2009).

2. Effect of time on the nutrient flow direction

Two factors contribute to the redistribution of N after its initial acquisition by microorganisms and roots (Figs 1, 2): N flow direction, and life cycle duration of rhizosphere microorganisms and plants. The N flows driven by competition between roots and microorganisms are directed to the roots (Fig. 2). Decomposition of SOM by some exoenzymes releases minerals and amino acids and some amino sugars, which can be acquired by microorganisms and, after mineralization to NH_4^+ or NO_3^-, by roots. Amino acids can also be used directly by roots, although compared with microorganisms, plant roots are often not very efficient competitors for this N source. As shown in Fig. 2, at the initial stage, microorganisms outcompete roots for inorganic N because of rapid growth rates and high surface-area-to-volume ratios compared with those of root hairs (Rosswall, 1982). Thus, even in soils with a high density of roots, for example in the upper 5 to 10 cm in grassland, most N will be allocated to microorganisms shortly after N addition or release from decomposing litter. This reduces N leaching losses as a result of the limited uptake capacity of roots.

At this stage, the second factor responsible for redistribution of N between microorganisms and roots arises: the duration of the life cycle of rhizosphere microorganisms and roots. The turnover time of the microorganisms is very short (a few days; Schmidt *et al.*, 2007) because of high C losses by respiration. In microorganisms,

the C released as CO_2 is lost, and their C:N ratio decreases. Despite this, the microbial C:N ratio is stable and ranges between 5 and 10 (average, *c.* 8; Cleveland & Liptzin, 2007). Mineral N is thus again available for microorganisms and roots. This cycle of the uptake and release of mineral N (and amino acid N) occurs within a few days according to the life cycle of the rhizosphere microorganisms.

Unlike the N flow in microorganisms, the net N flow to and in the roots is unidirectional. Despite some evidence for N rhizodeposition (Wichern *et al.*, 2008), the net N flow is directed to the roots, except in symbiotic diazotrophs. Although, in diazotrophy, the net flow of the sum of N species is directed to the roots, the minor efflux of the combined N obtained from the plant is offset by the influx of N generated during the fixation of N_2 by nodule bacteria. Therefore, roots acquire N in small portions, but more continuously and mainly unidirectionally. This leads to the continuous accumulation of N in roots and its depletion in the rhizosphere. Some of the N is involved in the synthesis of amino acids and proteins in roots, whereas another part is translocated to the shoots for further utilization. This indicates that, over long periods, plants acquire increasing amounts of N, which had already passed through a microbial cycle(s) and was initially stored in the SOM. At an ecosystem level, plants and microorganisms obtain the N as required (Kaye & Hart, 1997).

V. Potential of plants and microorganisms for N uptake by their competition

Using data collected from the literature, we calculated medians of K_m and V_{max} values separately for three groups of N species (NO_3^-, NH_4^+, and amino acids) for roots and microorganisms (Fig. 3, Tables 3, S1, S2). Despite the high variation in K_m and V_{max} values, we used these values to calculate the uptake depending on N concentration. The Michaelis–Menten uptake kinetics clearly showed that microorganisms have a higher capacity (V_{max}) for NO_3^- and NH_4^+ uptake compared with roots, across the whole concentration range. This advantage is particularly pronounced at low concentrations of mineral N (< 50–100 μM), as a small K_m indicates high affinity for NO_3^- and NH_4^+ (Table 3).

Table 3 Parameters of Michaelis–Menten kinetics: K_m (Michaelis constant) and V_{max} (maximum uptake capacity) for uptake of ammonia (NH_4^+), nitrate (NO_3^+) and amino acids by plants and microorganisms

	K_m (μM)				V_{max} (μM g^{-1} h^{-1})			
N species	Mean	± SE	Median	No.	Mean	± SE	Median	No.
Plants								
NH_4^+	289	114	64	68	37	5.9	49	68
NO_3^-	79	11	48	60	37	7.5	8.2	64
Amino acids	265	105	96	82	15	4.0	4.6	82
Microorganisms								
NH_4^+	48	20	13	59	188	86	48	7
NO_3^-	377	227	29	20	39	–	39	1
Amino acids	530	111	86	86	52	15	1.7	75

'No.' indicates the number of studies. All parameters from individual studies were recalculated for the same units.

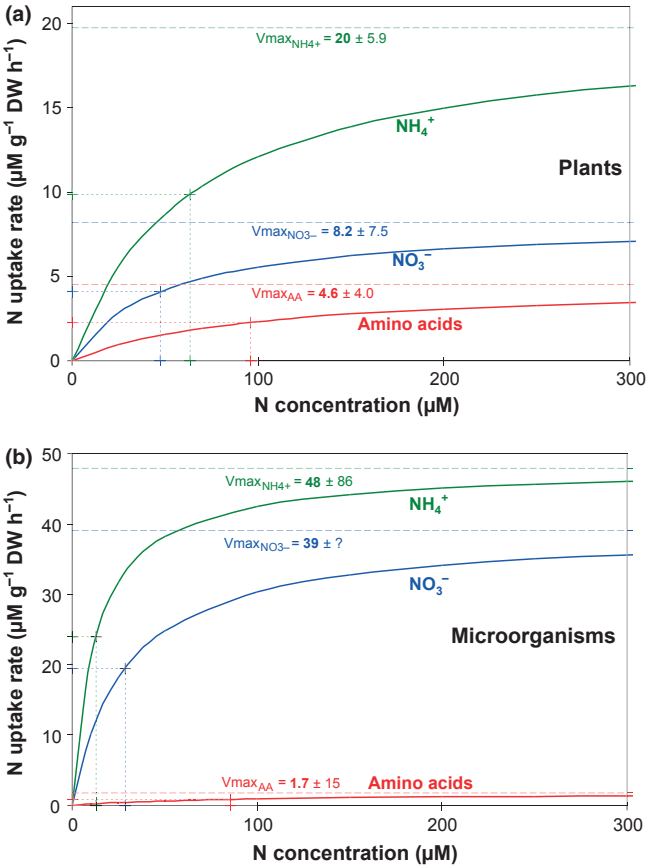

Fig. 3 Michaelis–Menten kinetics of nitrogen (N) uptake from nitrate (NO_3^-), ammonia (NH_3^-), and various amino acids (AA) by plants (a) and microorganisms (b). The lines were calculated on the basis of the medians of K_m (Michaelis constant) and V_{max} (maximum uptake capacity) values calculated from the database of studies with plants (35 studies; 436 K_m and V_{max} data points; see Supporting Information Table S2 for details) and microorganisms (42 studies; 249 K_m and V_{max} data points; see Table S1 for details). All V_{max} values are expressed as μmol g^{-1} DW h^{-1} (dry root weight used for plants and dry cell weight for microorganisms). The mean ± 1 SD of V_{max} values for NH_4^+, NO_3^-, and AA uptake by plants and microorganisms is also presented in the figure. The Michaelis–Menten kinetics clearly show that, within the N concentration range, but particularly at the low concentrations common in soils, NO_3^- and NH_4^+ will be taken up by microorganisms considerably more rapidly than by plants.

The analysis was conducted assuming that nearly all root uptake studies were performed using nutrient solutions. If this was the case, the N diffusion rate would be considerably higher than that under normal soil conditions. Considering a more even distribution of microorganisms in soil vs roots, we expected that the advantages of microorganisms are even higher under real soil conditions compared with those afforded by the theoretical curves (Fig. 3) estimated on the basis of nutrient solution studies.

The hypothesis regarding uptake rate was partly confirmed while summarizing the ^{15}N studies (Fig. 4). We related ^{15}N in plants to that in microorganisms after a pulse addition of ^{15}N as NO_3^-, NH_4^+, or amino acids to soil. Confirming our theory, most of the ^{15}N was allocated to microorganisms (there are nearly twice the number of points above the $x = y$ line in Fig. 4). Nonetheless, the red points in Fig. 4 clearly show a strong preference of

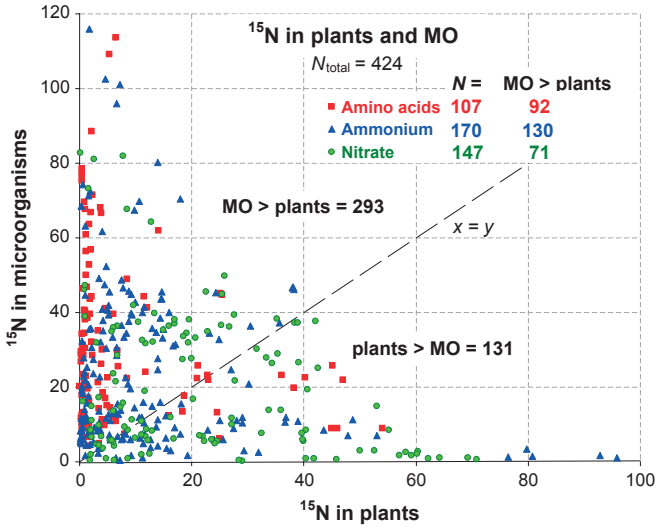

Fig. 4 Review of ^{15}N uptake by plants and microorganisms (MO) after ^{15}N pulse addition to soil. ^{15}N for plants and microorganisms is presented in the same mass units: in most studies, percentage of ^{15}N input and, in some studies, μg ^{15}N g^{-1} soil. There are nearly twice as many values above the $x = y$ line, suggesting that most of the added ^{15}N is taken up by microorganisms. Note the clear differentiation between the three N forms: ammonia is mainly allocated to plants, and amino acids are taken up mainly by microorganisms. Nitrate is allocated preferentially to plants. The Kruskal–Wallis one-way analysis-of-variance-by-ranks test was used to examine the difference among ammonium, nitrate, and amino acids. A significant difference among these values was observed at $P < 0.05$ (Dunn's method).

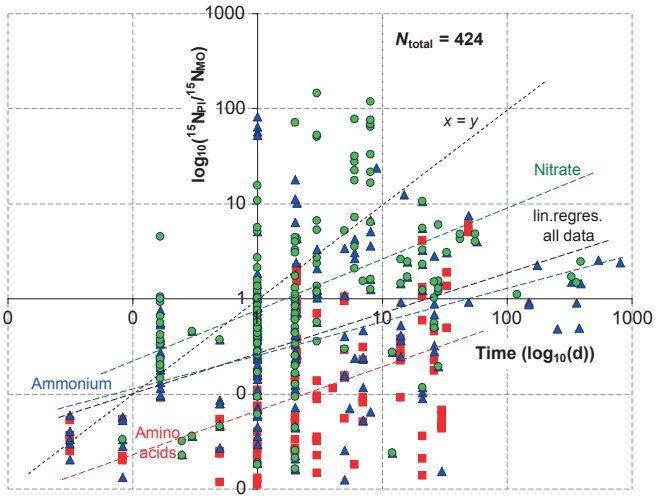

Fig. 5 Change in ^{15}N distribution between plants and soil microorganisms over time after ^{15}N input in soil. ^{15}N distribution is presented as the ratio between ^{15}N in plants and ^{15}N in microorganisms ($^{15}N_{PL}/^{15}N_{MO}$). Because of the enormous range of $^{15}N_{PL}/^{15}N_{MO}$ and the duration of various experiments (from < 1 h up to 3 yr), both variables are presented as decadal logarithms. The trend line (dashed lines) clearly shows that the ratio $^{15}N_{PL}/^{15}N_{MO}$ increases over time and, consequently, more ^{15}N will be relocated into the plants from microorganisms. For references see Table S3.

microorganisms for uptake of amino acids. This was not very obvious from Fig. 3, which shows K_m and V_{max} values, but clearly confirms our expectation that, under soil conditions, the competition will be shifted towards microorganisms. Accordingly, most of the amino acids appearing in the soil will be recovered in microorganisms and not in plants. This result partly confirms our previous suggestion that amino acid uptake is of minor importance for the N nutrition of plants in some ecosystems (Biernath *et al.*, 2008; Xu *et al.*, 2008; Rasmussen *et al.*, 2010).

The Michaelis–Menten kinetics (Fig. 3) reflect the uptake of N, but do not consider subsequent redistribution of N between roots and microorganisms after the uptake. When the level of ^{15}N in plants is compared graphically with that in microorganisms, the N dynamics within the system are still not clear (Fig. 4). We assumed that the life cycle of microorganisms and roots may have an effect on the later redistribution of N (see section VII). We therefore related the ratio between ^{15}N in plants and that in microorganisms to the time after the addition of ^{15}N to the soil (Fig. 5). This ratio clearly increased over time, indicating that, after initial preferential uptake by microorganisms, there is a redistribution leading to the relocation of N to plants.

VI. Ecological relevance of competition between roots and microorganisms for N

Previous studies have not focused on *why* the competition between roots and microorganisms for N is important and *what* are the ecological consequences of this competition (Kaye & Hart, 1997; Hodge *et al.*, 2000a). In our view, this competition and the fast uptake of N by microorganisms have at least three important consequences for ecosystem development and species evolution.

First, most N cycling in soils is through organic forms (Wanek *et al.*, 2010; Inselsbacher & Näsholm, 2012) and most plants have the capacity to take up organic N in the form of free amino acids (Näsholm *et al.*, 2009). Therefore, mineralization of SOM provides available N, including mineral N (i.e. NH_4^+ and NO_3^-) and amino acid-N, for plants and microorganisms (Schimel & Bennett, 2004). Very rapid trapping of mineral N and amino acids by microorganisms (Jones & Kielland, 2002; Fischer *et al.*, 2010) is ascribed to their inherent uptake capacity (i.e. high surface-area-to-volume ratios and V_{max}). This is an important adaptation of ecosystems against possible N losses by leaching. Allocation of N within the microorganisms (temporal immobilization) protects it against leaching. Therefore, in those natural ecosystems in which microorganisms retain nearly all N, the leaching losses are minimal, even in cases where the plants are unable to take up all N after its release by litter decomposition. This is partly confirmed by the fact that, in strongly N-limited ecosystems such as alpine grasslands, microorganisms rapidly trap N (Song *et al.*, 2007).

In contrast to natural ecosystems, areas with intensive agriculture have an excess of mineral N added as fertilizers that cannot be trapped by microorganisms because of the absence of available C, leading to a considerably lower microbial biomass and activity. Normally, agricultural soils contain < 70–50% of SOM compared with virgin soils (Lal, 2003). This decrease mainly reflects reduced pools of easily available SOM (Six *et al.*, 2002; Chen *et al.*, 2009). The inability of microorganisms to trap and retain all fertilizer N leads to considerably higher N losses by leaching in agricultural soils (Havlin *et al.*, 1999; Kirchmann *et al.*, 2002) and certain other

disturbed ecosystems compared with natural ecosystems. Therefore, high N losses from agroecosystems are associated not only with abundant mineral fertilizers (the annual N turnover in many natural ecosystems is even higher than in croplands) but also with the particular inability of microorganisms to retain excess mineral N.

Secondly, this fast preliminary microbial trapping of mineral N and amino acids probably affects plant species competition. Plants having close mutualistic relationships with rhizosphere microorganisms can store the temporary excess N in the microorganisms. Therefore, the excess N will not be leached (see the second paragraph of this section) and lost to other species, but will be temporarily secured in microbial biomass close to the root surface. This offers such plant species advantages for N (and probably other nutrient) acquisition. In particular, enhanced rhizodeposition provides a strong selection pressure for those microorganisms that are retained close to the root surfaces and promotes evolutionary selection for mutualistic interactions.

The third important ecological consequence is the continuous provision of mineral N for roots at the time of maximal plant demand. In temperate ecosystems, the input of litter in autumn is temporarily decoupled from the plant demand in spring. This decoupling ranges in duration from a few months (e.g. for alpine grasslands, only the unfrozen soil period is considered) to approximately half a year (the winter period in humid temperate forests and grasslands). In many ecosystems (boreal and deciduous forests, and Mediterranean ecosystems), the period in which plant growth ceases is often characterized by high precipitation. If no N is retained by microorganisms, natural ecosystems would experience high leaching losses. The N released by the decomposition of plant residues is initially stored in microorganisms until the following spring, providing protection against leaching. The soil temperature increase in spring accelerates microbial turnover, and N stored in microorganisms over winter (or the cold period) is released in spring and becomes available for plant growth. At this time, the plants have high photosynthetic and growth rates and a maximal demand for N. A noteworthy fact is that not only photosynthesis and plant growth rate but also soil temperature depend on solar radiation. Therefore, the N release by microorganisms, driven by soil temperature, corresponds to maximal plant growth driven by photosynthesis. Both processes depend on solar radiation, but there is a lag in maximum soil temperature and maximum irradiance.

On the basis of the ecological significance of fast N uptake by microorganisms and its subsequent slow release when plants need it most, we suggest that the competition between plants and microorganisms for N (and probably some other nutrients) prevents leaching losses. This is actually a strategy to maintain ecosystem stability from an evolutionary perspective. The C demand by soil microorganisms is met by plant photosynthesis. To stabilize and even increase plant growth (and thus the amount of C captured by photosynthesis), microorganisms use this C to mobilize nutrients and, after a delay, provide a part of this for plants. Accordingly, the plant–microorganism competition for nutrients is facilitated at the rhizosphere at the ecosystem scale. This phenomenon effectively converts 'competition' to cooperation, particularly in N-limited ecosystems.

Table 4 Effects of biotic and abiotic factors on competition between roots and microorganisms for nitrogen (N)

	N in plants	N in microorganisms	Competition	References
Biotic factors				
Root density ↑	↑↑↑	↓	↑↑	Cheng & Bledsoe (2004)
Mycorrhiza ↑	↑↑↑	↓	↑	Hodge *et al.* (2000a)
Root nodules ↑	↑	↑	↓	Kiers *et al.* (2003)
Photosynthesis ↑	↑	↓	↑	Xu *et al.* (2008)
Plant growth ↑	↑	↓	↑	
Abiotic factors				
Soil depth ↑	↓	↑	↓	Xu *et al.* (2011b)
Temperature ↑	↑	↓	↑	
N fertilization↑	↑	↑	↓	Bloor *et al.* (2009)
pH of soil ↑	↓	↑	?	
Ecosystem factors				
NPP ↑	↑	↑	?	

The table can be read as follows. For 'Root density', for example: if root density increases (↑), then plant uptake of N increases (↑), N in soil decreases (↓), and the root–microorganism competition increases (↑). A question mark indicates uncertain roles where further investigation is required. NPP, net primary production.

VII. Effect of biotic and abiotic factors on N flows between microorganisms and roots

Various factors may control N acquisition by roots and microorganisms and their competitive/mutualistic interactions. Unfortunately, very few studies have evaluated these effects. This hinders the statistical assessment presented in Table 4 and Figs 3–5. Therefore, we analysed individual studies that investigated biotic vs abiotic factors.

Ecosystem types – alpine or temperate grasslands, boreal or deciduous forests, and agricultural crops – feature important biotic factors that can modify interactions between roots and microorganisms for N acquisition. Note that most studies on such interactions were performed on grasslands (Table 2), and obtained results that were more reliable for such ecosystems than for forests and agricultural crops.

1. Root density

Root density is a key factor affecting the partitioning of available N between roots and microorganisms because of: the spatial occupation of soil volume; the high density of available C increasing microbial N immobilization; incomplete parallelism between nutrient uptake and water flux into the roots, depending on the plant's requirement for water and nutrients and the relative availability of these resources in soil (faster and more complete water uptake with dissolved nutrients, including N); and mycorrhiza formation intensity (see the following section). In all

ecosystems, most roots are typically located close to the soil surface. Accordingly, the most intense competition between roots and microorganisms should be in the topsoil. However, the N content and mineralization rates are substantially higher in the topsoil, leading to greater N availability. Additionally, microbial biomass decreases with soil depth and is strongly correlated with root biomass and SOM content (Foster, 1988; Fromm *et al.*, 1993; Ekschmitt *et al.*, 2008). To our knowledge, no studies have evaluated the competition between microorganisms and roots in soils deeper than 30 cm.

In alpine grasslands, we found that the ^{15}N ratio in grassland microorganisms and plants shortly after a ^{15}N pulse at various soil depths is clearly correlated with root biomass (Fig. 6). This relationship allows important conclusions to be reached. Primarily, increasing root density strongly shifts the competition to much higher N uptake by roots. If root biomass is < *c.* 30 kg DW m^{-3} – corresponding to *c.* 20–25 g roots per kg soil – the microorganisms outcompete roots by 5–10 times. Only an extremely high root density of *c.* 53 kg DW m^{-3} can enable root uptake to exceed that of microorganisms (Fig. 6).

2. Effect of mycorrhizas on the interactions of roots with other rhizosphere microorganisms

The roots of most plants are associated with one or more types of mycorrhiza (Allen, 1991; Newsham *et al.*, 1995; Smith & Read, 2008). Length, longevity, and branching of mycorrhizas are important in comparison with root hairs. The mutualism with mycorrhizas greatly increases the active surface of roots, thereby facilitating exploration of a larger soil volume for nutrients and water uptake (Read & Perez-Moreno, 2003; Allen, 2007), and also enhancing the translocation between the roots and shoots of the host plant (Li *et al.*, 1991; Osonubi *et al.*, 1991). From the root–microorganism competition perspective, this has one important consequence: most of the C released by roots will be released via hyphal turnover and not directly from the roots to the soil (Godbold *et al.*, 2006). Therefore, promoting rhizosphere microorganisms in the presence of well-developed mycorrhizas involves the turnover of dead mycorrhizal hyphae rather than the direct release of available C by roots into the soil (Rillig *et al.*, 2001; Godbold *et al.*, 2006). Such a redistribution of easily available root-derived C alters the interactions among rhizosphere microorganisms: The large surface of mycorrhizal hyphae per gram of dried soil leads to a larger and more evenly distributed depletion of soil N (Allen, 1991; Smith & Read, 2008). Therefore, the following interactions between roots and rhizosphere microorganisms can be expected in well-developed mycorrhiza formation:

- higher belowground C allocation;
- less C release directly to soil (mostly directed to hyphae);
- higher depletion of soil N (including free amino acids and inorganic forms) and other nutrients;
- later release of available C by rapid mycorrhizal hyphal turnover;
- lower C use efficiency because of absence of available N.

We conclude that a high degree of root mycorrhiza formation is a very important factor that enhances the competitive capacity of the plants relative to free microorganisms and consequently leads to less N allocation to microorganisms (except mycorrhizal fungi). However, to our knowledge, there have been no studies that provide information on N uptake by roots, mycorrhizas, and nonmycorrhizal microorganisms, and all the studies analysed in Figs 4–6 were performed using mycorrhizal plants.

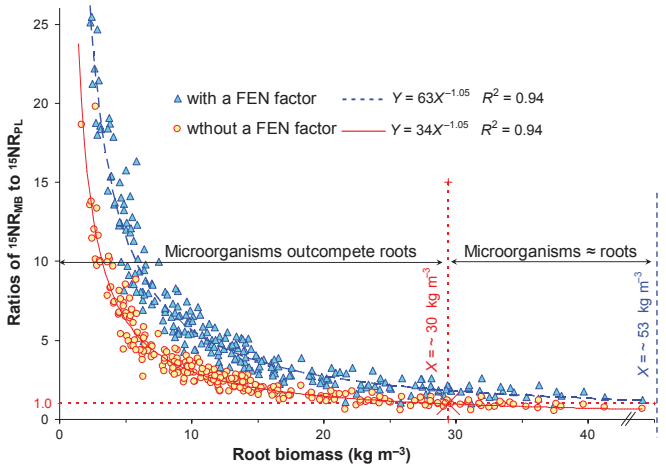

Fig. 6 Correlation between root density and plant–microbe competition in an alpine meadow. The plant–microbe competition for nitrogen (N) was investigated up to 48 h. The dashed curve indicates plant–microbe competition for inorganic N without using an extracable factor (FEN) to correct microbial ^{15}N uptake for incomplete extraction (referring to as a conservative estimate of microbial ^{15}N uptake), whereas the solid curve represents plant–microbe competition for inorganic N with a factor of 0.54 to correct microbial ^{15}N uptake. The value for the typical root density in this type of grasslands is *c.* 2.0 kg DW m^{-2} in the upper 15-cm soil depth. Root biomass below a threshold of 29.4 kg m^{-3} implies the condition where microorganisms outcompeted roots, whereas, at a root biomass > 52.9 kg m^{-3}, roots outcompeted microorganisms in this meadow (redrawn from Xu *et al.*, 2011b). which appears in the figure.

3. Effect of abiotic factors

The various abiotic factors affecting root–microorganism competition may be divided into two groups: factors affecting the intensity of nutrient limitation in the soil, and factors affecting the rate of soil water uptake, and consequently the rate of nutrient uptake, by roots.

The intensity of nutrient limitation can be absolute (very low N content in the soil) or relative (intensive immobilization of N by microorganisms). Very low N availability in the soil is typical, for example for alpine meadows, where microbial activities are depressed by low temperature. Nutrients are also limited in some subtropical and tropical soils because of human disturbance, for example when topsoil is eroded after the removal of vegetation. The remaining soil is then derived from the parent material, and nutrient concentrations in this soil are very low.

Very intensive N immobilization by microorganisms is usually associated with high input of plant residues with a high C : N ratio against the background of low N content in soil (Recous *et al.*, 1995). Such a situation is typical in agricultural soils after complete mineral N uptake by the harvested crop and the addition of straw. This usually significantly prolongs the mineralization of the straw

and delays N release by microorganisms (Mary *et al.*, 1996). Strong microbial N immobilization typically leads to N deficiency in crops and depresses the early development and yield of crops (Rathke *et al.*, 2006). This clearly indicates the imbalance between competition and mutualism in intensive agriculture.

Because nutrient acquisition by roots greatly depends on the delivery of nutrients to the surface of roots or mycorrhizas, the factors affecting water uptake by roots influence root N uptake (Inselsbacher & Näsholm, 2012). These factors depend directly on transpiration rates and include mainly the following factors: the intensity of photosynthetically active radiation, temperature, soil moisture, water pressure deficit, and wind velocity. The N increase attributable to all these factors also promotes the uptake of water and available N by roots before they can be taken up and used by microorganisms. Two factors – temperature and soil moisture – also directly affect microbial turnover. However, high temperature and soil moisture affect plant transpiration more than microbial turnover (Pregitzer & King, 2005). Therefore, competition is less important in warm and wet vs cold soils. This indirectly confirms the importance of initial microbial uptake of N, particularly in alpine grasslands, where transpiration is usually limited by low temperatures.

Soil pH may help determine root–microorganism competition. First, pH affects nutrient availability and changes the functions of some carriers located on the root surface (mainly in root hairs and mycorrhizal hyphae) responsible for ion uptake. Furthermore, pH greatly affects the activities and composition of microbial communities in the rhizosphere (Blagodatskaya & Anderson, 1998; Rousk *et al.*, 2010). Soil pH affects root growth and elongation (Edwards & Scott, 1974), as well as mycorrhizal colonization (van Aarle *et al.*, 2002; Read & Perez-Moreno, 2003). Accordingly, deviation of pH from the optimal (6–7) has impacts on both roots and microorganisms. The main question, however, is which of the two is suppressed more strongly. We speculate that acidification suppresses bacterial activities more strongly than those of roots: decreased soil pH therefore increases N uptake by plants. By contrast, alkalinization strongly limits N uptake by roots vs microorganisms, and the latter utilize more N than at neutral soil pH. Because root N uptake can alter rhizosphere pH (Raven & Smith, 1976; Allen, 1988), the ratio between NO_3^- and NH_4^+ uptake by roots could change the competition.

Competition between roots and microorganisms varies during the growth season (Jaeger *et al.*, 1999). This effect is mediated mainly by local climate and the phenological cycle of plants. These factors indirectly affect the competition via the mechanisms described above, involving temperature and precipitation and, in the rooting zone, exudate composition and root growth. In this regard, perennial grasses have an advantage in that they can acquire N early in the season: they overwinter with buds already formed and begin rapid growth as soon as the soils thaw in spring (Onipchenko *et al.*, 2009) by using stored nutrients as well as current-season N uptake (Jaeger & Monson, 1992). Additionally, plants differ in their capacity to acquire N during growth stages because the rhizosphere microbial composition changes as a result of the effects of different root exudates. We conclude that the temporal niche differentiation related to the duration of microbial and plant life cycles contributes to the decreased competition between microorganisms and roots for N in the rhizosphere.

VIII. Conclusions and outlook

The demand for the same nutrients leads to a significant competition between plants and microorganisms in the rhizosphere. The supply of easily available C by roots for growth and maintenance of microorganisms briefly increases this competition. Simultaneously, microbial nutrient mobilization by SOM decomposition increases, leading to an elevation in the level of mineralized nutrients available locally. This decreases the competition.

On the basis of 41 ^{15}N studies on plant–microbial competition for N, as well as 77 studies on the parameters of Michaelis–Menten kinetics of the uptake of nitrate, ammonium, and amino acids, we demonstrated that microorganisms show substantially faster initial uptake of all N forms. This makes them short-term winners in the competition. Conversely, the short life cycle of rhizosphere microorganisms and unidirectional N flux from soil to roots facilitates the relocation of N from microorganisms to roots. This enables plants to become winners over the long term. Thus, strong competition is weakened by mobilization of additional N from SOM, and temporal niche differentiation between microorganisms and roots.

This rapid trapping of available N by microorganisms and its subsequent slow relocation from microorganisms to plants have many ecological consequences, including maintaining ecosystem stability. First, the temporary excess of N released by litter mineralization in autumn (at periods of low N uptake by roots) allows a subsequent slow release of the N trapped by microorganisms – in spring when there is peak N demand by plants. Similarly, microbial N trapping prevents leaching from the soil or ecosystem losses. This property is probably more effective in natural ecosystems than in intensive agroecosystems, which are characterized by low microbial biomass and low available C in soils. Furthermore, plants releasing more available C in the rhizosphere are able to store more N mobilized from the SOM in microbial biomass close to their roots. This has long-term advantages for such plant species and may be beneficial from an evolutionary perspective.

We conclude that biotic factors have a strong effect on this competition, and that root density and mycorrhiza formation are crucial in shifting N acquisition to the roots.

Future studies are warranted to develop methods for quantitatively analysing the competition between roots and microorganisms for N uptake. These methods should be based on ^{15}N partitioning, its redistribution dynamics after uptake, and Michaelis–Menten uptake kinetics. Although the K_m and V_{max} parameters of N uptake by roots can be estimated easily in hydroponics, the relevance of these parameters under soil conditions remains unknown. Interfering processes such as diffusion; sorption; redistribution of water and nutrients between the liquid, solid, and living phases; and competition with microorganisms may completely change root uptake compared with the theoretical predictions. We assume that these interfering processes decrease the root uptake rate and thus increase the amount of N initially stored in microorganisms.

Experimental studies along with direct and inverse modelling would help test this hypothesis.

To better evaluate the competitive abilities of plant species, particularly mutualistic stimulation of rhizosphere microorganisms, we suggest coupling the ^{15}N-labelling of soil with ^{13}C- and/or ^{14}C-labelling of plants to investigate root exudation and rhizodeposition. This should then be related to the belowground allocated C and the N additionally mineralized from SOM.

The ecological relevance of root–microorganism competition for N suggested in this review needs to be shown by field studies that are conducted over more than a few months. This is important because the fast trapping of N by microorganisms is merely the first step of N (and probably other nutrient) retention in ecosystems. Therefore, the challenge is to investigate the second (and further) step(s) of the competition between roots and microorganisms, and to answer the question 'How does niche differentiation in the rhizosphere contribute to ecosystem stability and productivity?'

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Michaelis–Menten kinetics of nitrogen (N) uptake from NO_3^-, NH_4^+, and various amino acids by microorganisms; source publication for data in Table 3 and Fig. 3

Table S2 Michaelis–Menten kinetics of nitrogen (N) uptake from NO_3^-, NH_4^+, and various amino acids by plants; source publication for data in Table 3 and Fig. 3

Table S3 Publications of ^{15}N-labelling experiments used in this study to evaluate the competition for nitrogen (N) between plants and microorganisms

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