Received: 4 June 2023 | Revised: 2 February 2024 | Accepted: 4 February 2024

DOI: 10.1111/pce.14858

REVIEW

Plant, Cell & Environment | WILEY

Rhizosphere priming promotes plant nitrogen acquisition by microbial necromass recycling

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Abstract

Nitrogen availability in the rhizosphere relies on root-microorganism interactions, where root exudates trigger soil organic matter (SOM) decomposition through the rhizosphere priming effect (RPE). Though microbial necromass contribute significantly to organically bound soil nitrogen (N), the role of RPEs in regulating necromass recycling and plant nitrogen acquisition has received limited attention. We used ^{15}N natural abundance as a proxy for necromass-N since necromass is enriched in ^{15}N compared to other soil-N forms. We combined studies using the same experimental design for continuous $^{13}CO_2$ labelling of various plant species and the same soil type, but considering top- and subsoil. RPE were quantified as difference in SOM-decomposition between planted and unplanted soils. Results showed higher plant N uptake as RPEs increased. The positive relationship between ^{15}N-enrichment of shoots and roots and RPEs indicated an enhanced necromass-N turnover by RPE. Moreover, our data revealed that RPEs were saturated with increasing carbon (C) input via rhizodeposition in topsoil. In subsoil, RPEs increased linearly within a small range of C input indicating a strong effect of root-released C on decomposition rates in deeper soil horizons. Overall, this study confirmed the functional importance of rhizosphere C input for plant N acquisition through enhanced necromass turnover by RPEs.

KEYWORDS

$^{13}CO_2$ continuous labelling, ^{15}N natural abundance, crops, legumes, plant nutrition, soil respiration

1 | INTRODUCTION

Nitrogen (N) is one of the most important elements for plant growth and the nutrient that most often constrains the productivity of terrestrial ecosystems (LeBauer & Treseder, 2008; Vitousek & Howarth, 1991). In agriculture, soil mineral N is often limited and inadequate to meet crop needs, if continued supply of mineral N either from SOM-decomposition or from other sources is not assured. A high input of mineral N fertilisers aims to replace soil N mineralisation processes and thus directly supply N to plants (Berthrong et al., 2013). However, even with high synthetic N inputs, less than 50% of the N in crops is derived from current year N fertilisers (Yan et al., 2020). In addition, excessive N fertiliser usage poses a threat to water and air quality by leaching (mainly NO_3^-) or

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volatilisation (e.g., N_2O, NH_3) (Moreau et al., 2019). Crop production in sustainable agriculture without external inputs of mineral fertilisers therefore depends on intrinsic soil N reserves and is thus governed by the ability of organisms to recycle and retain limiting nutrients inside their ecosystem.

The vast majority of organic N in soil originates from microbial sources (Simpson et al., 2007). Microbial residues (hereafter 'necromass') are characterised by low C/N ratios relative to plant litter, making N-mining through necromass recycling (i.e., necromass consumption by living microbes) an efficient strategy for microbes to meet their N demand (Cui et al., 2020). Soil microorganisms synthesise extracellular enzymes to increase organic matter decomposition to mobilise organically bound N (Dijkstra et al., 2013). However, heterotrophic microbes are primarily limited in available C and energy (reviewed by Soong et al., 2020) which reduces their ability of metabolic investments in degradative enzyme production for resource acquisition (Wang et al., 2020). Carbon availability for microbes is enhanced in the vicinity of roots due to the input of root-released organic compounds. This input of labile C may accelerate the decomposition of soil organic matter (SOM), a process known as the rhizosphere priming effect (RPE; (Cheng & Kuzyakov, 2005; Kuzyakov, 2002; Zobel et al., 2005). The accelerated turnover of organics in soil is intimately linked to N cycling (reviewed by Holz et al., 2023). Various mechanisms, for example N-mining and stochiometric decomposition have been proposed to describe the linkage between the RPE and N availability in the rhizosphere (reviewed by Bernard et al., 2022; Daly et al., 2021; Kuzyakov, 2002; Mason-Jones et al., 2018). Generally, priming may have evolved from an evolutionarily stable mutualistic association between plants and rhizosphere microorganisms with benefits for both in terms of mineral nutrient acquisition (Cheng et al., 2014). To date, however, little is known about the sources of primed components in soil, and the contribution of priming-induced necromass recycling remains elusive. We hypothesise that priming is intimately linked to microbial necromass recycling, as the nutrient density of the necromass makes it a preferential source of nutrients. We further anticipate a more pronounced effect of C input on SOM cycling in subsoil than in topsoil, as microbial communities in the subsoil experience an even greater limitation of available C than those in the topsoil.

Conceptually, the rhizosphere-driven necromass N mineralisation represents a positive feedback loop potentially leading to a self-reinforcement of necromass N turnover by rhizosphere priming (Figure 1). This feedback loop can be described as follows: The starting point is the C exudation of plants into the rhizosphere. Microorganisms utilise this C together with mineral N as substrate for growth (Buckeridge et al., 2020). First, we consider a scenario in which the resource C–N stoichiometry closely matches the microbial demand, indicating that the microbes are not constrained by N availablility. This situation may occur in agricultural cropping systems with young plants and high N availability or in the region around the root tip, when the root enters new soil volumes from which available N has not yet been taken up. Fast growing organisms may benefit and preferentially utilise the available resources (C, N and other nutrients) likely causing decelerated mineralisation of organic matter (negative priming by preferential substrate utilisation (PSU), Figure 1, bottom right, (c.f. Kuzyakov, 2002). These fast growing organisms also die quickly upon substrate depletion (Biselli et al., 2020; Kästner et al., 2021), and thus contribute to the microbial necromass pool. With progressive nutrient limitation due to immobilisation by plants and microbes, a shift in microbial functions may occur resulting from alterations in physiology and/or changes in microbial community composition (Figure 1, top right). This could be the case for older plants that have already depleted the available N pool or in the region around the older root parts where N have been taken up from. Under nutrient limiting conditions, slow-growing cells may have an advantage over fast-growing cells. This is because slow-growing cells require less maintenance and can survive longer (Kästner et al., 2021; van Bodegom, 2007). Additionally, the surplus C or energy released by root exudates fuels the metabolic costs of producing exoenzmyes to acquire limited resources. Activities of enzymes involved in N

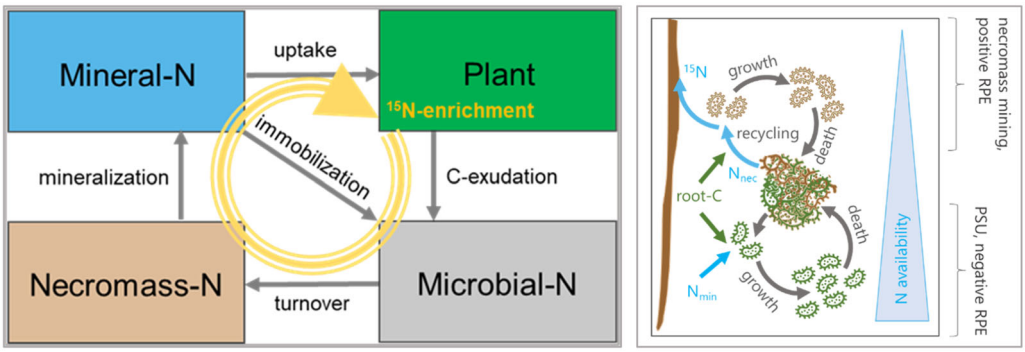

FIGURE 1 Conceptual figure representing process sequences triggering necromass recycling in the rhizosphere. Left: Feedback loop between root exudation, microbial N immobilisation and turnover, microbial necromass N recycling and benefits for plant growth. The yellow circles indicate a consistent ^{15}N-enrichment of plant tissue with increasing microbial necromass recycling. Right: Processes triggering priming effects depending on N availability. High N and C availability will promote preferential substrate utilisation (PSU) causing no or negative priming effects. With progressive N limitation, necromass recycling may become increasingly important to cover the microbial N-demands, resulting in positive rhizosphere priming and ^{15}N-enrichment of plant tissue. [Color figure can be viewed at wileyonlinelibrary.com]

cycling, for instance, were shown to be linked to RPE (reviewed by Holz et al., 2023). Further, slow-growing cells may preferentially recycle nutrient dense necromass to cover their N demand (Kästner et al., 2021). Finally, plants may benefit from the additional N mineralisation, and an improved plant growth will lead to an overall higher exudation that triggers further microbial turnover, thus completing the feedback loop (Figure 1, left). As microbial biomass is generally enriched in ^{15}N relative to total soil N (Craine et al., 2015; Dijkstra et al., 2006), enhanced microbial turnover and necromass recycling through exudate induced priming should cause a ^{15}N-enrichment of the plant available N. Therefore, our objectives were (1) to link the RPE to total N gains of plants, and (2) to show that $\delta^{15}N$ of plant tissues is a suitable proxy indicating increased recycling of microbial necromass N with higher RPEs.

2 | METHODS

2.1 | Experimental setup

To test our hypotheses, we combined a large data set with two different soil depths (topsoil and subsoil from an organic farm) from experiments with the same experimental conditions. Soil properties are given in Table 1. Plant species used in the experiments were *Triticum aestivum*, *Hordeum vulgare*, *Helianthus annus* and *Glycine max* (see also Table S1).

We collected data from six experiments with ^{13}C-continuous labelling of various plant species conducted at the University of California, Santa Cruz (Table S1). The plants were grown in a greenhouse equipped with the supplies for continuous labelling. The labelling approach is described in detail in Cheng and Dijkstra (2007). Plants were continuously labelled with ^{13}C-depleted CO_2 from the emergence of the first leaf until harvest. Briefly, a constant CO_2 concentration of 400 ± 5 ppm and a constant $\delta^{13}C$ value was maintained inside the greenhouse by regulating the flow of pure, ^{13}C-depleted CO_2 (99.9% CO_2, about −35‰) from a tank and setting CO_2-free air flow rate proportional to the leakage rate of the greenhouse (Zhu and Cheng, 2012). The $\delta^{13}C$ of the CO_2 inside the greenhouse ranged from −21.2‰ (Cheng & Dijkstra, 2007) to −15.2‰ (Pausch et al., 2013b). The CO_2-concentration inside the greenhouse was continuously monitored by an infrared gas analyser (Model LI-820, Li-COR) and stabilised at 400 ± 5 ppm by computer-controlled CO_2 injection from the tank. For more details see Cheng and Dijkstra (2007) or Pausch et al. (2013b).

2.2 | Analyses

The soil CO_2 efflux and its isotopic composition were measured from sealed pots at various growth stages of the plants by using a closed-circulation CO_2 trapping system (Cheng et al., 2003). CO_2 was trapped as Na_2CO_3 in 1 M NaOH. An aliquot of each NaOH solution was analysed for total inorganic carbon using a Shimadzu TOC-5050A Total Organic Carbon Analyser. Another aliquot was precipitated as $SrCO_3$ (Harris et al., 1997) and analysed for $\delta^{13}C$ (relative to V-PDB standard) using an Elemental Analyser interfaced to an Isotope Ratio Mass Spectrometer (EA-IRMS).

The dry weight of shoot and root biomass as well as C and N contents and the $\delta^{13}C$ and $\delta^{15}N$ values of shoots, roots and soils were determined using an elemental analyser—isotope-ratio mass spectrometer (EA-IRMS, with V-PDB and air-N_2 as isotope standards for C and N, respectively).

If reported, microbial biomass carbon (MBC) and nitrogen (MBN) contents were determined using the chloroform fumigation extraction method described by (Vance et al., 1987). The difference between fumigated and unfumigated soil extracts was calculated and corrected for the extraction efficiency with a factor k_{EC} of 0.45 for C and k_{EN} of 0.54 for N (Joergensen & Mueller, 1996; Wu et al., 1990).

2.3 | Calculation of RPE

The contribution of SOM- and root-derived CO_2 to total soil respiration was calculated using a linear two-source isotopic mixing model (Cheng, 1996):

$$C_{TOTAL} \cdot \delta^{13}C_{TOTAL} = C_{SOM} \cdot \delta^{13}C_{SOM} + C_{ROOT} \cdot \delta^{13}C_{ROOT} \quad (1)$$

$$C_{TOTAL} = C_{ROOT} + C_{SOM} \quad (2)$$

$$C_{SOM} = C_{TOTAL} \cdot \frac{\delta^{13}C_{TOTAL} - \delta^{13}C_{ROOT}}{\delta^{13}C_{SOM} - \delta^{13}C_{ROOT}} \quad (3)$$

$$C_{ROOT} = C_{TOTAL} - C_{SOM} \quad (4)$$

where C_{TOTAL} is the total CO_2 efflux of the planted soil (mg C kg^{-1} soil day^{-1}) and $\delta^{13}C_{TOTAL}$ is the corresponding $\delta^{13}C$ value (‰). C_{SOM} is the CO_2 derived from SOM decomposition (C_{SOM}, mg C kg^{-1} soil day^{-1}) and $\delta^{13}C_{SOM}$ is the $\delta^{13}C$ value of CO_2 from SOM decomposition measured in the unplanted soils (‰). C_{ROOT} is the root-derived CO_2 in the planted soils (mg C kg^{-1} soil day^{-1}) with $\delta^{13}C_{ROOT}$ as the corresponding $\delta^{13}C$ value (‰). The isotopic composition of root

TABLE 1 Selected properties of the soils used in the experiments from which the data were obtained.

	Topsoil (UCSC farm)	Subsoil (UCSC farm)
Soil type	Mollisol	Mollisol
Depth [cm]	0–20	70–90
C_{org} [%]	1.18	0.34
Total N [%]	0.13	0.05
C/N	9.10	7.27
$\delta^{13}C$ [‰]	−26.45	−24.69
$\delta^{15}N$ [‰]	7.12	6.94
pH	5.8	6.1

biomass (± an isotope fractionation factor) was used as a proxy for $\delta^{13}C_{ROOT}$. Except for (Dijkstra & Cheng, 2007), all studies considered a fractionation factor between root biomass and root-derived CO_2 ranging from 0.87 to 1.71 depending on the plant species (Zhu & Cheng, 2011).

The RPE (% of unplanted soil) on SOM decomposition was calculated by subtracting the CO_2 flux of the unplanted soil (C_{SOM} (*U*)) from the SOM-derived CO_2 flux of the planted soil (C_{SOM} (*P*)):

$$RPE = (C_{SOM}(P) - C_{SOM}(U))*100/C_{SOM}(U) \quad (5)$$

2.4 | Statistics

All statistical analyses were performed in R (version 3.3.1). Pearson correlations were calculated to estimate the association between the tested paremeters. The relation between all tested parameter pairs were described by linear function except for the relation between root-derived CO_2 and priming which was described by a rational function. To determine statistical differerence between the delta values (shoot and root) for legumes and non-legumes, the data were first checked for homogeinety of variances using a Levene's test. As the homogeinety of variances was not given, a general linear model was conducted, followed by a TukeyHSD post-hoc test with $p < 0.05$.

3 | RESULTS

3.1 | Rhizosphere priming improves plant N acquisition and microbial biomass N

Total plant N increased with increasing RPEs for nonlegume species in topsoil (Figure 2, left), while for the legumes the correlation between total plant N and the RPE was negative. However, this was caused by the very low total plant N data measured in one study (Zhu & Cheng, 2013) and must therefore be interpreted with caution. In subsoil, we did not find a significant correlation between total plant N uptake and the RPE (Figure 2, right).

We observed higher MBC in planted soils compared to unplanted soils, indicating a positive effect of roots on microorganisms (data not shown, cf. respective publications Table S1). However, there was a negative correlation between the RPE and MBC for topsoil, but no significant relationship between the RPE and MBC for subsoil was observed (Figure 3, left). Microbial biomass N increased significantly with increasing RPEs. Note, however, that MBN data were measured only in one study (Pausch et al., 2016) (Figure 3, right).

3.2 | RPEs increase the $\delta^{15}N$ of roots

In both top- and subsoil there was a significant positive relationship between the RPE and the $\delta^{15}N$ of roots of nonlegume species (Figure 5). The same pattern applied to the RPE and $\delta^{15}N$ of shoots, yet being only significant for nonlegume species in topsoil (Figure 4). The y-axis intercept (RPE = 0), that is, $\delta^{15}N$ of roots in the absence of rhizosphere priming, was higher for topsoil ($\delta^{15}N$ = 3.2‰) than for subsoil ($\delta^{15}N$ = 2.0‰) (Figure 5) which is in accordance with the higher $\delta^{15}N$ of total soil N in top than subsoil likely due to organic fertiliser input as part of the >50 years of organic farming practice at the site (Table 1). Organic fertilizeres are usually ^{15}N-enriched relative to mineral fertilisers (reviewed by Choi et al., 2017).

3.3 | Rhizosphere priming intensity

RPEs were plotted against root-derived CO_2 as depicted in Figure 6. Root-derived CO_2 comprises root respiration and the decomposition of rhizodeposits (i.e., rhizomicrobial respiration). Since the latter may contribute more than 50% to total root-derived CO_2 (Cheng et al., 1993;

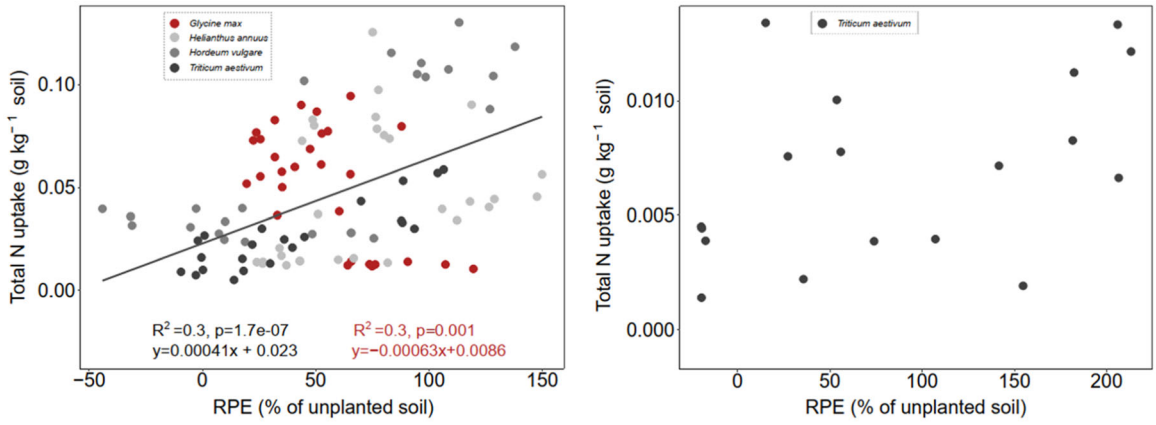

FIGURE 2 Relationship between RPE (% of unplanted control) and total plant N uptake (g N pot^{-1}) of legumes (red) and nonlegume species (grey) grown in a sandy loam (Mollisol) from the UCSC farm. Topsoil 0–20 cm (left); Subsoil 70–90 cm (right). Since the negative correlation for legume species was caused by the extremely low total N uptake data from one study (Zhu & Cheng, 2013), no regression line is shown. When excluding these data, the relationship between total N uptake and RPE was not significant for legumes. [Color figure can be viewed at wileyonlinelibrary.com]

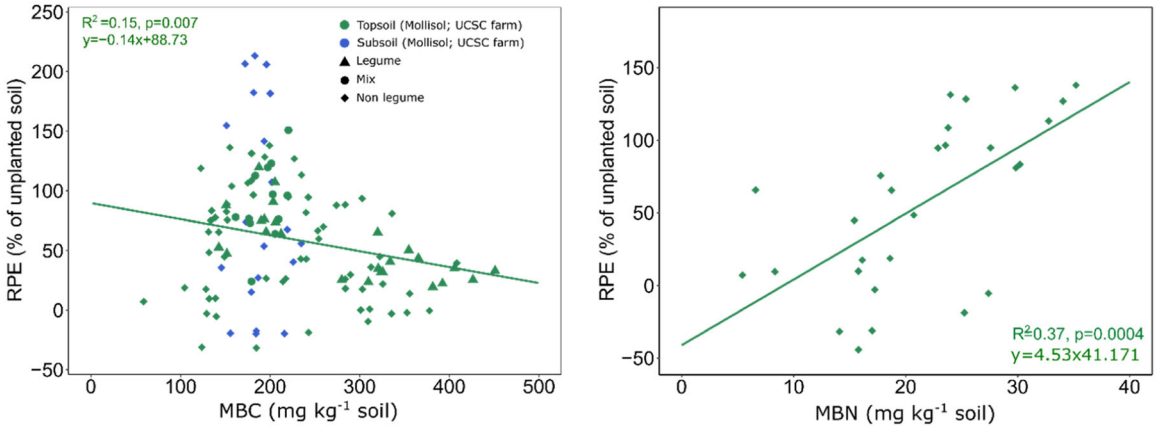

FIGURE 3 Relationship between RPE (% of unplanted control) and MBC (mg C kg^{-1} soil) (left) and MBN (mg N kg^{-1} soil) (right) of legumes, nonlegume species and a mixture of legume and non-legumes species (mix) in a sandy loam (Mollisol) from the UCSC farm. Green: Topsoil 0–20 cm; blue: Subsoil 70–90 cm. [Color figure can be viewed at wileyonlinelibrary.com]

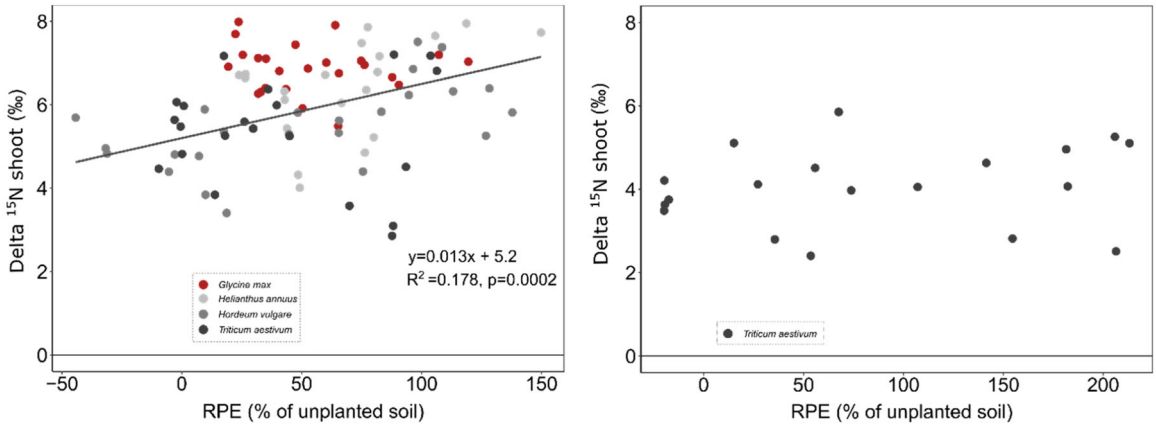

FIGURE 4 Relationship between rhizosphere priming effects (% of unplanted control) and $\delta^{15}N$ of shoots (‰) of legumes (red) and nonlegume species (grey) grown in a sandy loam (Mollisol) from the UCSC farm. Topsoil 0–20 cm (left); Subsoil 70–90 cm (right). [Color figure can be viewed at wileyonlinelibrary.com]

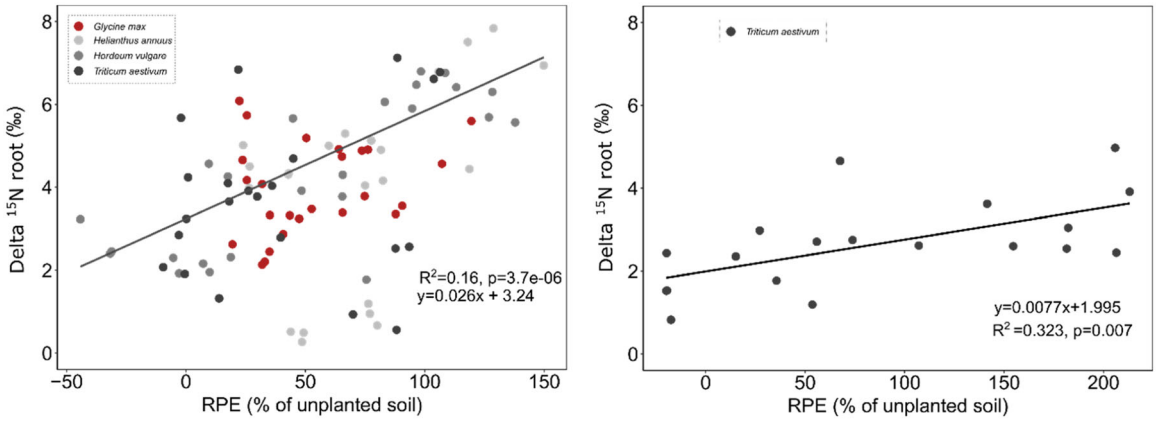

FIGURE 5 Relationship between rhizosphere priming effects (% of unplanted control) and $\delta^{15}N$ of roots (‰) of legumes (red) and nonlegume species (grey) grown in a sandy loam (Mollisol) from the UCSC farm. Topsoil 0–20 cm (left); Subsoil 70–90 cm (right). [Color figure can be viewed at wileyonlinelibrary.com]

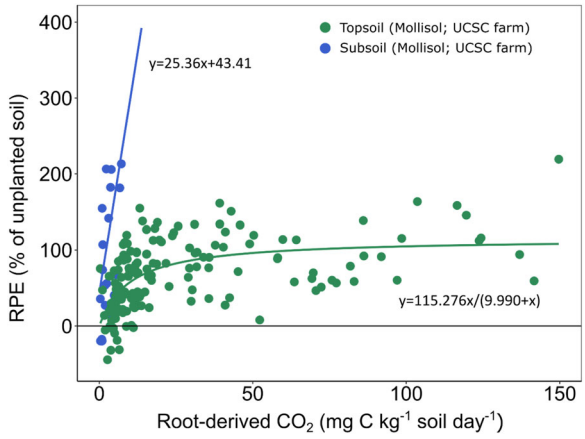

FIGURE 6 Relationship between the RPE (% of unplanted soil) and root-derived CO_2 (mg C kg^{-1} soil day^{-1}). Green: Topsoil 0–20 cm; blue: Subsoil 70–90 cm. For the topsoil of the organic farm, priming was saturated at 115%. The RPE in subsoil showed no saturation. [Color figure can be viewed at wileyonlinelibrary.com]

Pausch et al., 2013a), root-derived CO_2 was used as a proxy for C input by living roots into the rhizosphere.

The RPE was positive in most cases (91.5% of all data). Negative priming effects occurred only in young plants (30–35 days after planting) with root-derived CO_2 smaller than ~10 mg C day^{-1} kg^{-1} soil (Table S1). Rhizosphere priming in the topsoil was saturated at about 50 mg C kg^{-1} soil day^{-1} root-derived CO_2 and remained at a level of 115%. In contrast, organic matter decomposition was enhanced by up to 200% compared to the unplanted soil in subsoil (Table S1, and blue line in Figure 6). A small input of labile C, therefore, has a much larger effect on decomposition rates in sub-compared to topsoil. No saturation in the RPE was visible in subsoil.

4 | DISCUSSION

4.1 | Plant N acquisition via RPEs

We found an increase in total plant N uptake with increasing RPE for non-legumes (Figure 2), highlighting the tight connection between rhizosphere C availability and plant N nutrition as reported earlier (e.g. Dijkstra et al., 2009). With progressive N limitation due to plant N uptake and microbial N immobilisation, plants may increase the investments in exudates (Pausch & Kuzyakov, 2018) stimulating microbes to intensify N-mining from SOM, including necromass. This is in line with higher MBN as RPE increases (Figure 4). In contrast, MBC declined with increasing priming indicating decomposition of microbial remains. Under limiting conditions, microbes have developed strategies to reduce their energy consumption. Starvation may result in a substantial cell death with microbial necromass being recycled by the remaining active microorganisms (Dijkstra et al., 2022). Therefore, the decline in MBC and the simultaneous increase in MBN with increasing RPE suggest that microbial necromass is a source for N mining (see 4.2). A tight linkage between C and N cycling was also demonstrated by a positive relationship of the RPE and gross nitrogen mineralisation (GNM) in previous studies (reviewed by Holz et al., 2023).

For legumes, total plant N uptake did not show a conclusive pattern with RPE (Figure 2). With their N-fixing capability, legumes have an alternative strategy for N uptake which may lead to a decoupling of RPE and plant N uptake. Since the rhizobia in the root nodules are able to fix atmospheric N_2, which by definition has $\delta^{15}N$ values of zero, a legume that derives most of its nitrogen from N_2 fixation will have an isotopic composition close to that of the atmosphere (Huss-Danell & Chaia, 2005). The $\delta^{15}N$ values of legume shoots and roots, however, did not differ from those of nonlegume species (Figure S1). Legumes were reported earlier to produce higher priming compared to nonlegume species due to their high exudate quality with higher N contents promoting microbial turnover processes (Zhu & Cheng, 2012). This effect may even mask N_2 fixation resulting in a similarly high $\delta^{15}N$ values of legume and nonlegume shoots and roots (Figure 4; Figure S1).

4.2 | $\delta^{15}N$ of plant tissue as a proxy for the utilisation of microbial necromass

It is generally accepted that N in microbial biomass and necromass is ^{15}N-enriched compared to total soil N (Dijkstra et al., 2006). Hence, a positive relationship between rhizosphere priming and $\delta^{15}N$ of roots and shoots might indeed confirm that the N in microbial necromass is primed to cover the N demand of the plants. However, a basic assumption is that root $\delta^{15}N$ reflects the $\delta^{15}N$ of the N source acquired from soil. This assumption is only correct, if isotopic fractionation during N uptake and transport from roots to aboveground biomass remains constant. Isotope fractionation during N uptake was shown to be very low under low mineral N conditions (Craine et al., 2015). Given that we excluded N-fertilised soils in our analyses and that mineral N in most studies was <10 mg N kg^{-1} soil, fractionation during N uptake can be expected to be marginal. However, intra-plant fractionation between shoots and roots may have occurred. Indeed, we found that shoot tissue was enriched in ^{15}N by about 2‰ compared to roots (Figure S1). Autotrophic plant parts were also reported earlier to be ^{15}N-enriched relative to heterotrophic parts (Gebauer & Schulze, 1991). The ^{15}N enrichment of aboveground biomass compared to roots can be explained by isotopic fractionation occuring inside the plant, that is, by translocation of ^{15}N enriched nitrogen from roots to shoots where it is assimilated (reviewed by Kalcsits et al., 2014). This would lead to an underestimation of ^{15}N in roots. Nonetheless, under the condition of constant fractionation, we suggest that an increase in the $\delta^{15}N$ value of roots indicates an enhanced acquisition of necromass-N. In addtion, shifts in N isotopic composition between shoots and roots also occur when roots are intensively colonised by mycorrhizal fungi because arbuscular and ectomycorrhizal fungi are enriched in ^{15}N relative to plant tissue (Hobbie & Högberg, 2012; Klink et al., 2022).

A contribution of mycorrhizal fungal tissue in root measurements would however increase the isotopic signal of roots compared to shoots and not, as found in our study, vice versa.

In soils, $\delta^{15}N$ values have been used as indicators for the openness of the system (Wang et al., 2014). Increased $\delta^{15}N$ values of bulk soil inferes greater N cycling rates and N losses, whereby ^{14}N is preferentially lost from the system through processes such as nitrification, denitrification, N leaching or root uptake (Wang et al., 2021). Moreover, mineral N is generally ^{15}N-depleted relative to the total soil N pool (Craine et al., 2015) due to various transformation processes that cause fractionation (Denk et al., 2017). In contrast, microbial biomass N is ^{15}N-enriched compared to the bulk soil (Collins, 2000; Craine et al., 2015; Dijkstra et al., 2006) because microbes excrete ^{15}N-depleted compounds during their metabolism. Accelerated soil N cycling and intensified N losses cause an ^{15}N-enrichment of bulk soil, which we suggest is accompanied by an increasing contribution of ^{15}N-enriched necromass to total soil N. Finally, necromass-N recycling can gradually contribute to the N supply of the plants, which leads to an ^{15}N-enrichment of the plants.

Furthermore, there is a close link between soil N cycling rates and SOM priming as recently demonstrated by a positive relationship between gross N mineralisation and RPE (Holz et al., 2023).

As microbes are often limited in available C rather than nutrients (Soong et al., 2020), populations with high growth rates will react quickly to C additions such as root exudates in cases where mineral N is available. These organisms were suggested to have a high carbon use efficiency and thus use the root-released C for anabolic processes rather than respiration (Bernard et al., 2022). The new C allocated to microbial biomass production will ultimately end up as necromass in the soil after the microbes die, and provides an important source of SOM (Liang et al., 2019). In terms of priming, under circumstances of high N availability PSU may lower SOM decomposition (e.g., young plants or at the root tip region). Accordingly, our data showed lower RPE in younger plants together with lower ^{15}N-enrichment of roots (Figure S2). With an increasing N deficit over time, shifts in microbial physiology and/or community composition towards slow growing microorganisms may occur (Bernard et al., 2022). Imbalances in stoichiometry of available resources and microbial demands are compensated by overflow respiration and additional nutrient mineralisation (Manzoni et al., 2021; Wutzler et al., 2017) resulting in positive RPE. Under nutrient scarcity, necromass recycling may become increasingly important to cover the N demand of the active microorganisms. Necromass makes up a significant portion of the stabilised organic matter pool, accounting for about 50% in agricultrual soils (Angst et al., 2021). There is growing evidence that plants have developed multiple strategies to destabilise mineral-associated organic matter and use it as an important nutrient source (Jilling et al., 2018). Generally, recycling of N dense microbial necromass will lead to a release of ^{15}N-enriched compounds that become accessible to plant roots as plants repeatedly compete with microbes for resources due to slower turnover times (Kuzyakov & Xu, 2013). We therefore argue that the increase in $\delta^{15}N$ of shoots and roots results from enhanced microbial necromass recycling indicated by intensified RPE. This is further supported by a lower MBC but higher MBN with increasing RPE.

It has been suggested that recycling of necromass from fast-growing microorganisms by slow-growing organisms should technically cause negative RPE (Cui et al., 2020). This is because the fast growers incorporate root-derived C (especially exudates) into their biomass, hence biomass recycling should result in CO_2 fluxes that carry to a large portion the isotopic signal of the plants and hence, negative priming should be detected. However, our study demonstrates that necromass N turnover is strongly related to positive RPE (i.e., the higher the C fluxes via RPE, the higher the $\delta^{15}N$ of shoots and roots). As the C demand for catabolic and anabolic processes may exceed the supply from freshly formed necromass, we suggest that C and N sources are partly decoupled. Active microorganisms may consume exudates and plant residues with comparable wide C/N to meet their C requirements for metabolic processes and degradative enzyme production for nutrient acquisition but, in addition, they may recycle necromass as N source. A similar idea was proposed by Daly et al. (2021). The authors assumed degradation of particulate organic matter (POM) as C source, while mineral-associated organic matter (MAOM) would serve as N source for microbes after exudate induced desorption of MAOM (i.e., abiotic priming) (cf. (Jilling et al., 2018; Keiluweit et al., 2015). POM is largely made up of plant residues while MAOM consists to a large share of microbial residues (Lavallee et al., 2020). Hence organic matter desorbed from minerals is more nutrient dense and easily decomposed when freely available (Lavallee et al., 2020). We here argue that the technically measured initial negative priming effect caused by the recycling of microbial necromass carrying the plant isotope signal is overridden by positive priming. Continued turnover exploits 'unlabelled' necromass sources in the soil, considering that a large fraction of soil organic N comes from microbial necromass (Angst et al., 2021).

Future studies should consider necromass production and recycling of distinct microbial groups to disentangle their linkage to mechanisms of the RPE. Moreover, the assessment of total N and ^{15}N in various N pools, especially in the mineral N, the microbial biomass as well as in amino sugars, as a proxies for microbial necromass will allow to further disentangle the linkage between necomass recycling and rhizosphere priming.

4.3 | Saturation of RPEs

Our data for topsoil showed a saturation of rhizosphere priming intensity with increasing root-derived CO_2, which is a proxy for root-C input. The release of low molecular weight root exudates may stimulate saprotrophic activities for higher necromass turnover. This is in accordance to higher microbial biomass C in planted compared to unplanted soils (Pausch et al., 2013b). However, negative priming effects occurred but were restricted to young plants (30-35 DAP) with root-derived CO_2 smaller than ~10 mg C day^{-1} kg^{-1} soil (Table S1, Figure S2). This pattern is consistent with the proposed

concept (Figure 1) where fast-growing organisms benefit from the high availability of C and mineral N at early growth stages, resulting in 'preferential substrate utilisation' and no or negative priming (Table S1) (Bernard et al., 2022; Fontaine et al., 2003; Kuzyakov, 2010).

RPEs increased with increasing root-derived CO_2 leveling off at 115% above the unplanted control. Previous studies reported on priming saturation in the detritusphere, i.e., with increasing amounts of plant litter input (Guenet et al., 2010; Guenet et al., 2018; Xiao et al., 2015) or on priming saturation after the addition of increasing amounts of water-soluble C (Wang et al., 2015). Factors other than C supply may become increasingly limiting for microorganisms (Wang et al., 2015). Microbial processes are largely governed by stoichiometric ratios of nutrients. With increasing plant age and C input by the roots, N limitation for microorganisms is aggravated due to plant N uptake. This may cause shifts in microbial physiology and/or community composition. Organisms with low carbon use efficiency (i.e., the amount of microbial biomass produced per unit of resource consumed), mainly slow-growing organisms such as fungi, are thought to be favoured under these conditions (Bernard et al., 2022). On the one hand, these microorganisms will preferentially utilise the C released by roots causing a decline in priming. However, exudates are characterised by a rather wide C/N ratio. Thus, on the other hand, these microorganisms need to obtain additional N from organic sources. Organically-bound N is utilised via N mining by enhanced recycling of microbial necromass (Cui et al., 2020) or by exudate-induced desorption of low C/N compounds from mineral surfaces (Keiluweit et al., 2015). Moreover, intensified water uptake and rhizosphere respiration can lead to decreasing O_2 concentrations and moisture levels that counteract and limit priming effects. All these processes may shift rhizosphere priming intensity to a new equilibrium. Regardless of the specific mechanisms, our findings for agricultural topsoil suggests that as root-released C input increases, the relative importance of priming-induced SOM decomposition declines. Higher C input combined with lower SOM decomposition is favourable for carbon storage in soils.

In subsoil, on the other hand, we did not detect a saturation of priming intensity, likely due to the low range of root-derived CO_2 (< 10 mg C day^{-1} kg^{-1} soil; Table S1). If we assume that half of the 10 mg C day^{-1} kg^{-1} soil was released as exudation and a mean MBC in subsoil of about 200 mg C kg^{-1} soil (Figure 3), the C input per day would equal 2.5% of MBC. For the case that added substrate C was lower than 15% of MBC, Blagodatskaya & Kuzyakov (2008) reported a linear increase of priming effects with the amount added. Despite the small input of C to subsoil, relative RPE reached much larger values (200% of unplanted soil) in subsoil than in topsoil. Absolute CO_2 efflux by RPE, however, was much lower in subsoil than topsoil, suggesting that organic matter in deeper soil horizons is better protected from decomposition by sorption to minerals (Perveen et al., 2019). Moreover, Jones et al. (2018) suggested that microbial communities in subsoil are even more C than nutrient limited compared to topsoil communities, but their activity can be readily stimulated and can quickly adapt to new substrate addition resulting in enhanced RPE relative to basal respiration.

In conclusion, our findings demonstrate that the natural abundance of ^{15}N is a suitable proxy to determine necromass recycling via priming. Overall, our data highlight that microbial N turnover is a key mechanism of priming effects in the rhizosphere and that recycling of microbial necromass contributes significantly to N uptake by plants.

ACKNOWLEDGMENTS

Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Pausch, J., Holz, M., Zhu, B. & Cheng, W. (2024) Rhizosphere priming promotes plant nitrogen acquisition by microbial necromass recycling. *Plant, Cell & Environment*, 1–10. https://doi.org/10.1111/pce.14858