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REVIEW ARTICLE

Rhizosphere carbon priming: a plant mechanism to enhance soil nitrogen accessibility?

Maire Holz · Eric Paterson · Johanna Pausch

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Abstract

Aims Soil priming affects soil N transformation and plant N availability, but few studies have investigated these interactions to date.

Methods To address this, we reviewed the literature for studies quantifying soil priming, soil N transformation and plant N uptake.

Results Gross N mineralization was strongly controlled by soil priming in studies with plants, while abiotic factors had a minor influence on gross N mineralization. In contrast, soil priming was negatively related to gross N mineralization and had a low explanatory power in incubation studies where substrates are added as surrogates for root exudates. These results indicate that plants support increased N mineralization and that this is not adequately reflected in incubation studies. Additionally, we observed a positive relationship between soil priming and the % of N_{org}-derived N uptake as well as total N uptake, which demonstrates that priming enhances the availability of N that was previously organically bound and that at least part of the N mineralized during priming was available for plant uptake.

Conclusion Our results show that the effect of roots and rhizodeposition leads to a number of processes supporting N mineralization and availability through priming that are not well reflected in incubation studies. To fully capture the interactions between plant roots and their associated microbiota, we recommend focusing research on systems with plants. Additionally, the strong correlation between C and N transformation should be considered in biogeochemical modelling.

Keywords Gross N mineralization · Soil priming · Rhizosphere microbiota · Priming mechanisms · Plant N acquisition

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M. Holz (✉)
Leibniz Centre for Agricultural Landscape Research (ZALF), Eberswalder Straße 84, 15374 Müncheberg, Germany
e-mail: Maire.Holz@zalf.de

E. Paterson
Ecological Sciences, The James Hutton Institute, Aberdeen, Scotland

J. Pausch
Agroecology, Bayreuth Center for Ecology and Environmental Research BayCEER, University of Bayreuth, Bayreuth, Germany

Introduction

Even in agricultural systems, only approximately 50% of the N taken up by crops is current-year fertilizer derived (Gardner and Drinkwater 2009; Yan et al.

2020), indicating that plants are supplied with SOM-derived N to a large degree. Up to now, the extent to which plants are capable of affecting the mineralization of N from organic sources has not been well understood (Moreau et al. 2019), although reliance on organic N sources might help in reducing the environmental impacts of agriculture and the reliance on mineral N fertilizers (Drinkwater et al. 2017). This is of particular interest, considering recent drastic increased prices and reduced availability of those fertilizers.

Nitrogen mineralization in soil is microbially driven and involves the depolymerization of polymeric N containing organic compounds into monomers and the subsequent deamination of monomers to NH_4^+ and finally possibly nitrification from NH_4^+ to NO_3^- (Geisseler et al. 2010; Schimel and Bennett 2004). Although it is soil microorganisms that transfer N from organic into the mineral forms, plants might be able to effect gross N mineralization indirectly, for example by affecting C availability in the rhizosphere, the soil around the living roots.

Plant roots release up to 20% of their total photosynthetically fixed C into the soil as rhizodeposits (Haichar et al. 2014; Jones et al. 2009; Pausch and Kuzyakov 2018). The released C serves as an energy source for soil microorganisms that are normally C limited (Soong et al. 2020) and therefore enhances microbial activity and abundance in the rhizosphere (Gunina and Kuzyakov 2015; Philippot et al. 2013). The release of large amounts of available C into the rhizosphere through root exudates can lead to short-term changes in the turnover of soil organic matter (SOM), i.e. rhizosphere priming effects (Kuzyakov et al. 2000). Rhizodeposition can suppress SOM decomposition rates by 50% or stimulate it by 380% when compared to soil without plants (Cheng et al. 2014). Several mechanisms have been put forward to explain rhizosphere priming and it is likely that these mechanism do not work exclusively (Kuzyakov 2002; Mason-Jones et al. 2018). A microbial process that is common across N-mining (Fontaine et al. 2011) and activation theories (Mason-Jones et al. 2018) of priming is an increase in extracellular enzyme production resulting in increased SOM decomposition, following inputs of easily available rhizodeposits C. It is likely that rhizosphere priming also affects soil N cycling, because of the strong link between soil C and N decomposition, and it has been suggested that soil microorganisms, which are commomnly C limited, use rhizodeposit C as an energy source and decompose SOM to acquire additional N (Kuzyakov et al. 2000; Paterson 2003). Initially, large parts of this additional N will likely be immobilized into microbial biomass, because of the wide C/N ratio of rhizodeposits and because plant roots act as sinks for N and might also enhance microbial N limitation (Farrell et al. 2014; Geisseler et al. 2010; Paterson 2003). Once microbially immobilized, N can become available again by mechanisms such as microbial grazing by protozoa (microbial loop) or by predation through viruses (viral shunt). Due to the relatively low C/N ratio of microbial residues, these processes likely contribute to the release of mineral N (Bonkowski 2004; Kuzyakov and Mason-Jones 2018; Trap et al. 2016). Based on this concept, it can be expected that a) priming increases gross N mineralization and b) that at least part of this mineralized N becomes available to the plant through processes such as microbial grazing or viral predation. However, up to now there has been no comprehensive literature review on studies quantifying priming and N cycling as well as plant N availability and uptake following priming. We therefore conducted a meta-analysis on literature quantifying soil priming and parameters related to nitrogen turnover, such as gross N mineralization GNM, organic N derived N uptake (N_{org}-derived N uptake) by plants, total plant N uptake and soil exoenzyme activities. We focused the analysis on studies working with soil–plant systems, but also considered incubation studies in a separate data set. We hypothesized that (i) priming is positively related to GNM, particularly in plant studies, as several processes resulting in a strong relationship between GNM and priming might be directly linked to processes specific to the rhizosphere. We also hypothesized that (ii) the increase in GNM under soil priming will result in an increase in N_{org}-derived N uptake by plants and an overall increased plant N uptake.

Material and methods

Data collection and calculations

We searched the literature for studies related to the interaction between priming and soil nitrogen cycling and availability (Table 1). We created three

Table 1 Overview of the studies that were evaluated in the course of the meta-analysis. Studies where generally distinguished between those investigating systems with plants ("plant") and those investigating systems with soil only ("incubation"). SOC: Soil organic matter; TN: Total nitrogen; WHC: Water holding capacity

Dataset	Main parameters of interest	Study type	Number of studies	Number of data points	Additional parameters
Dataset 1	C input; C priming; Gross N mineralization	Plant, Incubation	20	221	Plant species; C-substrate added; amount of C substrate added; soil texture; SOC; TN; soil C/N ratio; temperature; days of experiment; soil WHC
Dataset 2	C priming; N-org-derived N uptake; C priming; Total N uptake	Plant	26	228	Plant species; soil texture; SOC; TN; soil C/N ratio; temperature; days of experiment; soil WHC
Dataset 3	C priming; Enzyme activities	Plant, Incubation	25	246	Plant species; C-substrate added; amount of C substrate added; soil texture; SOC; TN; soil C/N ratio; temperature; days of experiment; soil WHC;

data sets with studies quantifying 1) priming and GNM, 2) priming and SOM-derived N uptake and 3) priming and exo-enzyme activities.

Data set 1

In order to assess the effect of soil priming on soil N cycling, we firstly searched for studies quantifying soil C priming and gross N mineralization (GNM) (124 data points). The studies were differentiated into those with plants (52 data points) and incubation experiments with soil only (72 data points). Soil C priming was calculated as:

$$PE = SOMderivedCO2_{treatment} - SOMderivedCO2_{ctrl} \quad (1)$$

where PE is soil C priming, $SOMderivedCO2_{treatment}$ is the SOM-derived CO_2 efflux of the planted treatment or the treatment with C addition, and $SOMderivedCO_{2ctrl}$ is total CO_2 efflux of the unplanted or unamended control without C addition. Priming effects were expressed as percentage of the total CO_2 efflux of the unplanted or unamended soil which was calculated as follows:

$$PE\ (\%) = \frac{SOMderivedCO2_{treatment}}{SOMderivedCO2_{ctrl}} * 100 \quad (2)$$

In order to be able to compare GNM with PE, we calculated the excess of GNM as:

$$GNM_{excess} = GNM_{treatment} - GNM_{ctrl} \quad (3)$$

where $GNM_{treatment}$ is the rate of GNM in the planted treatment or the treatment with C addition, and GNM_{ctrl} is the unplanted or unamended control without C addition. Similarly to priming,GNM_{excess} was expressed as percentage of the N mineralization of the unplanted or unamended soil which was calculated as follows:

$$GNM_{excess}(\%) = \frac{GNM_{treatment}}{GNM_{ctrl}} * 100 \quad (4)$$

Additional parameters considered were soil texture, soil organic C (SOC), total N (TN), soil C/N ratio, temperature during the experiment, days of experiment, water content expressed as % of soil water holding capacity (% WHC), plant species, type of C-substrate added and amount of C-substrate added. As most studies reported % of soil water holding capacity instead of gravimetric water content (WC), for the latter studies WC was recalculated to WHC using the program RETC (van Genuchten et al. 2006) under consideration of soil texture data. The C/N ratio of mineralization was calculated using the following equations (Jiang et al. 2021; Murphy et al. 2015):

$$C/N_{ctrl} = SOMderivedCO2_{ctrl}/GNM_{ctrl} \quad (5)$$

$$C/N_{primed} = PE/GNM_{excess} \quad (6)$$

where Eq. 5 calculates the C/N ratio of mineralization in the control treatments (treatments without substrate addition/unplanted treatments) and Eq. 6 calculates the C/N ratio primed (treatments with substrate addition/planted treatments).

Data set 2

The second data set comprised studies quantifying priming and the portion of SOM-derived N uptake (N_{org}-derived N uptake) (32 data points). The latter is the N that was first released by SOM decomposition and then taken up by plants. In one study of this dataset priming was reported solely in mg C kg^{-1} soil and not in % and a recalculation of data was not possible. Priming for this dataset was therefore displayed in mg C kg^{-1} soil instead of %. This was legitimate, as there was a strong correlation between priming (%) and priming (mg C kg^{-1} soil) (Fig. S5). In this data set we only considered non-legume plants, as the fixation of N from the air through rhizobia complicates the calculation of N_{org}-derived N uptake. N_{org}-derived N uptake (% of total uptake) was calculated using the following equation:

$$N \text{ or } g_{derived}N \text{ uptake } (\%) = \frac{\left(atm\%^{15}N \text{ Shoot} - atm\%^{15}N \text{ Tracer}\right)}{\left(atm\%^{15}N \text{ Soil} - NA - atm\%^{15}N \text{ Tracer}\right)} * 100 \quad (7)$$

where atm%^{15}N Shoot is the ^{15}N enrichment in the shoot after harvest, *atm%^{15}N Soil-NA* is the ^{15}N natural abundance in the soil without ^{15}N addition and *atm%^{15}N Tracer* is the ^{15}N enrichment after ^{15}N-tracer application to the soil. We used shoot ^{15}N values and not total (shoot and root) ^{15}N values for the calculation because total ^{15}N values were not provided in all studies.

In addition, studies quantifying soil priming and total N uptake of plants were collected (188 data points). Similarly to above, we only considered data from non-legume plants here.

Data set 3

Finally, we collected studies that quantified soil priming and exo-enzyme activities in the respective soil samples. As for data set 1, these studies were differentiated into studies investigating systems with plants (23 data points) and those investigating systems with soil only (223 data points). Exo-enzyme activities were split into those exo-enzymes responsible for cleaving C-groups and those responsible for cleaving N-groups. Soil C related exo-enzymes included: amylase, peroxidase, alpha- and beta-glucosidase, cellobiohydrolase, xylanase and phenoloxidase. Soil N related exoenzymes included: peptidase, N-acetyl glucosaminidase, chitinase and leucine aminopeptidase.

In order to be able to compare priming with the soil exo-enzyme activities, we calculated the excess of soil exo-enzyme activity as:

$$Enz_{excess\ (\%)} = \frac{\left(Enz_{treatment} - Enz_{ctrl}\right)}{Enz_{ctrl}} \quad (8)$$

where $Enz_{treatment}$ is the exo-enzyme activity measured in the planted treatment or the treatment with C addition and Enz_{ctrl} is the exo-enzyme activity in the unplanted control or the treatment without C addition. The three complete datasets can be found in the supplementary tables 1–3.

Statistics

All statistical analysis as well as the plotting of the figures were performed in R (version 3.3.1). Plots were generated using ggplot2. To estimate the association between soil priming and GNM, N_{org}-derived N uptake, total N uptake and soil exoenzyme activities, Pearson correlations were calculated. Similarly, Pearson correlations were calculated to estimate the explanatory power that the amount of substrate added has on soil priming. Student t-tests were applied to determine statistical differences in C/N ratios of mineralization between Control and Treatment ($\alpha < 0.05$).

A random forest (RF) model was applied to test for the effect of soil properties and experimental parameters on GNM and N_{org}-derived N uptake using the r package randomForest. For the RF model for data set 1 and 2, we considered soil priming, temperature, soil WHC, soil C/N ratio, days of experiment

and plant species for studies with plants. For incubation studies, the same parameters were considered, but instead of plant species, the added substrate (classified into low vs. high molecular weight) as well as the amount of added substrate were considered. RF consists of a set of randomized classification (for categorical variables) and regression trees (for numerical variables) (Breiman 2001; Breiman et al. 1984). Therefore, the response as well as the predictor variables can be either categorical or numeric, providing an advantage over conventional regression analysis. Numerous trees (in our case 2000) are generated within the algorithm and finally aggregated to give one prediction. Each tree comes from a bootstrap sample of the dataset and for each tree only a subset of predictor variables is used. To find the predictor variables that best explain the data, the trees divide the dataset into successively smaller groups (nodes (t)) for each predictor variable.

Results

We compared the relationship between soil C priming and GNM for studies with plants and for incubation studies separately (Fig. 1; Data set 1). The range of soil C priming varied greatly between study types, with plant studies exhibiting priming values of 8.4 to 246.4%, while incubation studies ranged between -29.6 and 500.0%. GNM in excess of control ranged between approximately -200 to 500% for both plant and incubation studies. We found a significant positive relationship between soil C priming and GNM for studies with plants ($p = 0.00034$) (Fig. 1, left). Soil C priming explained 21% of the variation in GNM ($R^2 = 0.21$). For incubation studies, the relationship between soil C priming and GNM was significantly negative (Fig. 1, right), though with a lower statistical power ($p = 0.038$) and a very low explanatory power of soil C priming, indicated by a low R^2 of 0.056. The random forest model identified soil C priming and temperature as the two variables with the highest explanatory power on GNM in studies with plants (Fig. 2, left). Based on the model results, the omission of these parameters would result in an increase in mean square error (MSE) of around 40% for priming and around 30% for temperature. With an expected increase in MSE of 15–20% upon omission, the variables % of WHC, soil texture, days of experiment and soil C/N ratio ranked in the middle, while the variable plant species showed the lowest explanatory power, with less than 10% increase in MSE upon omission. The total variance explained by the model was 29.56%. At 45.25%, the explained variance in the random forest model adjusted to the incubation studies was higher than that for studies with plants (Fig. 2, right). For this model, the soil C/N ratio was the variable with the highest explanatory power, with an increase in MSE of around 38% upon omission. With an expected increase in MSE of 33–36% upon omission, the variables substrate

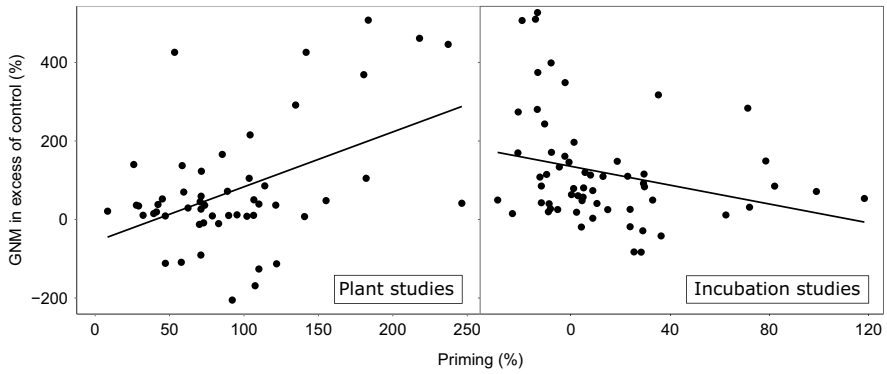

Fig. 1 Relationship between soil priming and gross N mineralization in studies with plants (left) and for incubation studies (right). For studies with plants, the correlation between the two variables was significant based on the Pearson correlation ($p = 0.00043$) with $R^2 = 0.21$ and was described by the following equation: $y = 1.398x - 56.55$. For incubation studies, the correlation between the two variables was significant based on the Pearson correlation ($p = 0.031$) with $R^2 = 0.056$ and was described by the following equation: $y = -0.36x + 117.30$

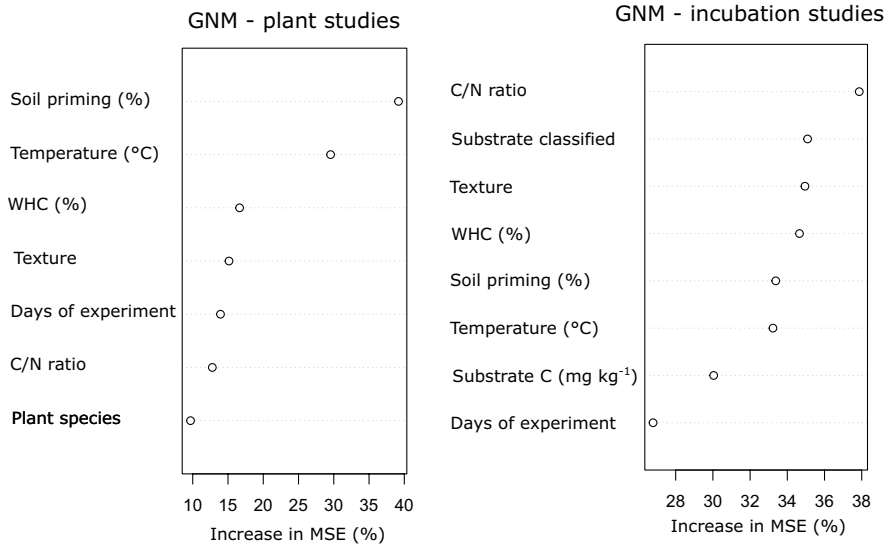

Fig. 2 Results of the random forest model, which was applied to evaluate the variables controlling gross N mineralization for studies with plants (left) and incubation studies (right). The x-axis displays the increase in mean square error (MSE) that can be expected if the respective variable was removed from the model. High x-axis values therefore indicate a strong explanatory power

classified, soil texture, % of WHC, soil priming and temperature ranked in the middle, while the variables amount of substrate C added and days of experiment showed the lowest explanatory power, with around 27–30% increase in MSE upon omission.

The C/N ratio of mineralization did not show significant differences between control and treatment for studies with plants. For incubation studies, however, the C/N ratio of mineralization was significantly lower (0.14 ± 10.26) for the treatment compared to the control (11.43 ± 9.22; Fig. S2). Overall, the C/N ratio of mineralization showed a very large variability, particularly for the treatment with substrate addition, ranging from -52 to 92 for studies with plants and from -163 to 179 for incubation studies. Note that negative values occur when C or N mineralized is lower in the treatment with substrate addition than in the control.

In the first data set, we related the amount of C substrate added in incubation studies to gross N mineralization. The correlation between the two variables was not significant and the amount of C added did not affect the magnitude of GNM (Fig. S3).

We found a significant positive correlation between soil C priming and the % of N_{org}-derived N uptake by plants ($p = 4.82e^{-07}$) (Fig. 3). Soil C priming explained 56% of the variation in N_{org}-derived N uptake ($R^2 = 0.56$). The strong correlation between soil priming and N_{org}-derived N uptake was confirmed by the random forest model, which identified priming as the variable with the

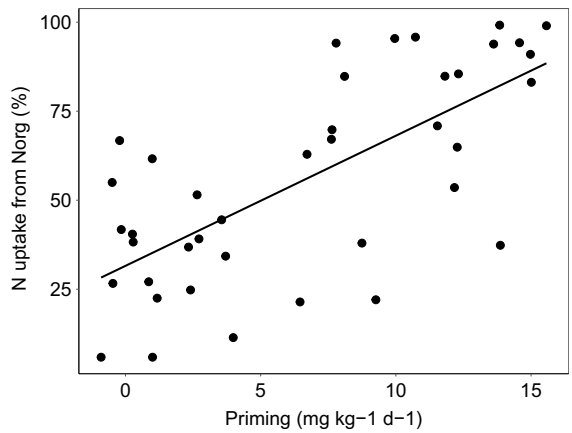

Fig. 3 Relationship between soil priming and N_{org}-derived N uptake. The correlation between the two variables was significant based on the Pearson correlation ($p = 4.82e^{-07}$) with $R^2 = 0.56$ and was described by the following equation: $y = 3.66x + 31.57$.

greatest explanatory power among all included variables, with an increase in MSE upon omission of this variable of over 40% (Fig. 4). With around 20% increase in MSE upon omission, the variables soil texture and C/N ratio showed the lowest explanatory power, while the remaining variables ranged in between. The total variance explained by the model was 62.69%.

Carbon priming and total plant N uptake showed a significantly positive correlation with a very low explanatory power ($R^2 = 0.037$), mainly due to a few

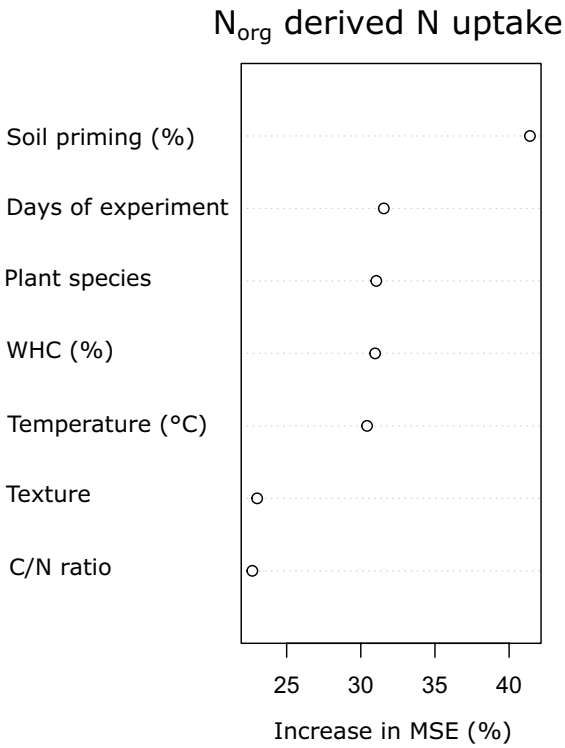

Fig. 4 Results of the random forest model, which was applied to evaluate the variables controlling N_{org}-derived N uptake. The x-axis displays the increase in mean square error (MSE) that can be expected if the respective variable was removed from the model. High x-axis values therefore indicate a strong explanatory power

outliers with very high N uptake values (Fig. 5, top). After removal of these outliers, R^2 increased to 0.21, indicating that 21% of the variance in plant N uptake is explained by soil C priming (Fig. 5, bottom).

Similarly to data set 1, the range of soil C priming in data set 3 varied greatly between plant and incubation studies, with plant studies exhibiting priming values of -65.3 to 204.2% (Fig. S6, left), while incubation studies ranged between -104.0 and 569.2% (Fig. S6). Note that for plant studies, only one negative priming value was observed (Fig. S6, left). Similar trends were observed for exo-enzyme activities, where plant studies exhibited values between -11.5 and 69.1% excess of control, while incubation studies showed values between -100.0 and 1008.7% excess of control. The relationship between soil C priming and exo-enzyme activities related to the C cycle was not significant for plant studies ($p=0.23$). For exo-enzymes related to the N cycle, this relationship was significantly positive on a level of $p=0.09$ (Fig. S6, left). For incubation studies, both, C and N cycle related exo-enzymes did not show a significant relationship to soil C priming (Fig. S6, right).

Discussion

We found that soil priming was related to increases in soil GNM in systems with plants but not in incubation setups (Fig. 1). This finding was confirmed by the random forest analysis for plant studies, where soil priming was the variable with the strongest explanatory power for GNM. In contrast, for incubation studies, soil priming had only moderate explanatory power for GNM. One main difference between plant and incubation studies was the duration of the experiments, which was on average 110 days for plant studies but only 25 days for incubation studies. However, based on the random forest analysis, the duration of experiment had only a small effect on priming and GNM in both plant and incubation studies (Fig. 2, S1). Apart from this, both study types differ in a) the way the substrate was added to the soil, and b) the composition of the substrates added to the soil. Substrate addition can be differentiated into continuous and pulse input. For incubation studies, substrates are commonly added to the system once, at the beginning of the experiment, as a pulse. In contrast, for plant studies, the substrate is added to the soil continuously in the form of rhizodeposition as the roots grow. However, the substrate addition approach (pulse vs. continuous input, i.e., plant vs. incubation studies) did not have a strong effect on priming or GNM either. The contrasting results in the relationship between priming and GNM for plant and incubation studies may be explained by the composition of substrates added. For incubation studies, commonly one substrate that includes C but no N is added at a time, while for plant studies a mixture of substrates is added through rhizodeposition. Rhizodeposits include primary metabolites, such as sugars, amino acids and organic acids, as well as secondary metabolites, such as flavonoids and other compounds, such as exoenzymes, mucilage or root border cells (Farrar et al. 2003).

Our results indicate that the combination and interplay of different substances released by plants into the rhizosphere and possibly direct effects of

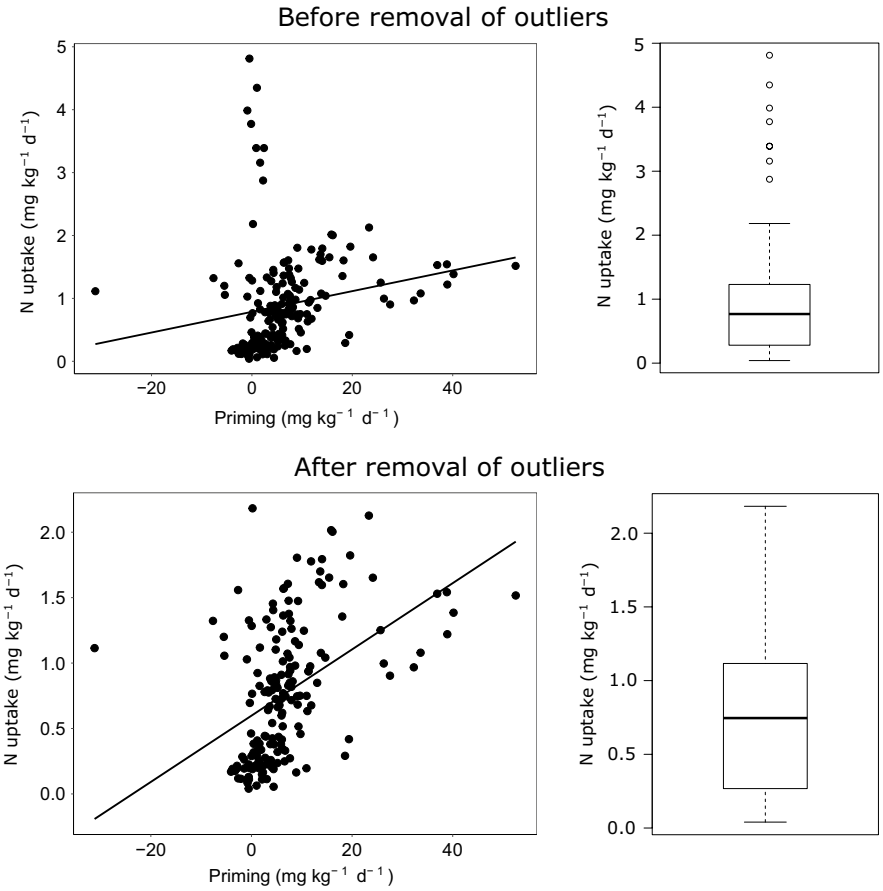

Fig. 5 Relationship between soil priming and plant N uptake. Before removal of outliers, the correlation was significant ($p = 0.0085$) but had a low R^2 of 0.037 (top). After removal of outliers, R^2 increased to 0.21 ($p = 1.53e\text{-}10$) (bottom). The boxplots to the right show the distribution of N uptake data before and after removal of outliers

roots result in an increase in GNM with soil priming. For example, it has been shown that N efficient plants support growth of rhizosphere microorganisms that contain high numbers of genes related to N metabolism (Zhang et al. 2019). In this way, plants may promote the abundance of bacteria utilizing organic nitrogen, thus increasing GNM and possibly the availability of mineral nitrogen to the plant by ammonification. Additionally, the plant is a sink for nitrogen, and the removal of mineral nitrogen from the soil solution by the plant root will affect soil priming and GNM (Paterson 2003). These processes cannot be reflected in incubation setups, where usually only one substance is added to soil and where nitrogen is not removed from the soil. However, it is worth noting that, compared to incubation studies, measuring priming in planted systems involves a greater complexity, as plants need to be either labelled continuously or the natural abundance approach (C4 plant on C3 soil or vice versa) needs to be applied. This explains why many studies have used added substrates (incubation), while incubation setups may be justified, depending on the question addressed.

We found that soil priming was not only positively related to GNM but also to the proportion of N_{org}-derived N uptake as well as total N uptake (Fig. 4, 5). Though, it has to be considered, that in our study, the proportion of N_{org}-derived N uptake was calculated based on shoot delta^{15}N values, not on the whole plant (shoot and root) delta^{15}N values. In the case of an uneven distribution of ^{15}N in shoot and root, this could possibly lead to and over or under estimation of the proportion of N_{org}-derived N uptake. Our finding on the positive relation between priming and N_{org}-derived N uptake indicates that not only N mineralization was increased due to soil priming, but also N availability and plant N uptake. One way of increasing not only GNM but also plant N availability might possibly be the desorption of mineral associated

organic matter (MAOM) from minerals surfaces through the exudation of organic acids into the soil, a process termed abiotic priming (Jilling et al. 2018; Keiluweit et al. 2015; Li et al. 2021). It has been suggested thatMAOM, once it is released into soil solution, is exposed to soil microorganisms which might result in net N mineralization due to its high N content (Cotrufo et al. 2019; Schimel and Bennett 2004). In previous studies the C/N ratio of mineralization was used as an estimate of preferential mineralization of N rich compounds in treatments with substrate addition compared to the control (Jiang et al. 2021; Murphy et al. 2017). Low C/N ratios of mineralization in treatments compared to the control would indicate that substrate addition results in preferential N- compared to C mineralization (Jilling et al. 2018; Murphy et al. 2015). Although this was not confirmed in our study, the lack of difference between C/N ratio of mineralization between treatments with substrate addition compared to the control for our data could be caused by the extremely high data variability (Fig. S2).

Apart from abiotic priming, several other mechanisms can result in increased plant N availability following root exudation and soil priming. The high C input through root exudates is likely to lead to microbial N limitation and microbes might therefore start mining for organic N by enzyme production and immobilize this N into their biomass so that it is not available to the plant (Farrell et al. 2014; Geisseler et al. 2010). Only few of the studies considered within this meta-analysis quantified soil exo-enzymes, which hampers the interpretation of these results. Nevertheless, for plant studies, the relationship between N-cycle related enzymes and GNM was positive, though only to a level of $p = 0.09$. Once labile root exudate C is exhausted, e.g. in the region behind the root tip, a shift in microbial communities towards low CUE microorganisms may occur in combination with an increasing N deficit due to N immobilization (Bernard et al. 2022). The "new" microbial community may recycle nutrients from "old" communities, i.e. from microbial necromass (Cui et al. 2020; Kaiser et al. 2014). Due to the low C/N ratio of the necromass, net N mineralization will occur, enhancing plant N availability particularly in the root regions behind the root tip, where N uptake is greatest (Eshel and Beeckman 2013). Beside shifts in microbial communities, also N released by mechanisms such as grazing and viral shunt (microbial loop) likely contribute to the release of mineral N from microbial residues (Bonkowski 2004; Kuzyakov and Mason-Jones 2018; Trap et al. 2016).

Recently, it has been suggested that the amount of substrate added to soil is positively related to soil priming (Liu et al. 2017; Lloyd et al. 2016; Mason-Jones et al. 2018). For plant systems, this would indicate that GNM and finally also plant N availability increases with rhizodeposition. In priming studies, rhizodeposition is usually not quantified, while the plant-derived CO_2 flux could be used as a parameter to estimate substrate addition. As only few studies reported these data, we were not able to relate substrate addition to priming and GNM in plant studies. We therefore strongly encourage authors to provide data on plant-derived CO_2 efflux in priming studies in order to be able to link the amount of released rhizodeposits to soil priming and N mineralization.

Finally, it has to be considered that the datasets on priming and N cycling were relatively small which limits the robustness of the study. More studies that relate C priming in soil to N turnover and plant N uptake could greatly increase our understanding on the interrelation of both processes. Additionally, most of the studies included in this meta-analysis were conducted in agricultural soil and with agricultural crops which limits the scope of this study to those systems. However the age of the plants at the time points of measurements ranged from 21 to 140 and therefore covers a wide range of developmental stages which positively affects the significance of the study.

Conclusions

We found that gross N mineralization was most strongly controlled by soil priming and that abiotic factors such as soil moisture or soil texture had a far lower influence on gross N mineralization for studies conducted with plants. This indicates that the presence of plants caused an increase in soil N mineralization. This increase might be caused by plant N uptake and the resulting microbial N limitation and by C priming caused by root exudation. In contrast to plant studies, the correlation between soil priming and gross N mineralization was significantly negative for incubation studies, indicating that plants, by root exudation, support increased N mineralization, and that this is not adequately reflected in incubation studies.

Additionally to this increase in N mineralization, we observed a positive correlation between soil priming and the % of N_{org}-derived N uptake by plants and total plant N uptake. This shows that at least part of the N mineralized during priming was available for plant uptake. In conclusion, our meta-analysis indicates that rhizodeposition results in a number of processes leading to increased N mineralization and plant N availability. We therefore recommend focusing research on priming and related N cycling in systems with plants, so that diverse influences of roots on soils and microbial communities can be represented. We further suggest that the strong relationship between C cycling (i.e. priming) and N transformation be considered when modelling soil C and N transformation.

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Author contributions MH and JP planned and designed the research. MH conducted the meta-analysis and analyzed the data. MH, JP and EP wrote the manuscript.

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Data availability The data that supports the findings of this study are available in the supplementary material of this article (Suppl. Table 1–3).

Declarations

Competing Interests "Financial interests: The authors declare they have no financial interests.

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