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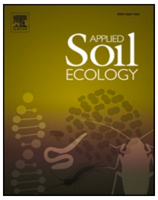

Research paper

Distinct interaction between management history and nitrogen source drive microbial nitrogen processes in soil

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ABSTRACT

Microbial processes in soil primarily govern nitrogen (N) availability to plants. However, microbial processes can be altered by farming history due in part to resource adaptation by microbes and such changes could further modify N dynamics between fertiliser and plants. Here, using a two-months greenhouse experiment, we investigated plant N uptake from applied fertilisers as well as microbial parameters in N cycling modified by management history and fertiliser types. Sixteen soils were collected from either organically or conventionally managed fields and fertilised with $(^{15}NH_4)_2SO_4$ (mineral N fertiliser) or ^{15}N-*Lolium multiflorum* (organic N fertiliser). Among microbial parameters tested, ammonia-oxidizing archaea (*amoA*) and membrane-bound nitrate reductase (*narG*) gene abundance responded to management × fertiliser interaction. Organically managed soils exhibited greater gene abundances with organic fertiliser compared to mineral fertiliser, and the opposite trend was observed with conventional management and mineral fertiliser. Plant fertiliser N uptake was associated with all microbial parameters tested, however, no positive interactions between management history and fertiliser type was observed. A clear management × fertiliser interaction effect was found exclusively in microbial biomass N with mineral fertiliser application where its association with plant N uptake was negative with organically managed soil but positive with conventionally manged soil at first harvest. Our results suggested that soil microbes are highly versatile and respond strongly to current nutrients conditions. Thus, fertiliser type and timing would be a key driver of short-term plant N uptake and warrant consideration to improve plant N recovery.

1. Introduction

Nitrogen (N) is one of the most vital nutrients for terrestrial primary productivity, and limited soil N availability is a common constraint of plant growth. In agroecosystems, N fertilisation is used excessively to circumvent N limitation and assure crop yield. More than 100 Tg N yr^{-1} are applied on agricultural lands, yet only about half is taken up by crops (Cross et al., 2025; You et al., 2023). As a result, N often leaches into soil and freshwater systems or is emitted as nitrous oxide (N_2O), contributing to environmental pollution (Di and Cameron, 2002; IPCC, 2023). Reducing these detrimental N losses is of paramount importance, therefore it is essential to improve the coupling between N supply from fertilisation and crop N demand to achieve a more efficient use of N in agroecosystems.

Microbial processes largely govern the availability of N in soils. Microbes decompose organic N and provide mineral N to the soil system (i.e. N mineralisation). However, they also assimilate mineral N to support growth and thus bind N in their biomass (i.e. N immobilisation). Nitrogen immobilisation could compete with the crop N uptake but may also help stabilise excess N in the soil, reducing N losses. Microbial N may later be gradually re-mineralised and become available for crops during subsequent growing season. However, the (re)mineralised N could also fuel nitrification – the microbial oxidation of ammonium to nitrate – which increases the risk of N loss via leaching (Beeckman et al.,

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2018). Nitrate may then undergo sequential reduction steps which transform nitrate to dinitrogen gas, ultimately leading to N loss into the atmosphere (Stein and Klotz, 2016). Thus, processes governed by soil microbial communities are crucial for regulating soil N availability and, ultimately, the N acquisition of plants.

Farming systems can alter functional traits of soil microbial communities (Chou et al., 2017; Lori et al., 2024), which in turn may change subsequently soil N dynamics. Recent work shows that organic inputs often increase the microbial abundance and activity in N cycling – including higher gene abundances in denitrification and N transport, and enhanced mineralisation enzyme activity, – relative to conventional, mineral-based fertilisation, which indicates a greater capacity to process complex organic substrates under organic farming (Hu et al., 2024; Jezierska-Tys et al., 2020; Yu et al., 2024). Further, Chou et al. (2017) showed a greater microbial versatility to degrade different carbon (C) sources in organically managed soils than conventionally managed soils. Recent meta-analyses suggest that organic amendments can tighten soil N cycling by concurrently accelerating gross mineralisation and immobilisation, thereby expanding transient mineral N pools and improving opportunities for crop N interception relative to synthetic fertilisers (Breza and Grandy, 2025). Similarly, studies comparing N use efficiency in organic and conventional systems find higher nutrient use efficiency under organic management (Maeder et al., 2002; Sanders et al., 2025). Recent studies highlighted further that soil functions such as N cycling can differ depending on management systems where less intensive farming systems could have enhanced ecosystem multifunctionality (van Rijssel et al., 2025; Yu et al., 2024). Together, these advances support a mechanistic view in which long-term exposure to complex organic inputs such as under organic farming selects for microbial traits that enhance mineral N supply to plants from organic sources, and also regulate downstream nitrification and denitrification pathways through temporal immobilisation. Such shifts in microbial communities provides a plausible pathway for a tighter coupling between N supply and plant uptake in organically managed soils receiving organic amendments.

This study aims to experimentally explore such potential soil microbes' resource adaptation due to organic management history and its impact on plant N uptake by means of microbial immobilisation, mineralisation, nitrification and nitrate reduction. To this end, we employed a greenhouse study with 16 soils of either organic or conventional management history. We used ^{15}N labelling to trace fertiliser-derived plant N uptake and calculated plant ^{15}N recovery from organic and mineral fertiliser. Besides microbial biomass N, we assessed mineralisation, nitrification and nitrate reduction using qPCR targeting chitinase (*chiA*), archaeal and bacterial ammonia monooxygenase (*amoA*) and nitrate reductase (*narG*), respectively. Under the assumption that long-term organic management enriches microbial functional traits, we expect these microbes to respond more strongly to complex organic substrates. As a result, key microbial N processes – such as mineralisation, immobilisation, nitrification and nitrate reduction – may interact differently with plant N uptake in organically than in conventionally managed soils. Therefore, our central hypotheses were;

(1) Soils with a history of organic management harbour higher microbial abundances than conventionally managed soils when organic fertiliser is applied as microbes under long-term organic management are adapted to organic inputs and better positioned to exploit such resources.
(2) Plant ^{15}N recovery is facilitated by high N mineralisation but hindered by N immobilisation, nitrification and nitrate reduction as mineralisation supplies plant available N while the other processes compete with plant N demand.
(3) The relationships mentioned in (2) are most significant in organically managed soil with organic fertilisation, reflecting enhanced microbial capacity to utilise organic sources and subsequent increase in those microbial processes.

2. Materials and methods

2.1. Field sampling and greenhouse experiment

Sixteen soils were collected in February 2019 from the top 0–20 cm layer of farmer-managed fields, with eight samples from organically managed (hereafter BIO) and eight from conventionally managed (hereafter CON) fields. Organically managed fields solely relied on organic fertilisers whereas conventionally managed fields were fertilised mainly with synthetic fertilisers alongside regular organic fertiliser inputs. The management practices at each field followed the guidelines of BioSuisse, the Federation of Swiss Organic Farmers (Bio Suisse, 2025) or the 'Proof of Ecological Performance' guidelines of the Federal Office for Agriculture, Switzerland (Federal Office for Agriculture (FOAG), 2025), respectively. All fields were located in the northeast of Switzerland. Soils were classified as Cambisols and contained 10–39 g SOC kg^{-1}, 1.1–4.8 g total N kg^{-1}. There was no fertilisation activity at least 2 months ahead of the sampling. The soils were sourced from fields where crop residues, plant debris, and grass cover were removed prior to sampling to ensure consistency in soil conditions for the greenhouse experiment. The soils were then passed through a 8 mm sieve and stored at 4 °C until its use. Physicochemical characteristics of 16 soils are detailed in Table S1. The initial status of the microbial parameters of the 16 soils was not determined.

Soils were filled into 3 l pots by volume to ensure the same growing space for all treatments. Soils were amended with either 1.45 atom% excess $(^{15}NH_4)_2SO_4$ (mineral N fertiliser) or 2.00 atom% excess ^{15}N-*Lolium multiflorum* litter (organic N fertiliser) at a rate of 90 kg N ha^{-1}. Both amendments were fully mixed with soil upon the application. ^{15}N labelled plant litter was produced following Toda et al. (2023) and had C/N ratio of 9.94. In our experiments, we used the two N inputs to simulate contrasting N fertiliser sources, which we will refer to as the "mineral" and "organic" fertiliser treatments. This terminology simplifies the complex nature of real-world fertilisers. We adopted this simplification to maintain clarity and focus in our study, ensuring a clear distinction between the effects of purely mineral versus organic sources of N. The pots were arranged in a completely randomized block design with six replicates for each soil and fertiliser combination resulting in a total of 192 pots (2 management histories × 8 soils × 2 fertiliser treatments × 6 replicates). *Plantago lanceolata* was chosen as a model plant following earlier works (Edlinger et al., 2022; Nuccio et al., 2013). Soil water content was controlled by weighing and adjusted to 60% of field capacity throughout the experiment by watering every other day. Shoot and soil samples were taken from the same individual pots two times (3 weeks of establishment phase followed by one growing periods of 5 weeks). At each harvest, plants were cut 2 cm above the soil surface and dried at 65 °C for 24 h. After determining aboveground biomass, the plant material was homogenised using a blender and sub-samples were further ground with a ball mill for shoot N concentration and ^{15}N isotopic ratio analysis. Soils were collected with three soil cores (2 cm diameter, equivalent to pot depth) from each pot at each harvest. Three cores were thoroughly mixed by hands prior to subsampling for molecular analysis. Soil subsamples for molecular analysis were taken into 2 × 2 ml Eppendorf tubes, snap-frozen in liquid N_2 and stored at −80 °C until freeze-drying processing. The remaining soil sample was placed into 50 ml falcon tubes and stored at −20 °C until the microbial biomass measurements (Stenberg et al., 1998). After the first harvests, the void spaces due to core sampling were refilled with the same field soils used to fill in the pots initially.

2.2. Determination of plant ^{15}N recovery

Dried shoot samples were ground with a ball mill and the N concentration and ^{15}N isotopic ratio were determined with an elemental analyser interfaced with an isotope mass spectrometer. The plant ^{15}N recovery at each harvest was calculated as follows (Wu et al., 2010):

$$\text{Ndff}\ (\%) = \text{Es}/\text{Ef} \times 100$$

$$\text{Plant}^{15}\text{N recovery}\ (\%) = \left(\text{Shoot N} \times \text{Ndff}/\ ^{15}\text{N applied}\right) \times 100$$

where Ndff is N derived from fertiliser, Es is ^{15}N enrichment of shoot samples (atom%) at each harvest and Ef is the ^{15}N enrichment of applied fertiliser. ^{15}N recovery was calculated based on shoot biomass at each harvest. The data for shoot biomass and shoot N content were reported elsewhere (Toda et al., 2023).

2.3. Microbial biomass N measurement

Soil microbial biomass was determined using the fumigation extraction method with slight modification for K_2SO_4 concentration (Brookes et al., 1985). The frozen soil sample was acclimated at 5 °C overnight before the extraction. The soil was passed through a 2 mm sieve to remove roots and stones. Then, 15 g of the soil were fumigated with chloroform for 24 h at 25 °C. Fumigated and non-fumigated samples were extracted with 75 ml of 0.05 M K_2SO_4 (Bruulsema and Duxbury, 1996; Makarov et al., 2015) on an overhead shaker for 1 h. Total dissolved N in the filtrate was measured using a TOC/TNb analyser (Elementar Analysensysteme GmbH, Langenselbold, Germany). Microbial biomass N (MBN) was calculated as follow:

$$\text{MBN}\ \left(\text{mg N kg}^{-1}\right) = \text{N}_{\text{fumigated}} - \text{N}_{\text{unfumigated}}$$

where $N_{\text{fumigated}}$ and $N_{\text{unfumigated}}$ refers to extractable N in fumigated and unfumigated samples. A conversion factor was not applied in the current study to make the comparison easier with other studies using different conversion factors. Thus, MBN mentioned here is equivalent to the extractable N-flush.

2.4. Soil DNA extraction and quantitative real-time PCR

The frozen soils subsamples were freeze-dried using a freeze dryer prior to the DNA extraction. Soil DNA was extracted from 0.15 g of dry soil using NucleoSpin® 96 Soil 96-well kit (MACHEREY-NAGEL GmbH & Co. KG, Düren, Germany) following the manufacturer's instructions with slight modification. Briefly, DNA was extracted twice from the same soil samples and pooled as one sample. The quantity of the extracted DNA was measured with a Spark 10 M Multimode Microplate Reader (Tecan Trading AG, Männedorf, Switzerland) and normalized to a working concentration of 5 ng μl^{-1}. The abundance of genes encoding ammonia monooxygenase (archaeal and bacterial *amoA*), membrane-bound nitrate reductase (*narG*) and chitinase (*chiA*) was determined by qPCR assay with a CFX Opus 384 Real-Time PCR System (Bio-Rad Laboratories, Inc., CA, USA). A total of 5 μl qPCR mixture contained 1 μl of 5 x HOT FIREPol® Blend Master Mix (Solis BioDyne, Tartu, Estonia), 0.5 μl of 30 μg μl^{-1} bovine serum albumin (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany), 0.25 μl of 10 μM of each primer, 2.75 μl of double-distilled water (ddH2O), and 0.25 μl of normalized DNA. The thermal cycler condition consisted of an initial denaturation at 95 °C for 12 min, followed by 40 cycles of denaturation at 95 °C for 45 s, annealing at the primer specific temperatures for 45 s, elongation at 72 °C for 45 s, and a stepwise melting curve from 95 to 55 °C in 1 min to check for PCR product specificity. The primers employed and the corresponding nucleotide sequence and annealing temperatures are described in detail in Table S2. Standard curves were obtained using serial 10-fold dilutions of a known amount of plasmid DNA (6.92 to 9.18 $\times 10^6$ gene copies) containing each target gene fragment. The details of each plasmid standard are described in Table S2. All standards and samples were measured in triplicate. The Cq value of standards and samples were normalized by multiplying with PCR efficiency averaged by standard samples (standards) or by field site (samples) using the LinRegPCR program (version 2016) (Brankatschk et al., 2012).

2.5. Statistical analysis

All statistical analyses were performed using R version 4.5.1 (R core team, 2025). Field 60 was considered an outlier due to its extremely small biomass (on average, Field 60: 4.19 g and the other field: 7.81 g). This was presumably attributed to extremely low soil phosphorus availability compared to all other sites (Table S1), and Field 60 was excluded from all statistical analysis incorporating plant parameters – such as plant ^{15}N recovery.

Generalised linear mixed models were fitted with microbial parameters (MBN or AOA *amoA* and AOB *amoA*, *chiA* or *narG* gene abundances) or total dissolved N (TDN) as the response variable and management history, fertiliser type, harvest and all interactions as explanatory variables. The models were specified with Gaussian or Gamma distribution either with log or identity link. The residual variance was allowed to differ among management history, fertiliser type and harvest to ensure normality and homoscedasticity, if necessary. The details for fitted models were summarised in Table S3.

The relationship with plant N uptake was also analysed with generalised linear mixed models where plant ^{15}N recovery was the response variable and microbial parameters or TDN, management history, fertiliser type, harvest, and all interactions were explanatory variables. For MBN and AOA *amoA*, or *chiA*, Gamma distribution either with identity (MBN and AOA) or log (*chiA*) link was used with different residual variance permitted between fertiliser type and harvest. For AOB *amoA* or *narG* and TDN, a Gaussian distribution with log (AOB) or identity (*narG* and TDN) link was used, and different residual variance was set between management history and fertiliser type.

In all models, field and replicate and their interaction were treated as random factors. Type II Wald tests were conducted to infer the effect of each fixed factor and their interaction. Subsequent pairwise comparison was performed based on estimated marginal mean with *P*-values adjustment according to the Tukey method. All generalised linear mixed models were performed using the package glmmTMB ver.1.1.12 (Brooks et al., 2017) and slope trend analysis and pairwise post hoc test were performed using the package emmeas ver.1.11.2-8 (Lenth, 2024). The significance level was set to 0.05 for all analyses.

3. Results

3.1. Initial soil properties and total dissolved N dynamics

There was no significant effect of management history on any initial soil parameters measured, yet total organic C, total C, total N and aggregate stability measured as mean weight diameter tended to be higher in BIO soil while Olsen-P tended to be lower compared to CON soil (Fig. S1, and all statistical details were provided in Table S4).

The unfumigated fraction of total dissolved N (TDN) was used as a proxy for mineral N fraction in the soil (Brookes et al., 1985). There was significant interaction effect between management history and fertiliser type where BIO soils showed 1.8–1.5 times higher TDN than CON soils but it was statistically significant only under mineral fertilisation (Tukey HSD, $P = 0.032$, Fig. S2). There was also significant effect of fertiliser type but the effect depended on harvest. TDN was 1.7 times higher with mineral fertiliser compared to organic fertiliser at first harvest (Tukey HSD, $P < 0.0001$, Fig. S2).

The association between TDN and plant ^{15}N recovery was conditional on fertiliser type and harvest (3-way interactions: $\chi_1^2 = 18.8$, $p < 0.0001$). The significant negative associations were found at 1st harvest across fertiliser types (marginal slope estimate, $P = 0.002$ or smaller, Fig. S3) and at the second harvest with organic fertiliser (marginal slope estimate, $P = 0.037$, Fig. S3).

3.2. *Effect of management history and fertiliser type on microbial parameters*

The application of organic fertiliser led to higher MBN by 1.41 times at 1st harvest and 1.25 times at 2nd harvest compared to mineral fertiliser (Tukey HSD, $P < 0.0001$, Fig. 1) while mineral fertiliser application resulted in 1.20 times higher AOB *amoA* abundance than organic fertiliser across two harvests (Tukey HSD, $P < 0.0001$, Fig. 1). For AOA *amoA* and *narG* abundance, the effect of fertiliser type varied among management history and harvest (Fig. 2, Table S5). Organic fertiliser led to higher AOA *amoA* abundance by 1.18 times at 1st harvest (Tukey HSD, $P = 0.038$) and *narG* abundance by 1.10 times at 2nd harvest (Tukey HSD, $P = 0.005$) in BIO soils compared to mineral fertiliser application (Fig. 2). Contrary, in CON soils, mineral fertiliser application led to higher AOA *amoA* abundance by 1.42 and 1.19 times than organic fertiliser at 1st and 2nd harvests respectively (Tukey HSD, $P = 0.029$ or smaller, Fig. 2). Among microbial parameters tested, management history had the least effect, showing only marginal effect for AOA *amoA* and *narG* abundance (Table S5).

3.3. *Influence of soil microbial parameters on plant ^{15}N recovery*

Plant ^{15}N recovery was associated with all five microbial parameters tested, suggesting microbial influences on plant available N.

The relationships varied with management history, fertiliser types or harvests. For instance, at the first harvest, plant ^{15}N recovery was negatively associated with MBN in BIO soils, whereas a positive association was observed in CON soils under mineral fertilisation (Fig. 3a). At the second harvest, all relationships were similar and clearly positive independent from management history (Fig. 3b). In contrast, with organic fertilisation, we observed consistently positive relationships between MBN and plant ^{15}N recovery across two harvests (Fig. 3d, e). Besides MBN, we also observed a positive association with the abundance of the *chiA* gene – used here as a proxy for organic N mineralisation – but only at the second harvest (marginal slope estimate, $P = 0.005$, Fig. 4).

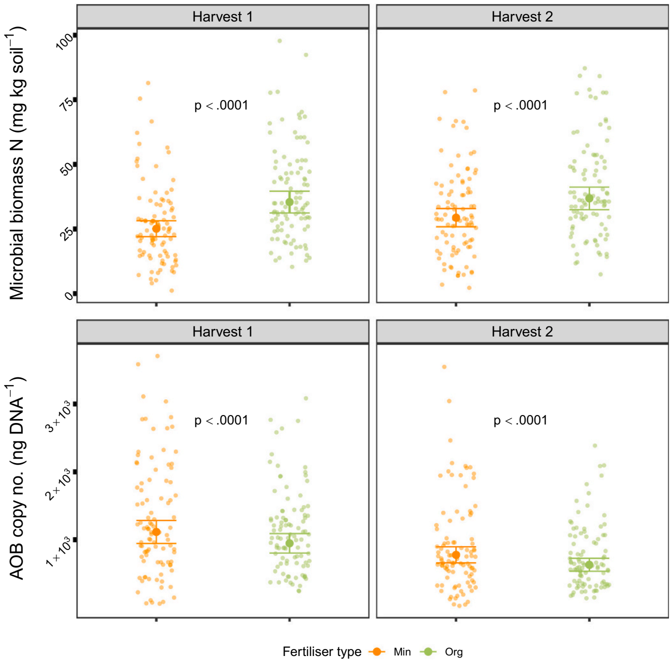

Fig. 1. The model estimated microbial biomass N and AOB *amoA* gene abundance with different fertiliser application across two harvests from eight farms. The large points show model estimated means (± SE) and the small points show the measured microbial abundances. Data was pooled across management history since no significant management history main or interaction effect was detected. Generalised linear mixed models (GLMM) were used to calculate estimated means (see in Section 2.5). The significance between fertiliser types at each harvest was indicated by *P*-value in each panel.

The association between plant ^{15}N recovery and ammonia oxidisers' abundance – *amoA* of AOA and AOB – was dependent on fertiliser type and harvest (3-way interactions, AOA: $\chi^2_1 = 8.01$, $P < 0.005$, AOB: $\chi^2_1 = 5.79$, $P < 0.016$). AOA *amoA* gene abundance was associated positively with plant ^{15}N recovery at the first harvest but shifted to a negative association at the second harvest (Fig. 4). For AOB *amoA* abundance, only mineral fertiliser application had significant relationships which showed inverse trends compared to AOA *amoA* abundance (Fig. 4). A significant negative association of plant ^{15}N recovery with the abundance of the *narG* gene was found under both fertiliser type, but only at the first harvest (marginal slope estimate, $P = 0.014$, Fig. 4).

4. Discussion

In our study, we set out to investigate the role of soil microbial processes on plant N acquisition upon two different types of fertilisation and with contrasting management histories. Our results show only weak effect of management history, while fertiliser type had a dominant impact. Microbial processes were strongly linked to plant N uptake, demonstrating their importance in the soil-plant nexus.

4.1. *Effect of resource legacies on microbial-mediated N processes*

Overall, fertiliser type dominated over management history × fertiliser interaction, where organic fertiliser increased MBN while mineral fertiliser increased AOB abundance irrespective of management history (Fig. 1).

The majority of soil microbes are characterised as heterotrophs and utilise organic C as an energy source (Jin et al., 2024). Soil C is often depleted in agricultural soils (Beillouin et al., 2023), and the soils used in the current study contained relatively low SOC (ave. SOC / clay = 0.082, data not shown). Adding organic fertiliser likely supplied the C substrate needed for microbial growth. Consequently, this additional C input could explain the greater microbial biomass observed under organic compared to mineral fertiliser independent of the management history.

The availability of ammonia greatly impacts ammonia-oxidizers due to niche differentiation between AOA and AOB, suggesting that AOB is more prevalent in nitrogen-rich environments (Hink et al., 2018). In line with this, a meta-analysis by Carey et al. (2016) reported that nitrogen addition led to an increase of AOA and AOB abundances on average by 27% and 326%, respectively. They also showed that AOB abundance increased to a greater extent with mineral fertiliser compared to organic fertiliser, which aligns with our results.

Beyond fertiliser effects, initial soil conditions between management histories appeared broadly comparable, although initial N availability tended to be higher in BIO soils (Table S1, Fig. S2). This has been expected to promote higher initial microbial biomass in soils with organic management history (Li et al., 2024). Yet no such difference was detected in MBN pointing to high microbial versatility in adapting to new nutrients conditions. Similarly, no significant differences between management histories were found for other important soil parameters, such as pH. Thus, one might assume that the two management histories resulted in broadly comparable soil microbial community composition at the start of the experiment.

However, we found some evidence that the microbial response to different fertiliser types depends on management history. The abundance of AOA and *narG* showed a positive response based on management history and fertiliser types (Fig. 2), – for example, BIO soils harboured higher microbial abundances with organic than mineral fertilisers, while similar pattern was observed from CON soils with mineral fertilisers. Such history dependent response was not clearly observed in MBN, yet there was a trend showing higher MBN with organic than mineral fertilisation in BIO soils ($\chi^2_1 = 3.36$, $P = 0.067$, data not shown).

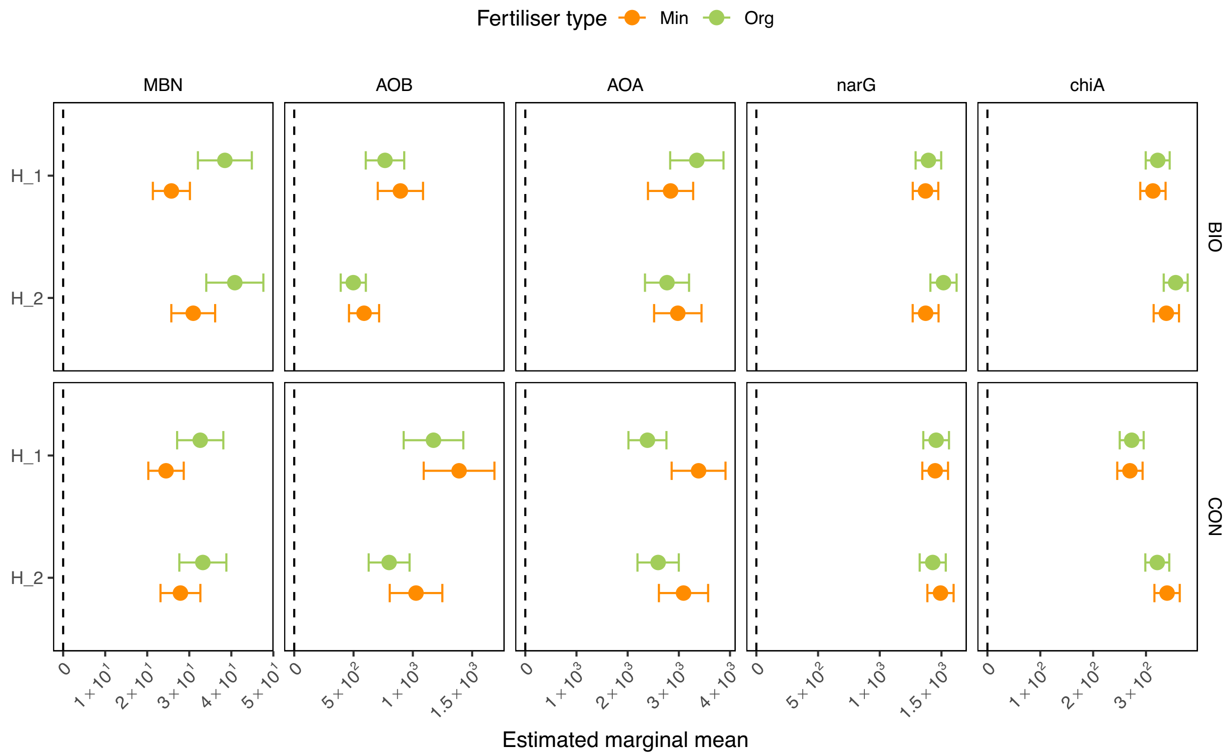

Fig. 2. The model estimated marginal means (± SE) for soil microbial parameters, as affected by management history and fertiliser types across tow harvests. MBN: microbial biomass N, AOB: bacterial *amoA*, AOA: archaeal *amoA*, narG: membrane-bound nitrate reductase, chiA; chitinase gene abundance, H_1: Harvest 1, H_2: Harvest 2. MBN are shown as mgN kg soil^{-1} and gene abundances are shown as copy number ng DNA^{-1}. Generalised linear mixed models (GLMM) were used to calculate estimated means (see in Section 2.5).

This provides some indication for the adaptation of microbial guilds to farm management, as we initially hypothesised, however, the effects were comparatively small and mainly fertiliser dependent. Yet, earlier studies indicated that microbes in organically managed soils are better adapted to convert organic substrates while possessing augmented enzyme capacities (Chou et al., 2017; Flieβbach and Mäder, 1997; Jezierska-Tys et al., 2020). The limited positive responses in the present study might be partly due to farming practices in Switzerland, where conventional farming still applies a substantial amount of organic amendments and does not rely solely on mineral fertilisers (Büchi et al., 2019).

4.2. *Effect of microbial processes on plant ^{15}N recovery*

4.2.1. *Microbial immobilisation and mineralisation*

Microbial biomass N showed a clear relationship with plant ^{15}N uptake. However, the relationships were not intensified in BIO soils with organic fertiliser (Fig. 3). Instead, strong management × fertiliser interactions were found with mineral fertiliser. For instance, BIO soils showed a negative relationship between MBN and plant ^{15}N recovery with mineral fertilisation at the first harvest, while CON soils showed a positive one (Fig. 3a), which may indicate differences in MIT dynamics depending on the management history. Differences in N dynamics between managements could be attributed to differences in total organic carbon (TOC) content, which tended to be higher in BIO soils than CON soils (Fig. S1). Carbon sufficiency – e.g. soils under organic management – generally accelerates N immobilisation since the heterotrophic lifestyle of most microbes results in a strong demand for C as an energy source to metabolise N (Mooshammer et al., 2014). Following mineral N fertilisation, microbial communities may more rapidly immobilise the additional N in soils with a history of organic management, facilitated by the higher availability of C (Cao et al., 2021). This rapid immobilisation enhances the N retention and thus intensifies competition between plants and soil microbes for N. In contrast, CON soils may have limited competition for N due to C limitation rather than N deficiency. The negative relationship in BIO soils turned into positive at second harvest, which indicates N release through re-mineralisation of microbial biomass (Pausch et al., 2024).

In line with these patterns, the dissolved nitrogen (TDN) fraction was higher in BIO soils than CON soils under mineral fertilisation (Fig. S2), indicating the greater supply of soil-derived N in BIO soils. The high availability of soil-derived N could attenuate plant N uptake from applied fertiliser as suggested by the significant negative relationships between TDN and plant ^{15}N recovery especially at first harvest (Fig. S3). These findings together suggest that plants in BIO soils primarily relied on the readily available soil N fraction during the first harvest, while the applied fertiliser N was temporarily immobilised by the microbial community. At later stages, the soil-derived N pool may have become depleted and plant likely relied increasingly on re-mineralisation of previously immobilised N, as discussed above.

In contrast to mineral fertiliser, the relationships between MBN and plant ^{15}N recovery under organic fertiliser application were generally weaker (Fig. 3d, e), yet consistently positive (Fig. 3f), pointing to the importance of microbial mineralisation and/or re-mineralisation when organic amendment is added to the system. This interpretation is further supported by positive relationship between *chiA* abundance and plant ^{15}N uptake under organic fertilisation across two harvests (Fig. 4), corroborating the importance of microbial mineralisation of organic substrates for N release to plants when organic amendments are applied.

4.2.2. *Nitrification*

The effect of ammonia oxidizers on plant ^{15}N uptake was influenced mainly by fertiliser type and harvest instead of management history × fertiliser interactions. The negative relationship between ammonia oxidizer's abundances and plant ^{15}N uptake indicate N loss from the system probably due to nitrifier denitrification or N_2O emission via nitrification

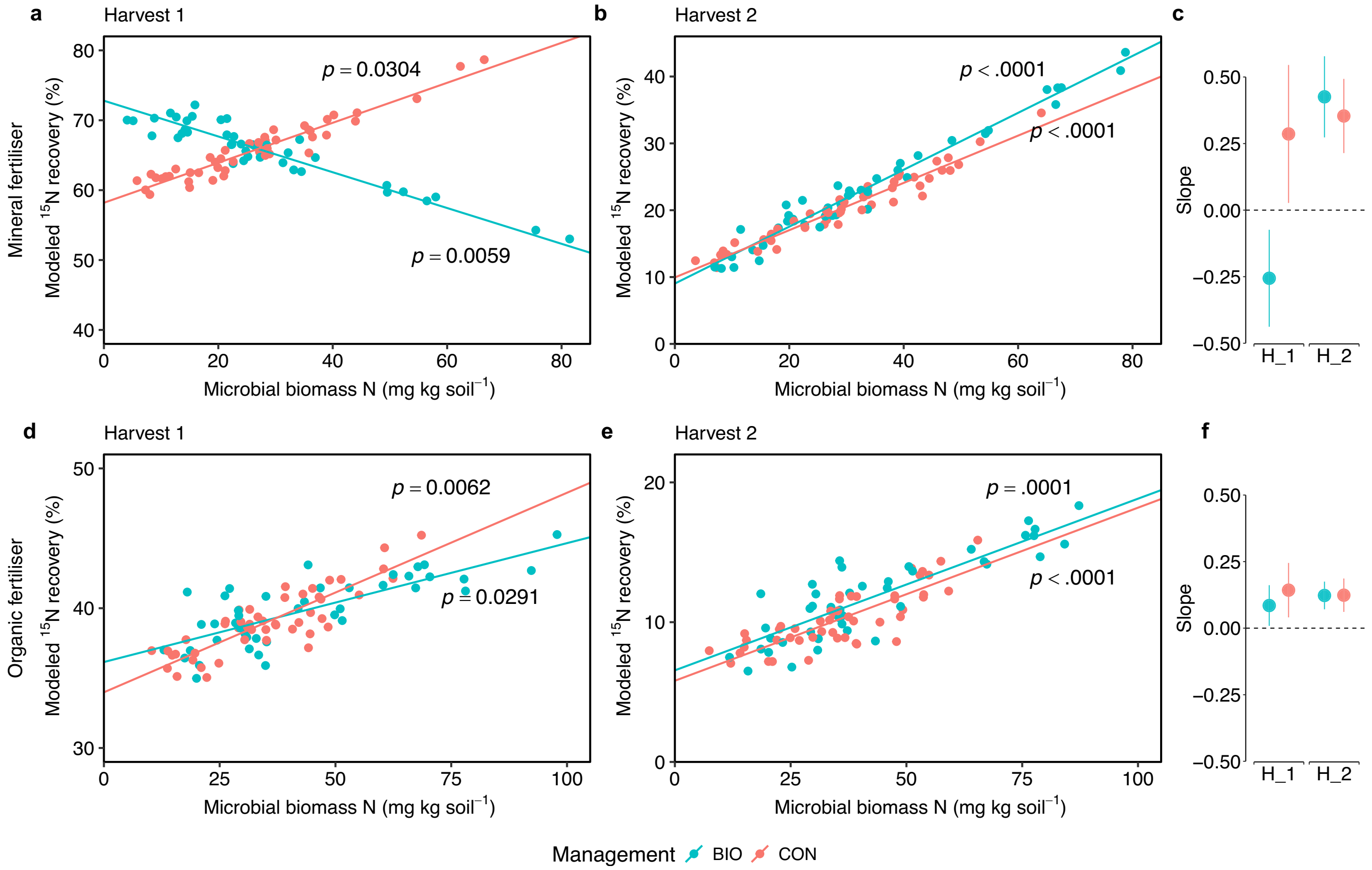

Fig. 3. Relationship between microbial biomass N and plant ^{15}N recovery at (a, d) first and (b, e) second harvest based on model estimated marginal mean. Data were obtained from organically (BIO) or conventionally (CON) managed soils receiving mineral N fertiliser (a, b) or organic N fertiliser (d, e). Regression lines are shown as group average based on generalised linear mixed models (see in Section 2.5). The slope estimates with 95% confidence intervals are shown by fertiliser type (c; mineral fertiliser, f; organic fertiliser) where statistical significance can be inferred with confidence intervals relative to zero. Note that y axes were truncated at first harvest to improve visual clarity and different axis ranges were used across fertiliser types and harvest timing due to the inherent differences in recovery rates. The significance of the slope estimate is shown by *P*-value in the plot.

as soil moisture was maintained at 60% of field capacity throughout the experiment and risk of leaching was generally low. Nitrification can be a dominant N_2O production pathway at water-filled pore space (WFPS) below 50–60% (Congreves et al., 2019; Davidson, 1993), which aligns with the range of WFPS in the present study (ave. 30.8 ± 0.13%). Furthermore, there were also significant positive relationship between ammonia oxidizer's abundances and plant ^{15}N uptake (Fig. 4). Previous studies indicated that NO_3^- produced via nitrification could support plant N uptake (Dan et al., 2022; Kirk and Kronzucker, 2005). *Plantago lanceolata* was used in the current study and it was reported to prefer NO_3^- over NH_4^+ as its N source (Blacquière et al., 1988; Falkengren-Grerup, 1995). Thus, it is probable that nitrification provided NO_3^- to plants and supported plant N uptake. Observed positive and negative associations switched between two harvests and exhibited the inverse trends between AOA and AOB (Fig. 4). This dynamic likely reflects shifts in N availability, though whether such changes are linked to ecological interactions such as niche specialisation remains to be tested (Rütting et al., 2021).

The most of significant relationship between ammonia oxidizers and plant ^{15}N uptake was found with mineral fertiliser application (Fig. 4). We can generally attribute such a response to the ammonia oxidisers' distinct ability of utilising ammonia as an energy source and thriving when NH_4^+ availability increases (Monteiro et al., 2014; Norton and Ouyang, 2019; Ouyang et al., 2017). Also, the more evident relationships under mineral fertilisation might be because mineral N is directly accessible to both plants and microbes, allowing for more precise identification of specific microbial pathways. Conversely, organic fertilisation depends on decomposition processes that provide mineral N to ammonia oxidizers, which can make it more challenging to discern the relationship between plant N uptake and microbial processes, potentially leading to less clarity.

4.2.3. Nitrate reduction

The gene abundance of *narG* was negatively correlated with plant ^{15}N uptake, which could be ascribed to NO_3^- removal from the system due to denitrification. Nitrate and soil organic C pools are major determinants of denitrification (Pan et al., 2022), and earlier studies reported that denitrification potential was positively correlated with NO_3^- and labile C availability in soil (Surey et al., 2020; Wang et al., 2013). Such progressive substrate depletion, consistent with the decline in soil-derived N and MBN dynamics discussed above, could explain the significant harvest effect where negative relationship was found only at 1st harvest (Fig. 4).

4.2.4. Microbial N transformation pathways

Nitrogen cycling in soil is integrated system in which multiple processes produce and consume mineral nitrogen species such as NH_4^+ and NO_3^-. Plant N uptake can be fostered by any processes which increase these mineral N pools; organic N mineralisation, direct dissolution of synthetic fertiliser or NO_3^- production via nitrification. Contrary, it can be restrained due to immobilisation, NH_4^+ removal via nitrification or NO_3^- removal via denitrification as mentioned earlier. Thus, the relationship between one microbial process and plant N uptake can be bidirectional, which largely agrees with our findings. With mineral

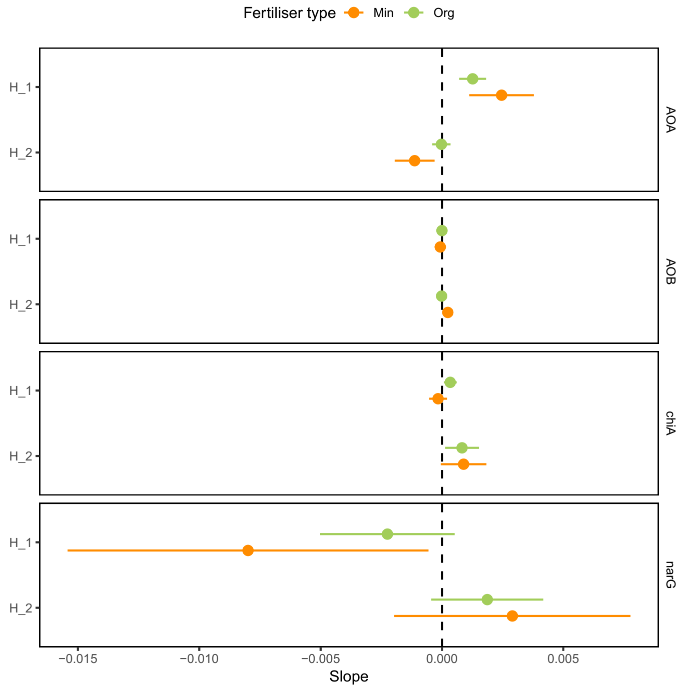

Fig. 4. The slope estimates of relationship between gene abundances and plant ^{15}N recovery affected by fertiliser types and harvest. The error bar shows 95% confidence intervals where statistical significance can be inferred with confidence intervals relative to zero. AOB: bacterial *amoA*, AOA: archaeal *amoA*, narG: membrane-bound nitrate reductase, chiA; chitinase gene abundance, H_1: Harvest 1, H_2: Harvest 2. Data was pooled by management history since no four-way interaction was significant. Generalised linear mixed models (GLMM) were used to calculate estimated slopes (see in Section 2.5).

fertiliser, BIO soils showed a negative MBN-^{15}N relationship at the first harvest but a positive one at the second, consistent with rapid early immobilisation followed by re-mineralisation that later released N back to plants. This tight coupling between immobilisation and re-mineralisation reflects microbial turnover dynamics (MIT) that may help synchronise N release with plant uptake. Under organic fertiliser, relationships with MBN were weaker but generally positive, and *chiA* abundances were positively associated with ^{15}N uptake across harvests, indicating that mineralisation and/or re-mineralisation supported plant N supply more when complex substrates were added. For nitrification, we observed both negative and positive associations between AOA/AOB and ^{15}N uptake. Negative links likely reflect N losses via N_2O leaking from nitrification (hydroxylamine oxidation), nitrifier denitrification and/or coupled nitrification-denitrification where nitrification fuels denitrification by providing NO_3^- as substrate (Congreves et al., 2019; Petersen et al., 1991). Contrary, positive links are consistent with NO_3^- provision to a NO_3^--preferring plant (Plantago). As these processes occur simultaneously, the net effect of any single process on plant N uptake may be smaller or larger than simple correlation suggests. Together, these examples show that plant ^{15}N recovery integrates counteracting flows, which can hide or invert expected bivariate microbial parameter-N uptake patterns. Explicitly accounting for the coupling between immobilisation and re-mineralisation (MIT dynamics), as well as the sequential linkage by which nitrification provides NO_3^- substrate for denitrification, would help characterise how these processes interact to shape net plant N availability. For instance, larger datasets that include temporal NH_4^+/NO_3^- pools and short incubations of net rates, combined with integrative models (e.g., path analysis/SEM), could better disentangle direct and indirect contributions of multiple processes to plant N uptake.

This study relied on static measurements of microbial abundances based on microbial biomass and gene abundances, which provide only a partial view of dynamic processes such as mineralisation, immobilisation, and nitrification. Net process rates using direct measurement of N pools and fluxes would offer clearer insights into how microbial activity contributes to plant N uptake. Furthermore, the use of unlabelled pools limits our ability to trace fertiliser-derived N within the soil-microbe-plant system. Investigating ^{15}N-labelled mineral and microbial N pools, for instance by combining ^{15}N-MBN extractions with sequential fractionation of soil N, would enable more detailed tracking of N flows and support stronger mechanistic interpretations. Finally, the management contrast between BIO and CON soils, as found under realistic farming conditions in Switzerland, may not have been strong enough to reveal the full ecological consequences of long-term organic inputs. Future studies could employ more extreme management contrasts for instance by employing long-term field experiments comparing mineral versus organic fertilisation over decades to better capture adaptation of microbial communities to different fertilser regimes. Integrating ^{15}N-labelling with dynamic measurements of different N pools, together with clearer contrast in soil management history would together advance our understanding of the role of soil microbial processes and their resource adaption in plant N acquisition.

5. Conclusion

This greenhouse study investigated shifts in microbial functional traits and its effect on plant N uptake as a function of management history and fertiliser types. Legacies of management history had marginal effects on microbial abundance and only AOA *amoA* and *narG* gene abundances showed positive interactions according to management history and fertiliser type. Similarly, freshly applied fertiliser, rather than management history was the dominant driver of plant-microbial relationships. Majority of significant relationships were found with mineral fertiliser irrespective of management history. The significant interaction of management × fertiliser found in link between MBN and plant ^{15}N uptake was probably related to different C availability due to management history and subsequent impact on MIT. Our results suggest that fertiliser form and timing strongly control short-term plant N uptake, and that aligning them with plant demand is critical for near-term N recovery.

CRediT authorship contribution statement

Misato Toda: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Michael Scheifele:** Writing – review & editing, Methodology, Investigation. **Jochen Mayer:** Writing – review & editing, Methodology. **Marcel G.A. van der Heijden:** Writing – review & editing, Conceptualization. **Florian Walder:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107075.

Data availability

The data are deposited in Zenodo and publicly available at 10.5281/zenodo.17988695

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