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Organic management and soil health promote nutrient use efficiency

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Abstract

Introduction: Nitrogen is a key nutrient for plants. Often less than 50% of the applied nitrogen fertilisers is acquired by crops and nitrogen can be easily lost into the environment causing environmental pollution. Thus, to make agriculture more sustainable, it is important to investigate which factors determine nitrogen use efficiency (NUE). We investigated whether NUE was higher in organically managed soils compared to conventionally managed soils.

Materials and Methods: To test this, we carried out a pot experiment in a greenhouse using soils from 16 fields. The soils were collected from conventionally (eight fields) or organically managed fields (eight fields). In addition, plants received two different ¹⁵N enriched N sources (mineral ¹⁵N or an organic fertiliser source, namely ¹⁵N enriched plant litter). Plants were harvested at three time points, and growth and nitrogen uptake were assessed at each time point.

Results: NUE depended on management type and harvest time and the higher NUE of organically managed soils became more evident towards the second and third harvest. The average NUE at the end of the experiment was 93% and 55% for mineral fertiliser and litter application, respectively. This indicated that mineral fertilisers were immediately acquired by the plants, while nutrients in organic amendments had a lower availability and probably would be supplied later but steadier. Further, NUE was positively linked to microbial biomass, soil organic carbon content, and aggregate size, indicating that enhanced soil quality and soil health leads to a more efficient use of fertilisers.

Conclusion: Our results indicate that organic management and soil health promote a more efficient use of nutrients and contribute to a more sustainable agriculture.

KEYWORDS

¹⁵N labelled fertiliser, conventional and organic farming, nitrogen use efficiency, soil health

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1 | INTRODUCTION

Conventional farming systems rely heavily on chemical nitrogen (N) fertilisers to sustain crop productivity (Erisman et al., 2008). Global N fertiliser consumption has reached to 108 Mt N year⁻¹ in 2017 (IFA, 2019), however, less than half of the applied N is taken up by crops, with a huge fraction lost into the environment (Ladha et al., 2005). Nitrogen loss causes a number of environmental issues including eutrophication, contamination of drinking water, bio-diversity loss and greenhouse gas emission (Midolo et al., 2019; Stark & Karl Richards, 2008). It is thus essential to seek for alternative agricultural practices to mitigate these deleterious N losses and achieve a more efficient use of N in agroecosystems.

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Organic farming relies on soil ecological processes and does not allow any synthetic fertiliser or pesticide use (FAO, 2003; IFOAM General Assembly, 2008). This practice tends to decrease crop yield compared to conventional farming, however, often improves soil health (Mäder et al., 2002; Wittwer et al., 2021). Soil health can be defined as 'the continued capacity of soil to function as a vital living ecosystem that sustains plants, animals, and humans' (https://www. nrcs.usda.gov/conservation-basics/natural-resource-concerns/soils/ soil-health) and various soil physico-chemical and biological properties can be used as soil-health indicators including soil organic carbon content, microbial biomass soil aggregation state (Lehmann et al., 2020). Several studies showed that organic farming increases aggregate stability and prevents soil crusting and runoff (Morvan et al., 2018; Seitz et al., 2019). Soil organic matter and cation exchange capacity (CEC) also increases under organic farming, which could retain nutrients for later growing periods while preventing leaching (Moharana et al., 2017; Smith et al., 2019). Moreover, organic farming generally harbours a more abundant, stable, and diverse soil life compared to conventional farming (Lupatini et al., 2017; Smith et al., 2019). For instance, Banerjee et al. (2019) reported that organically managed fields exhibited more complex microbial networks with a larger number of keystone taxa compared to conventionally managed fields. They further showed that keystone taxa in organic farming was dominated by arbuscular mycorrhizal fungi and a member of the Sebacinales, both of which are known to deliver soil nutrients to plants (van der Heijden et al., 2015; Weiß et al., 2016). Furthermore, earlier studies showed that organically managed soil exhibited higher enzyme activities in N mineralisation and greater versatility in C utilisation than conventionally managed soil (Chou et al., 2017; Jezierska-Tys et al., 2020). This suggests that soil microbes under organic farming where only organic fertilisers (manure, slurry, etc.) are applied would thrive with more complex nutrients sources such as organic amendments compared to microbial communities from conventionally managed fields where mineral fertilisers (e.g., ammonium and nitrate) are the main N inputs. These highly developed microbial communities in organically managed soils could more effectively supply plant nutrients to crops. Together, this enhanced soil health could be a reason why nutrients are more efficiently utilised (e.g. higher N use efficiency [NUE]) in organically managed systems.

Several experimental studies indeed demonstrated that NUE was higher under organic management (Liu et al., 2016; Mäder et al., 2002). However, other studies also observed reduced NUE (Wittwer et al., 2021) and similar amounts of N losses have been reported in organically managed fields compared to conventionally managed fields (Autret et al., 2020) and thus it is still unclear whether organic management generally has higher NUE. Moreover, field experiments that directly compare organically and conventionally managed treatments cannot be extrapolated as they are based at one particular location. To test whether NUE in organically managed soils is generally higher, soils from different fields under organic and conventional management need to be compared. In earlier work (Walder et al., 2023), we compared 40 fields, 20 each from organic and conventional management. We observed based on field fertilisation data supplied by the farmers that NUE was higher under organic management. Yet, precise NUE from applied fertiliser remains obscure as this NUE value didn't differentiate crop N uptake from fertiliser and soil. Therefore, another approach is required to capture a more accurate NUE.

Nitrogen use efficiency has been widely used to evaluate N cycling and assess N management in agroecosystems (Mäder et al., 2002; Omara et al., 2019; Panel, 2015). Nitrogen use efficiency is the ratio of the amount of N taken up by crops to the amount of N fertilised. Thus, low NUE leads to high N loss indicating negative impacts on the environment (Panel, 2015). There are two common approaches to estimate NUE—the N balance approach (NUE_{bala}) and ¹⁵N tracer approach (NUE_{15N}). NUE_{bala} is estimated as N output in relation to N input and the required data set to calculate NUE (grain yield and N fertiliser rates) is straightforward and enables NUE to be calculated even at commercial farms (Panel, 2015; Xie et al., 2020). The ¹⁵N tracer approach applies ¹⁵N labelled fertiliser and calculates the proportion of plant N derived from fertiliser (Liang et al., 2013; Quan et al., 2021; Wu et al., 2010). NUE_{15N} is thus considered a more accurate estimation than NUE_{bala} (Quan et al., 2021).

In this study, we employed a ¹⁵N tracer technique with soils collected from the same sites as in Banerjee et al. (2019) and Walder et al. (2023) to compare fertiliser-derived plant ¹⁵N uptake between conventionally or organically managed soils. We collected soils from eight conventionally managed fields and eight organically managed fields. A pot experiment was subsequently set up with those soils in combination with two ¹⁵N enriched N sources-mineral and plant litter N-this enabled us to assess the possible microbial adaptation to management, complex N sources and its effect on plant N recovery. Plant ¹⁵N recovery was evaluated at three different time points to follow temporal change over 18 weeks. Our main hypotheses were;

- organically managed soils have higher NUE than conventionally managed soils and the results from the ¹⁵N tracer approach to test NUE is consistent with field data;
- (2) organically managed soil exhibits a particularly high ¹⁵N recovery with organic fertilisation as these soils are conditioned to acquire nutrients from organic amendments;

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(3) soil health measures such as soil carbon content and microbial biomass are related to NUE.

2 | MATERIALS AND METHODS

2.1 | Site selection and sampling

Soil samples were collected in February 2019 from 16 agricultural croplands in the northeast of Switzerland. Each sampling point was identified with a GPS tagged point, where the previous sampling was conducted in May 2016 (see Walder et al., 2023). For the current study, eight conventionally managed and eight organically managed fields were chosen. Each field was from a different farm. Both cropping systems (organic or conventional) were implemented for at least the last 5 years. All fields were regularly tilled with a mouldboard plough. Synthetic fertilisers were the main form of N input combined with regularly organic fertiliser application in conventionally managed fields. Conventional management followed the 'Proof of Ecological Performance' guidelines of the Federal Office for Agriculture, Switzerland (Federal Office for Agriculture [FOAG], 2015). Organic fertilisers were the sole N input in organically managed fields and they were managed according to the guidelines of BioSuisse, the Federation of Swiss Organic Farmers (Bio Suisse, 2020). The average mineral and organic N fertiliser input for the period 2011-2016 were 141 and 19 kg N ha⁻¹ for conventional fields and 0 and 61 kg N ha⁻¹, for organic fields respectively (Büchi et al., 2019). The crop rotation of the last two years is shown in Supporting Information: Table S1. The soil was collected from 0-20 cm after the removal of the top layer (crops growing upon the sampling). Soil samples were crumbled over 8 mm sieve by hand to keep the aggregate structure and stored at 4°C until its use. Soil total carbon (TC), total N (TN), total organic C (TOC), plant available phosphorus (Olsen-P) and soil pH were measured for each 16 field soils using the Swiss standard protocols (FAL, 1996; Olsen et al., 1954). The aggregate stability of each 16 field soils was also determined as mean weight diameter (MWD) using the aggregate fractionation method (Six et al., 1998; Van Bavel, 1950). The basic soil properties of the 16 soils are described in Supporting Information: Table S1.

2.2 | Experimental design

A greenhouse experiment was conducted from June to October 2019. Three litres of soil were filled into 3 L pots by volume. Two different N sources, either ¹⁵N-labelled ammonium sulphate (1.45% of which was ¹⁵N enriched) or plant litter (*Lolium multiflorum*, 2% of which was ¹⁵N enriched) were applied to each pot by fully mixing N sources with soil. The ¹⁵N labelled plant litter was produced by fertilising the plants with ¹⁵N labelled NH₄NO₃. At harvest, leaves were collected, dried and chopped into 2–3 cm. For each N source (¹⁵N enriched mineral N fertiliser or ¹⁵N labelled litter) a total N input of 90 kg N ha⁻¹ was added as a one-time, nonrecurring application. A total of 192 pots were set up (eight soils × two cropping systems ×

two fertiliser treatments × six replicates) and arranged in a complete randomised block design. Five *Plantago lanceolata* seedlings were planted and 2 weeks later from the planting, one seedling was thinned resulting in four plants in each pot. We used *P. lanceolata* as a model plant as it is widely used for pot experiments, grows in a wide range of soil types and has a broad distribution (Edlinger et al., 2022). The soil water content was adjusted to 60% by weighing every other day over the entire growing period.

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2.3 | Plant harvest and ¹⁵N signal measurement

Three harvests were conducted from the same individual pot over the growing period (3 weeks of establishment phase followed by 3 consecutive periods of 5 weeks). The shoots including flowers were cut 2 cm above the soil surface and dried at 65°C for 24 h. Upon the third harvest, the whole root system was harvested, washed and dried at 65°C for 24 h. The dried samples were weighed to determine root biomass. Dried shoot samples were weighed to determine aboveground biomass and then analysed to determine N concentration and ¹⁵N isotopic ratio. The dried shoot sample was ground with a ball mill and the N concentration and ¹⁵N abundance were determined with an elemental analyser equipped with an isotope mass spectrometer at the University of California Davis (UC-Davis) Stable Isotope Facility (first harvest) or at Agroscope, Reckenholz, Switzerland (second and third harvest). The plant N derived from applied fertiliser (Ndff) and soil (Ndf_{soil}), and NUE_{15N} were calculated as follows (Wu et al., 2010):

- 1) Ndff (%) = $E_s/E_f \times 100$,
- 2) Ndf_{soil} (%) = (1 Ndff) × 100,
- 3) Recovery of ${}^{15}N$ (%) = (Shoot N × Ndff/ ${}^{15}N$ applied) × 100,
- 4) NUE_{15N} (%) = cumulative ¹⁵N recovery,

where E_s is ¹⁵N enrichment of shoot samples (atom%) and E_f is the ¹⁵N enrichment of the labelled fertiliser (Mineral fertiliser: 1.45 atom % and organic fertiliser: 2.00 atom%). ¹⁵N recovery was calculated based on shoot biomass at each harvest and NUE_{15N} was sum of recovered ¹⁵N up to each harvest (e.g., NUE_{15N} at third harvest = sum of ¹⁵N recovery from first to third harvest).

2.4 | Soil sample harvest and microbial biomass measurement

Soil was sampled at each harvest by taking three soil cores from each pot to make a composite sample. These soil samples were thoroughly mixed and stored at -20° C until the microbial biomass measurements. After each harvest, the empty spaces due to soil sampling were refilled with the same field soils used at the initial pot setup. Soil microbial biomass was determined by the fumigation extraction method with slight modification for K₂SO₄ concentration (Brookes et al., 1985). Briefly, 15 g of the soil were fumigated with chloroform

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for 24 h at 25°C. Both fumigated and non-fumigated samples were extracted with 75 mL of 0.05 M K₂SO₄ (Bruulsema & Duxbury, 1996; Makarov et al., 2015) on an overhead shaker for 1 h. The C concentration of the extract was measured using a TOC/TNb analyser (Elementar Analysensysteme GmbH, Langenselbold, Germany). Microbial biomass was calculated as follow:

Microbial biomass (mg C kg⁻¹) = $C_{\text{fumigated}} - C_{\text{unfumigated}}$,

where $C_{\text{fumigated}}$ and $C_{\text{unfumigated}}$ refer to extractable *C* in fumigated and unfumigated samples. Due to logistical constraints, microbial biomass was determined only for the first two harvests. The average was used as an index for microbial biomass after confirming the high correlation in microbial biomass data between the two harvests (*p* < 0.001).

2.5 | Statistical analysis

All statistical analyses were performed using R version 4.1.2 (R Core Team, 2021). Field 60 was considered as an outlier due to its extremely small plant biomass and very low plant available soil P concentration and excluded from all statistical analysis containing plant parameters. Because of an issue during sample processing, two samples at third harvest (conventionally managed soil, one with mineral and the other with organic fertiliser) were lost and data were treated as NA. The effect of management, N source and harvest on plant parameters (biomass, N concentration, N content, root/shoot ratio, Ndf_{soil} , ¹⁵N recovery, NUE_{15N}) were analysed using linear mixed effect models. The effect size of organic management as well as 95% confidence intervals were calculated based on linear mixed effect models. For field data in 2016, the effect of management on NUE was reanalysed for the 16 fields used in the current study with one-way analysis of variance (ANOVA).

The effects of soil parameters on NUE_{15N} were analysed also using linear mixed effect models. For each slope estimate, the pairwise post hoc multiple comparisons with a *p*-value adjustment equivalent to the Tukey was used. For field data in 2016, the effect of soil parameters on NUE was analysed for the 16 fields with linear models. The relationships in soil parameters between data in 2016 and the current study was analysed with linear models. All linear mixed-effect models were performed using the package lmerTest (Kuznetsova et al., 2017) with field, replicate and pot fitted as a random effect in every model. Slope trend analysis and pairwise post hoc test were performed using the package emmeas (Lenth et al., 2018). Conditional R^2 (Nakagawa & Schielzeth, 2013) was calculated for linear mixed effect models using the package MuMln (Bartoń, 2022).

3 | RESULTS

3.1 | Effect of management and N source on plant performance

The effect of management and N source on plant biomass and plant N content was strongly driven by experimental duration (Supporting

Management <u>_____</u>10.0 Bio Shoot biomass 7.5 Con 5.0 2.5 C (b) 0.4 (g N content 0.3 0.2 0.1 (c) <u>©</u>0.10 Indfsoil 0.05 H 1 H 2 H 3

(a)

FIGURE 1 Shoot biomass (a), shoot N content (b), and soil N uptake (c) over three harvests. The plots show mean values by management and harvest. Values with different lowercase letters are statistically significantly different at p < 0.05 (n = 96 for conventionally managed soil [Con] and n = 84 for organically managed soil [Bio]). Statistical details for the corresponding analysis of variance are shown in Supporting Information: Table S2.

Information: Table S2). In several cases, we found a pattern (effect, correlation) without statistical significance. In such cases, we used the word 'tended' to indicate potential links and always clearly stated P value in brackets. Plant biomass and plant N content were highest at harvest 1 and lowest at harvest 3 (Figure 1) and the management effect was only visible over the course of the experiment. This was also revealed by a significant interaction term between management and harvest (Supporting Information: Table S2). The positive effect of organic management increased with experiment duration except for root/shoot ratio where conventionally managed soils tended to have higher root/shoot ratio than organically managed soils (Supporting Information: Figure S1, p = 0.07). Organically managed soils tended to exhibit higher total shoot biomass (Figure 2, S2a; p = 0.443) and shoot N content (Figure 1b; p = 0.119) than conventionally managed soils, however, these trends were not statistically significant. Similarly, total N uptake was significantly higher in organically managed soil than conventionally managed soil at the end of the experiment (Figure 2, Supporting Information: Figure S2b). Furthermore, higher NUE_{15N} and Ndf_{soil} were found in organically managed soils than conventionally managed soil and this trend was consistent between two fertiliser types (Figures 2 and 3; p = 0.261, S3; p = 0.188). Reanalysis of field NUE_{bala} using the 16 fields used in this study showed no significant difference between conventional farming

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Effect size 2 C -2 H_1 H 2 Н'З FIGURE 2 Effect size analysis showing plant parameter changes over three harvests between organic management and conventional management. Positive values indicate that organic management had a

positive effect on the parameters while the negative values indicate that conventional management had a positive effect. Error bars represent 95% confidence intervals. All parameter values were analysed as cumulative value up to each harvest (e.g., Total shoot biomass at third harvest = sum of shoot biomass from first to third harvest).



FIGURE 3 NUE_{15N} over three harvests. The plots show mean values for management, N source, and harvest. Results for an analysis of variance performed using N source (N), harvest (H), management (M), or their interaction terms are shown. Asterisks indicate the statistical significance of the variable (*p < 0.05; **p < 0.01; ***p < 0.001). The dashed line shows average NUE_{15N} at the end of the experiment (93% and 55% under mineral and organic fertiliser, respectively) (n = 48 for conventionally managed soil [Con] and n = 42 for organically managed soil [Bio]).

system and organic farming system although the trend was similar to the previous report (Supporting Information: Figure S4).

N source also showed a clear effect on plant performance but its interaction effect with harvest depicts a different pattern from that with

FIGURE 4 Change in (a) shoot biomass, (b) shoot N concentration, and (c) shoot N content over three harvests. The plots show mean values by N source and harvest. Values with different lowercase letters are statistically significantly different at p < 0.05(n = 90). Statistical details for the corresponding analysis of variance are shown in Supporting Information: Table S2.

H 2

H 3

management. At the first harvest, organic fertilisers (plant litter) gained more shoot biomass than mineral N fertiliser (Figure 4a, p < 0.05), and this effect was reversed in the second harvest (Figure 4a, p = 0.097) while the value became similar at third harvest, resulting in no difference between fertiliser types in total shoot biomass. Shoot N content and N concentration was higher with mineral N fertiliser than plant litter up to second harvest (Figure 4b,c). Further, shoot N content didn't change over three harvests with litter whilst it significantly reduced at third harvest with mineral N fertiliser (Figure 4c). Moreover, the N source effect was particularly noticeable with ¹⁵N recovery. The NUE_{15N} of the mineral N fertiliser showed much higher values than organic fertiliser at all harvests (Figure 3). On average, the mineral N fertiliser had 65%, 22% and 6.0% of ¹⁵N recovery at first, second and third harvest, which was significantly higher than plant litter with 39%, 11% and 4.2% of ¹⁵N recovery, respectively and yet, no interaction effect between management and N source was found (Supporting Information: Table S2). Average NUE_{15N} at the end of the experiment was 93% and 55% under mineral N fertiliser and plant litter indicating almost no N loss in the systems.

3.2 Effect of soil parameters on NUE

Soil parameters measured at the current study in 2019 were highly correlated with the data from previous studies from 2016 (Supporting



FIGURE 5 Relationships between soil properties and cumulative ¹⁵N recovery (NUE_{15N}). Data were obtained for pots receiving mineral fertiliser (a, c, e) or plant litter (b, d, f). Shown are relationships between total organic carbon (TOC) and NUE_{15N} (a, b), soil aggregation expressed as mean weight diameter (MWD) and NUE_{15N} (c, d) and the relationship between microbial biomass and NUE_{15N} (e, f). Regression lines are shown as group (random factor) average based on linear mixed models where field, replicate, and pot were treated as random factors (conditional R² = 0.97 [TOC], 0.96 [MWD], 0.96 [microbial biomass]). The significance of the correlation is shown using solid lines (p < 0.05) and dotted lines (NS).

Information: Figure S5). In a next step, we analysed whether soil characteristics were linked to NUE. A significant positive correlation between NUE_{15N} and total soil organic carbon, soil aggregation and positive trend with microbial biomass was observed for both fertiliser types, indicating that soil quality influences NUE (Figure 5). However, this pattern was not observed in field data (data not shown).

4 | DISCUSSION

The principal goal of the current study was to evaluate NUE under organic and conventional farming, and its dependence on the type of applied N fertilisers. Our results show that organic management had a higher NUE than conventional management and this positive trend was more pronounced towards later growing periods. Interestingly, NUE was positively linked to various parameters of soil quality and soil health (e.g., total soil organic carbon, soil aggregation, microbial biomass), indicating the importance of soil health in plant nutrient uptake.

4.1 | Effect of organic and conventional management on NUE

In the current experiment, the effect of management varied with time and the NUE_{15N} of organically managed soils exceeded that

of conventionally managed soils towards a later growing period at harvest 2 and 3 (Figures 2 and 3). The positive effect on NUE in organic management could be linked to better plant growth followed by enhanced plant N uptake in organically managed soils. A range of studies showed that organically managed soils often contain higher amounts of soil nitrogen compared to conventionally managed soils (Bosshard et al., 2009; Escanhoela et al., 2019; Friedel et al., 2001). Our study is in agreement with this and the organically managed soils exhibited an increased trend in soil N compared to conventionally managed soils for both analysed year (n = 8/management, p = 0.17, 0.34, data in 2016 and 2019 respectively, Supporting Information: Figure S6a), probably due to repeated application of organic amendments in earlier years (Supporting Information: Table S1, Büchi et al., 2019). This N stock in soil can be released over the course of experiment through mineralisation and subsequently support plant growth. Indeed, organically managed soils were dependent more on soil N than fertiliser N compared to conventionally managed soils, which led to substantial increase in plant N uptake in organically managed soils (Figure 2, Supporting Information: Figures S2b and S3). Similar to our result, Langmeier et al. (2002) comparing organically and conventionally managed soils also reported increased plant N uptake from soils with organic management. Also, plants allocate more resources to belowground under the nutrient limited conditions (Poeplau, 2016). The enhanced root/

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shoot ratio in conventional soils points in this direction (Supporting Information: Figure S1).

4.2 | Effect of N source on plant performance

This study demonstrated that plants utilise mineral N fertiliser much more efficiently compared to organically applied N litter. Almost all applied mineral N fertiliser was taken up by plants over the course of experiment while about half of plant litter N remained in the soil. These observation are congruent to earlier studies comparing ¹⁵N labelled mineral and organic fertilisers (Langmeier et al., 2002; Wu et al., 2010). The effectiveness of mineral fertiliser in terms of plant N uptake was also confirmed by the significantly higher shoot N content and concentration with mineral N fertiliser up to second harvest (Figure 4b,c). Thus, mineral N fertiliser could swiftly provide nutrients when plant nutrients demand is high (e.g. vegetation period). However, it is important to synchronise nutrients supply and plant demand to avoid N loss to the environment.

Despite the large difference in plant nutrient availability, plant biomass was affected by fertiliser type to a lesser extent compared to NUE_{15N}. Shoot biomass was greater with plant litter than mineral N fertiliser at the first harvest and this pattern was reversed in the second harvest, which resulted in no overall difference in total shoot biomass during the experiment (Figure 4a). This contrasting fertiliser effect between two harvests may arise from the difference in limited nutrients by plants, which is not necessarily only N. For instance, plants require other macro- and micronutrients in addition to N such as potassium and manganese, which can be supplied through crop residue amendments (Moyin-Jesu, 2007). Earlier studies showed that crop residues can release those nutrients in a relatively short time span (<30 days) through its decomposition (Masunga et al., 2016; Suvain et al., 2021). However, after the quick decomposition of labile materials, certain amounts of crop residue remain as organic form that is non-plant available nutrients. Thus, the growth enhancement under litter application at first harvest would be attributed to more balanced nutrients supply from litter. Contrary, the reversed trend at the second harvest would be ascribed to possible leftovers of NH4⁺-N under mineral fertiliser treatment, which could better support plant growth at second harvest when N limitation was presumably more severe.

4.3 | Effect of soil properties on NUE

The significant relationships between improved soil properties and NUE_{15N} highlight the importance of soil health on plant nutrients uptake. In the current experiment, aggregate size, total organic carbon and microbial biomass were significantly linked to increased NUE_{15N} for both fertiliser types (Figure 5). Soil aggregate and TOC are tightly linked to soil microbial biomass and activities, which could

further elucidate these positive relationships between soil properties and NUE_{15N}. Several studies showed that soil microbes play a pivotal role in aggregate stabilisation by producing binding substances (e.g. microbial polysaccharides and mucilages) and/or mechanically holding the structure (e.g fungal hyphae network) (Six et al., 2004; Totsche et al., 2018). Moreover, aggregate acts a major habitat for soil microbes (Li et al., 2018; Wilpiszeski et al., 2019). Wan et al. (2021) also reported the positive relationship between TOC and microbial biomass across different terrestrial ecosystems. Indeed, we found a positive relationship between soil aggregate size, TOC and the microbial biomass (Supporting Information: Figure S7). The increased microbial biomass could act as an engine for soil N cycle through various microbial metabolic processes (Kuypers et al., 2018). Among those, microbes can decompose organic N and supply mineral N to plants (N mineralisation) while they also assimilate mineral N into their biomass (N immobilisation). Further, microbial N can become plant-available upon microbe's death and subsequent release of mineral N (N remineralization) (Chen et al., 2014; Liang et al., 2013). Thus, the positive relationship between microbial biomass and NUE with mineral fertiliser could be attributed to ¹⁵N release through N remineralization whereas that of plant litter could be resulted mainly from mineralisation as plant litter needs to be decomposed first to release plant available N (Figure 5e,f). Interestingly, the positive relationship between microbial biomass and NUE was stronger with mineral N fertiliser than plant litter (Figure 5e,f). This further implies that remineralization from microbial biomass might have more profound impact on N turnover compared to decomposition process in the current experiment setting.

5 | CONCLUSION

Here we examined whether N uptake efficiency was higher in organically managed soils compared to conventionally managed soils using ¹⁵N tracer approach in the greenhouse. Furthermore, two ¹⁵N enriched N sources-mineral N fertiliser and plant litterwere used to test if higher NUE in organic management is enhanced with plant litter application. Our results demonstrate that organically managed soils showed higher NUE_{15N} than conventionally managed soils towards a later growing period and this trend was consistent between two fertiliser types. The positive effect on NUE under organic management could be deduced from increased plant growth which was supported by better nutrient supply from organically managed soil. Interestingly soil properties such as soil aggregation, soil organic carbon content and soil microbial biomass showed a positive relationship with NUE suggesting that enhanced soil health influences nutrient use efficiency. In conclusion, this study suggests to the importance of soil health for a better N fertillizer use by crops especially in soils from organically managed farming systems. Future efforts to develop mechanistic understanding of high NUE in organic farming should focus more on microbial function in nutrients supply from soil to plants.

AUTHOR CONTRIBUTIONS

Misato Toda: Conceptualisation; writing—original draught; writing review and editing; visualisation; formal analysis; data curation. Florian Walder: Conceptualisation; writing—review and editing. Marcel van der Heijden: Conceptualisation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ETHICS STATEMENT

The authors confirm that they have adhered to the ethical policies of the journal.

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SUPPORTING INFORMATION

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

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