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Short communication

Increased plant uptake of native soil nitrogen following fertilizer addition – not a priming effect?

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ABSTRACT

Fertilizer inputs affect plant uptake of native soil nitrogen (N), yet the underlying mechanisms remain elusive. To increase mechanistic insight into this phenomenon, we evaluated the effect of fertilizer addition on mineralization (in the absence of plants) and plant uptake of native soil N. We synthesized 43 isotope tracer (^{15}N) studies and estimated the effects of fertilizer addition using *meta*-analysis. We found that organic fertilizer tended to reduce native soil N mineralization (-99 kg ha^{-1} year^{-1}; $p = 0.09$) while inorganic fertilizer tended to increase N priming (58 kg ha^{-1} year^{-1}; $p = 0.17$). In contrast, both organic and inorganic fertilizers significantly increased plant uptake of native soil N (179 and 107 kg ha^{-1} year^{-1}). Organic fertilizer had greater effect on plant uptake than on mineralization of native soil N ($p < 0.001$), but inorganic fertilizer had similar effects. Fertilizer effects on mineralization and plant uptake of native soil N were not influenced by study location (laboratory or field) and duration, soil texture, carbon and N content, and pH. Fertilizer addition variably affected native soil N mineralization but consistently increased plant uptake of native soil N. The positive effect of organic fertilizer on plant uptake of native soil N can not be explained by its negative effect on native soil N mineralization, suggesting that increased plant uptake of native soil N was caused mostly by plant-mediated mechanisms (e.g., increased root growth, rhizosphere N priming) rather than by soil microbe-mediated mechanisms.

1. Introduction

Plants often grow faster with supplemental nitrogen (N), which is applied to agricultural fields as fertilizer (Asagi and Ueno, 2009; Bosshard et al., 2009) or enters natural ecosystems in the form of atmospheric deposition (Reich et al., 2001; Schimel and Bennett, 2004). Although this added N directly increases N availability and plant growth, it can also affect the release of N from soil organic matter (SOM) (hereafter, "native soil N").

Nitrogen priming (or "added N interaction" in older literature) is defined as the increase or decrease in the amount of native soil N released by microbial mineralization or taken up by plants with fertilizer addition compared to treatments without added N (Jenkinson et al., 1985). Priming is best measured using ^{15}N-enriched fertilizers to distinguish added N from the unlabeled native soil N (Barraclough, 1995). Plant uptake of native soil N can be boosted either by the increase in native bulk soil N mineralization or by plant-mediated processes, such as increased root growth and rhizosphere N priming (Ashraf et al., 2004; Jenkinson et al., 1985; Schimel and Bennett, 2004). Native soil N priming dynamics are thought to be affected by soil type, fertilizer type, and environmental factors (Ghaley et al., 2010; Glendining et al., 1997; Hgaza et al., 2012; Liu et al., 2017; Recous et al., 1988; Rowlings et al., 2016; Westerman and Kurtz, 1973). However, it remains unclear what mechanisms regulate native soil N dynamics following fertilizer inputs. Hence, we used *meta*-analysis to assess the effect of fertilizer addition on mineralization and plant uptake of native soil N, testing for broad patterns across experiments performed to date.

2. Materials and methods

2.1. Data collection

We used the ISI Web of Science and Google Scholar to exhaustively search papers published before March 2017. Several terms ("soil nitrogen priming", "nitrogen 15", "soil ^{15}N", "added nitrogen interaction", "labeled ^{15}N fertilizer", "nitrogen

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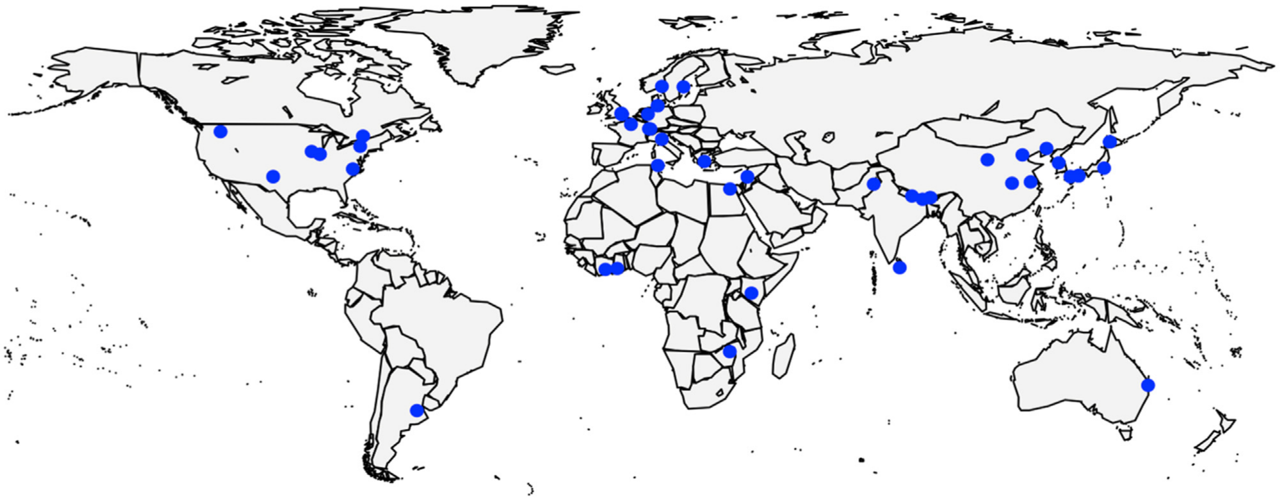

Fig. 1. The location of studies included in this *meta*-analysis.

fertilization", and "nitrogen mineralization") were used to identify studies that compared mineralization or plant uptake of native soil N in control (no-fertilizer applied) and fertilizer treatments. To be included in our dataset, studies were required to have used ^{15}N isotope tracers to separate unlabeled native soil N from labeled fertilizer N, and to report data for both fertilizer and control plots. We tabulated studies where organic fertilizers (e.g., animal manure, compost, crop residues) or inorganic (chemical) fertilizers were added. Study location (laboratory or field) and duration, soil texture (sand, silt, or clay), carbon and N content, and pH were tabulated when available. Soils classified as silty loams were included in the silt category, clayey loams in the clay category, and sandy loams in the sand category. Our dataset did not include studies on soils that were classified as loam. For studies with multiple observations over time (e.g., multiple growing seasons or years), data were averaged across time to avoid the temporal pseudoreplication. Our final dataset included 43 studies that were conducted on all continents except Antarctica (Fig. 1), involving a wide range of plant species, fertilizer types, and soil physicochemical characteristics (Tables 1 and 2).

We expressed results of N priming as kg N ha^{-1}. Other units (e.g., g N kg^{-1} soil) for fertilizer N rate, mineralization or plant uptake of native soil N were converted to kg N ha^{-1} as described in Li and Evanylo (2013):

$$\text{kg N ha}^{-1} = \rho_b \times N_m\ (\text{or } N_p) \times d \times 10^{-1}$$

where ρ_b is soil bulk density (g cm^{-3}), N_m and N_p are the amount of native soil N mineralized from SOM or taken up by plants (mg N kg^{-1} soil), and d is soil depth (cm). We assumed ideal bulk densities for sand, silt, and clay (1.6, 1.4, and 1.1 g cm^{-3}) and a soil depth of 15 cm (Rowell, 2014) when data were not reported in the original publications.

2.2. Meta-analysis

To determine the response of mineralization and plant uptake of native soil N to fertilizer addition, the effect size (ES; kg N ha^{-1} year^{-1}) was calculated as the difference between fertilizer and control treatments:

$$ES_i = (V_f - V_c)/\text{length of study (days)} \times 365\ (\text{days/year})$$

where V is mineralization or plant uptake of native soil N (kg N ha^{-1}) for fertilizer (V_f) and control (V_c) treatments of the ith observation in the dataset.

A few studies in our dataset used the same control for multiple fertilizer treatments, e.g., three levels of inorganic N fertilizer addition (Blankenau et al., 2000). To avoid using multiple non-independent effect sizes, we averaged all experimental observations corresponding to the same control to obtain one independent effect size. Effect sizes were weighted by the number of experimental replicates (Adams et al., 1997):

$$W_i = (n_c \times n_f)/(n_c + n_f)$$

where n_c and n_f are the number of replicates for the control and fertilizer treatments for the i^{th} observation in the dataset. For studies that used the same control for multiple fertilizer treatments, n_f is the sum of number of replicates of all fertilizer treatments.

Mean effect size (MES) was calculated as:

$$\overline{MES} = \Sigma(ES_i \times W_i)/\Sigma W_i$$

Table 1
Literature data for mineralization of native soil nitrogen used in the *meta*-analysis.

Fertilizer type	Reference	Soil pH	Soil texture	Study duration (days)
Organic	Azam and Mulvaney (1993)	5.7/7.7	Silt	28
	Gentile et al. (2008)	4.7/5.5	Sand/clay	272
	Kawaguchi et al. (1986)	5.6/6.3	Clay	196
	Muriuki et al. (2001)	6.3	Sand	182
	Pare and Gregorich (1999)	5.9/7.2	Silt/clay	42
Inorganic	Gentile et al. (2008)	4.7/5.5	Sand/clay	272
	Muriuki et al. (2001)	6.3	Sand	182
	Wickramasinghe et al. (1985)	4.0/6.8	Silt/clay	40

Table 2
Literature data for plant uptake of native soil nitrogen used in the *meta*-analysis.

Fertilizer type	Reference	Soil pH	Soil texture	Study duration (days)	Study location	Plant species
Organic	Asagi and Ueno (2009)	6.2	Sand	85	Field	Rice
	Ashraf et al. (2004)	7.8	Sand	100	Lab	Rice
	Barbanti et al. (2011)	7.7	Silt	99	Lab	Sorghum
	Bergstrom and Kirchmann (1999)	6.2	Sand	365	Field	Barley
	Bergström and Kirchmann (2004)	7.2/8.2	Sand	94	Field	Barley
	Breland and Hansen (1998)	5.6	Silt	57	Lab	Ryegrass
	Choi et al. (2004)	6.5	Sand	45	Lab	Cabbage
	Ebid et al. (2008)	6.6	Sand	119	Lab	Radish/spinach
	Ghoneim (2008)	6.8	Sand	105	Lab	Rice
	Kurdali (2004)	8.1/8.3	Silt	70	Lab	Sorghum
	Lu et al. (2013)	6.3	Silt	365	Field	Rice
	Takahashi et al. (2003)	5.7	Clay	66	lab	Rice/maize
	Westerman and Kurtz (1973)	5.6	Silt	84	Field	Sudangrass
	Wu et al. (2010)	5.0/7.3	Sand/clay	120	Lab	Rice/wheat
Inorganic	Asagi and Ueno (2009)	6.2	Sand	85	Field	Rice
	Asagi et al. (2015)	5.4	Clay	30	Field	Spinach
	Ashraf et al. (2004)	7.8	Sand	100	Lab	Rice
	Bergstrom and Kirchmann (1999)	6.2	Sand	365	Field	Barley
	Bergström and Kirchmann (2004)	6.2	Sand	94	Field	Barley
	Blankenau et al. (2000)	5.5	Sand	90	Lab	Wheat
	Blesh and Drinkwater (2014)	6.1	Clay	104	Field	Rye
	Bosshard et al. (2009)	6.4	Silt	112	Field	Maize
	Bronson et al. (2000)	7.1	Clay	95	Lab	Rice
	Ebid et al. (2008)	6.6	Sand	119	Lab	Radish/spinach
	Ehaliotis et al. (2010)	7.8	Sand	105	Lab	Pepper
	Ghaley et al. (2010)	5.4	Clay	45	Field	Rice
	Glendining et al. (1997)	7.3/7.5	Silt	110	Field	Barley
	Hgaza et al. (2012)	5.4	Sand	167	Field	Yam
	Khelil et al. (2005)	8.5	Sand	80	Field	Sudangrass
	Leon et al. (1995)	5.8	Silt	28	Field	Ryegrass
	Lin et al. (2004)	6.7	Sand	35	Lab	Wheat
	Macdonald et al. (1997)	6.6/7.8	Sand/silt /clay	128/170	Field	Wheat/rape /potato/bean
	Nannen et al. (2011)	5.5	Sand	120	Field	Maize
	Pan et al. (2012)	5.6	Silt	36	Field	Rice
	Pilbeam et al. (2002)	5.4/6.0	Silt/clay	143	Field	Maize/millet
	Rao et al. (1991)	5.5/7.2	Silt	60	Lab	Wheat
	Recous et al. (1988)	7.8	Silt	154	Field	Wheat
	Rimski-Korsakov et al. (2012)	5.9	Silt	143	Field	Maize
	Rowlings et al. (2016)	6.1	Clay	130	Field	Grass
	Stevens et al. (2005)	5.6	Silt	135	Field	Maize
	Wang et al. (2016)	8.3	Silt	141	Field	Maize
	Westerman and Kurtz (1973)	5.6	Silt	84	Field	Grass
	Wu et al. (2010)	5.0/7.3	Sand/clay	120	Lab	Rice/wheat
	Zhang et al. (2012)	8.6	Silt	92	Field	Rice

MetaWin (version 2.1) was used to calculate mean effect sizes and 95% confidence intervals (CIs) by bootstrapping (9999 iterations). Individual treatment effects were considered significant if their 95% CIs did not overlap with zero. We used randomization tests in MetaWin to determine significant differences in treatment effects between study categories and treatment effects of mineralization vs. plant uptake of native soil N ($p < 0.05$).

3. Results

Averaged across fertilizer type, fertilizer addition tended to reduce mineralization of native soil N ($p = 0.16$; Fig. 2). Organic fertilizer tended to decrease native soil N mineralization by 99 kg N ha^{-1} year^{-1} ($p = 0.09$), whereas inorganic fertilizer tended to increase it by 58 kg N ha^{-1} year^{-1} ($p = 0.17$). Treatment effects of organic and inorganic fertilizers were not affected by soil texture or study location (Table 3). Other factors, such as soil pH, fertilizer N rate, soil C and N content, and study duration, were not different between organic and inorganic fertilizers (Table S1).

In contrast, fertilizer application increased plant uptake of native soil N across fertilizer type (Fig. 2; $p < 0.001$). Organic

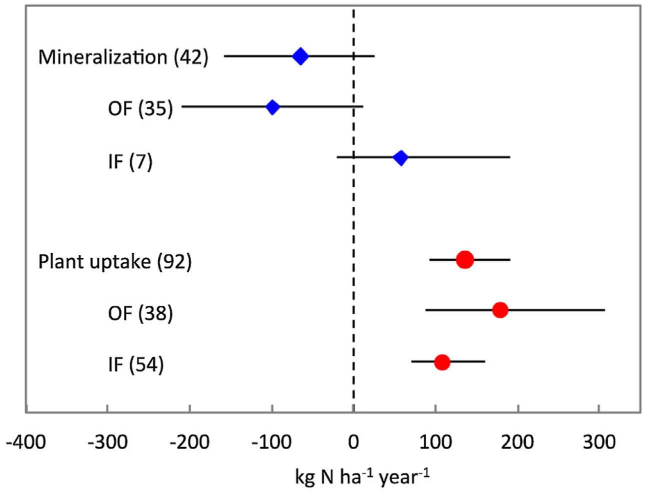

Fig. 2. Effects of fertilizer addition on mineralization and plant uptake of native soil N (OF = organic fertilizer; IF = inorganic fertilizer). Numbers in parentheses are number of independent observations. Error bars indicate 95% confidence intervals.

Table 3
Mineralization and plant uptake of native soil nitrogen (kg N ha^{-1} year^{-1}) in response to fertilizer addition as affected by soil texture and study location.

Parameters	Classes	Soil mineralization			N[a]	Plant uptake			N
		Mean	95% CI			Mean	95% CI		
			Lower	Upper			Lower	Upper	
Soil texture	Sand	−13	−86	57	9	91	47	147	41
	Silt	−102	−255	44	24	193	99	326	33
	Clay	−26	−173	139	9	135	60	241	17
Study location	Field	–	–	–	–	95	53	148	50
	Lab	−65	−158	26	42	181	103	290	41

[a] Number of independent observations.

fertilizer increased plant uptake of native soil N by 179 kg N ha^{-1} year^{-1} ($p < 0.001$), and inorganic fertilizer increased it by 107 kg N ha^{-1} year^{-1} ($p < 0.001$). Yet, the effects of organic and inorganic fertilizers on plant uptake of native soil N did not differ. Treatment effects on plant uptake of native soil N were not affected by soil texture or study location (Table 3). Furthermore, studies on organic and inorganic fertilizer were implemented under comparable experimental conditions and soil characteristics (Table S1).

Across the entire dataset, the average fertilizer effect on plant uptake of native soil N was greater than its effect on native soil N mineralization (Fig. 2; $p < 0.001$). With organic fertilizer, plant uptake of native soil N was greater than mineralization of native soil N (179 vs. −99 kg N ha^{-1} year^{-1}; $p < 0.001$). With inorganic fertilizer, however, no significant difference was observed between plant uptake and mineralization of native soil N. Because all studies on native soil N mineralization were conducted in the laboratory, whereas those on plant uptake of native soil N were done in both laboratory and field, the difference in treatment effects between mineralization and plant uptake of native soil N could be confounded by study location. However, further analyses suggest that this was not the case: laboratory and field studies on plant uptake of native soil N showed similar responses to fertilizer addition (Table 3).

4. Discussion

Across 43 published N tracer studies, fertilizer addition had variable effects on mineralization but consistently positive effects on plant uptake of native soil N. Fertilizer addition tended to reduce native soil N mineralization, although the effect was not significant and variance was high, suggesting that interactions between native soil N mineralization and fertilizers are not identified in our analysis. The C:N ratio of organic fertilizer was proposed to affect the direction of effects on mineralization (Masunga et al., 2016; Trinsoutrot et al., 2000; Turmel et al., 2014), such that fertilizers with lower C:N ratios would stimulate greater N mineralization, microbial biomass, and abundances of bacteria and fungi (Masunga et al., 2016). However, the C:N ratio was not a reliable predictor for native soil N mineralization in our dataset. Our results corroborate those by Azam and Mulvaney (1993) who reported that three organic fertilizers (with different C:N ratios) showed negative effects on native soil N mineralization in one soil, but positive effects in another soil, despite the fact that the two soils exhibited similar nutrient concentrations and physicochemical characteristics. Other nutrient additions, such as phosphorus (P), have been reported to increase net soil N mineralization and abundances of ammonia-oxidizing bacteria but to decrease enzyme activities related to N-mineralization (Chen et al., 2016). Yet, it is impossible to quantify the amount of mineralized native soil N from studies that did not use ^{15}N tracers. In general, results from our synthesis and others suggest that the C:N ratio of the fertilizer has little influence on the direction of native soil N mineralization with fertilizer addition. Possibly, soil microbe-related mechanisms involving N transformations play a stronger role.

There are several possible explanations for the variable fertilizer effects on native soil N mineralization. Negative effects of organic fertilizer on native soil N mineralization can occur when microbes are energy-limited, shifting from SOM to organic fertilizer for energy (Liu et al., 2017) and N (simultaneous preferential utilization of C and N) (Cheng, 1999; Spohn et al., 2016), reducing native soil N mineralization (Ekschmitt et al., 2005). For example, fresh organic matter (wheat straw) addition not only provided microbes with energy, but also provided 10% of N for microbial biomass, and increased soil total N (Shindo and Nishio, 2005). Alternatively, interactions, where microbes decomposing fresh organic fertilizer outcompete those decomposing native SOM (Fontaine et al., 2003; Liu et al., 2017), might lead to the decrease in native soil N mineralization.

On the other hand, positive effects of fertilizer (organic and inorganic) on native soil N mineralization can be explained in several ways. Increased N availability, such as fertilizer addition, might trigger C limitation for microbes when microbial C demands exceed C supply. As a result, microbes would have to increase production of extracellular enzymes to break down SOM (Drake et al., 2013) and gain energy (the C priming) (Liu et al., 2017). Because of the low C:N ratio of SOM, microbial C priming can result in simultaneous release of native soil N (Schimel and Weintraub, 2003). Increased mineralization of native soil N could also be associated with remineralization – the accelerated microbial (biomass) N turnover (Shindo and Nishio, 2005), a process in which microbe-immobilized (native soil) N is released to the environment after microbial death (Redin et al., 2014).

In contrast to variable fertilizer effects on native soil N mineralization, both organic and inorganic fertilizers significantly increased plant uptake of native soil N. These consistently positive effects suggest that the increased plant uptake of native soil N was primarily controlled by plant-mediated mechanisms, instead of by soil microbe-mediated mechanisms. Indeed, fertilizer addition is known to stimulate root growth and density, increase root biomass, and extend rooting depth (Ashraf et al., 2004). These changes in plant morphology and size increase the soil volume explored by plant roots (Kurdali, 2004), thereby enhancing plant uptake of native soil N (Azam and Mulvaney, 1993). Under nutrientlimitation, if the N from fertilizers does not meet plant demands, plants can outcompete microbes by suppressing their growth and enzyme activity related to mineralization of native soil N (Kaye and Hart, 1997), increasing microbial turnover (death) and remineralization of microbe-immobilized native soil N (Breland and Hansen, 1998). Furthermore, fertilizer addition might stimulate rhizosphere N priming by increasing the root exudation that fuels microbial growth and enzyme production (Dijkstra et al., 2013; Liu et al., 2017), increasing the amount of mineralized native soil N.

5. Conclusions

Our findings demonstrate that fertilizer application variably affected native soil N mineralization, but consistently increased plant uptake of native soil N. This inconsistency in fertilizer effects on native soil N mineralization suggests complex interactions between fertilizer addition and microbial immobilization and mineralization of N, indicating the need for further study. Strongly positive responses of plant uptake of native soil N to fertilizer addition, as compared with negative responses of native soil N mineralization (especially to organic fertilizer addition), suggest that plant-mediated mechanisms (e.g., increased root growth, rhizosphere N priming) play an more important role than soil microbe-mediated mechanisms in enhancing native soil N utilization by plants with fertilizer application.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2017.03.011.

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