



Nitrogen fertilization altered arbuscular mycorrhizal fungi abundance and soil erosion of paddy fields in the Taihu Lake region of China

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Abstract

Arbuscular mycorrhizal (AM) fungi were of importance in mitigating soil erosion, which was highly influenced by biotic and abiotic factors, such as host plant growth and soil nutrient. To investigate the impact of nitrogen (N) fertilization on seasonal variance in AM colonization and soil erosion, we conducted a field experiment with rice cultivation under four N fertilizer levels (0 kg N ha⁻¹, 270 kg N ha⁻¹, 300 kg N ha⁻¹, and 375 kg N ha⁻¹ plus organic fertilizers) in the Taihu Lake region, China. We investigated AM colonization before rice transplantation, during rice growth, and after rice harvest. We also assessed soil splash erosion of intact soil cores sampled at tillering and after rice harvest. We found that AM colonization (indicated by percentage of root length colonization) varied from 15 to 73%, which was attributed to rice growth, N fertilization, and their interaction. Soil loss due to splash erosion was cut down by organic N fertilizer at tillering, while higher inorganic N fertilization significantly increased soil loss after rice harvest. Additionally, we found significantly negative relationships of AM colonization to soil loss but positive relationships to soil aggregate stability. We highlighted the potential role of AM fungi in decreasing soil erosion and suggested that high N fertilization should be considered carefully when seeking after high yields.

Keywords Nitrogen · Arbuscular mycorrhiza · Splash erosion · Aggregate stability · Rice · Fertilization

Introduction

As a key component of the environment, agricultural soil is significant for food and water security. Agricultural soil erosion causes “on-site” problems for food security and “off-site” problems for water security (Borrelli et al. 2018; Mardhiah et al. 2016). In agricultural food production, the main “on-site” problem is the decrease in food productivity due to loss of upper layer soils with high nutrient availability (Olson and Nizeyimana 1988). For water security, the “off-site” effects

include sedimentation of waterways and eutrophication (Xie and Yue 2018). Sustainable development requires both increase in agricultural production and decrease in waterway sedimentation and water eutrophication. Thus, novel approaches that systematically improve agricultural production without decreasing water security are highly demanded.

Arbuscular mycorrhizal (AM) fungi might be the sustainable alternative to achieving food security (Thirkell et al. 2017; Zhang et al. 2019) and improving water security (Bowles et al. 2017; Cavagnaro et al. 2015). AM fungi form symbiosis with and obtain organic carbon from most crops (Jiang et al. 2017). As a return, they provide host plants with both macronutrients (i.e., nitrogen, phosphorus, and potassium) (Delavaux et al. 2017) and micronutrients (e.g., zinc, copper, manganese, and selenium) (Lehmann and Rillig 2015). In addition to nutritional function, they were reported to increase plant tolerance to both biotic and abiotic stresses, including pests, pathogens, heat, heavy metals, drought, ozone, and parasites (Cabral et al. 2016; Cui et al. 2018; De La Peña et al. 2006; Li et al. 2011; Louarn et al. 2012; Yang et al. 2014; Zhang et al. 2016a). Furthermore, they showed great potential in controlling nutrient loss from agricultural

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eco-systems via leaching (Bowles et al. 2017; van der Heijden 2010), runoff (Zhang et al. 2016b, 2015a), and gas emission (Bender et al. 2015; Storer et al. 2017; Zhang et al. 2015b). More importantly, they play a significant role in reducing soil erosion (Mardhiah et al. 2016) via improving soil aggregate stability (Leifheit et al. 2015). Therefore, sustainable farming would benefit from good understanding of the variance in AM colonization and effects on soil erosion under changing environments, such as varying nitrogen fertilization.

AM colonization, usually indicated by percentage of root length colonization, was depended on both biotic and abiotic factors. For rice inoculated with AM fungi, AM colonization on the 35th day (51.4%) after sowing was different from that on the 122nd day (harvesting stage, 36.3%), indicating that AM colonization varied with rice growing (Solaiman and Hirata 1997). In another AM fungi inoculation experiment, Solaiman and Hirata (1998) reported that AM colonization was depended on status of soil and water: AM colonization was greater for seedlings cultivated in wet seedling nursery when compared to the seedling in wet nursery. This was in agreement with an investigation on semi-aquatic grasses along a wide hydrologic gradient, which indicated that flooding had an inhibitory effect on AM colonization (Miller 2000).

AM colonization was also altered by fertilization. Camenzind et al. (2016) found that in a tropical montane forest, nitrogen additions decreased AM colonization along an elevational gradient. A meta-analysis integrating nutrient responses across independent field-based studies also found that compared with the non-fertilized control, AM colonization decreased 15% under N fertilization (Treseder 2004). Additionally, AM colonization decreased with increasing dosage of N fertilization in an alpine meadow on the Tibetan (Liu et al. 2012). This was explained by the “trade balance model” based on the functional equilibrium hypothesis: N fertilization removed N-limitation and then plants were limited by carbon; carbon-limited plants tended to allocate less carbon to AM fungi and then AM colonization decreased (Johnson 2010; Kleczewski et al. 2011).

AM fungi played a role in enhancing the stability of soil aggregates (Lehmann et al. 2017; Rillig et al. 2019; Wu et al. 2014a, b; Xu et al. 2015). Specifically, AM fungi increased soil accumulation of glomalin-related soil proteins (GRSP), a component of hyphae cell wall (Driver et al. 2005), leading to enhanced soil aggregate stability (Wu et al. 2014a). In addition, AM fungi enhanced the stability of soil aggregates via twining smaller aggregates with their extraradical hyphae (Mardhiah et al. 2016). Furthermore, AM fungi increased soil organic matter content by enhancing growth of other soil microorganisms as AM fungi were large conduits of carbon flow below-ground (Nuccio et al. 2013). Importantly, the effect of AM fungi on soil aggregate stability could be detectable after 30 days of inoculation and the effect was significant even under low colonization (Xu et al. 2015). As soil aggregate

stability is often acknowledged for their resistance to soil erosion (Barthès and Roose 2002), any biotic or abiotic factors impacting on AM colonization might increase the risk of soil erosion.

Although there are many studies focusing on the effect of N fertilization on AM colonization at given plant growth stage, little is known how this effect vary within the whole growing season during which both soil temperature and water management are changing. Additionally, the direct impact of fertilization on soil erosion was investigated in previous studies (Gholami et al. 2016), whether fertilization altered soil erosion indirectly, such as via manipulating the abundance of AM fungi, is unknown. In our study, we aim to answer the following questions by running a field experiment involving four nitrogen (N) fertilizer treatments in the Taihu Lake Region:

- (i) Does N fertilization impact seasonal variation in AM colonization and soil erosion?
- (ii) What are the relationships among AM colonization, soil erosion, and soil aggregate stability?

Materials and methods

Description of the study area

The field experiment was carried out in Changshu Agro-ecological Experimental Station, Chinese Academy of Sciences, Changshu City, Jiangsu Province, China (31°32' 93"N, 120°41'88"E). In the experimental year, the mean annual temperature of this region was around 17 °C and the mean annual rainfall was about 1345 mm, indicated by the automatic meteorological station (Vaisala, Finland) located at the Changshu Agro-ecological Experimental Station.

The soil is classified as Gleyi-Stagnic Anthrosol (CRGCST2001) developing from lacustrine sediments. The soil texture is silt clay loam, with 13.3% sand, 54.8% silt, and 31.9% clay. Soil particle size was determined with a laser particle size analyzer (LS13320, Beckman Coulter, Brea, CA, USA). The soil in this region contained 2.83 g kg⁻¹ total nitrogen, 26.6 g kg⁻¹ soil organic carbon, 0.87 g kg⁻¹ total phosphorous, and had a pH of 6.99 (soil: MiliQ water = 1:2.5) at the beginning of the experiment. The crop succession was winter wheat (*Triticum aestivum* L.) lasting from mid-October of the first year to mid-June of the second year and summer rice (*Oryza sativa* L.) going from mid-June to mid-October of the second year.

Experimental design

Before our investigation, the fertilization treatment had been conducted for 1 year, which covered summer rice and winter

wheat. During the experimental year, all of the treatments were applied to the same rice cultivar ‘Changyou 5’ and the same field management practice. For rice seedling cultivation, rice seeds were grown in soil collected from paddy fields where seedlings would be transplanted to. During this seedling cultivation process, no fungicide or other alternatives that were harmful to AM fungi were applied, indicating that the indigenous AM fungi was not inactive before transplantation. Rice seedlings were cultivated for 5 weeks and the percentage of AM root colonization was 6% before transplantation. Therefore, in our study, all the AM fungi involved were indigenous.

Four nitrogen fertilization treatments with four replicates in completely four randomized blocks were established, that is, a total of 16 plots ($6 \times 7 \text{ m}^2$). The plots were separated by a 30-cm earthen ridge and lined with polyvinyl chloride (PVC) boards. The PVC boards were placed into the soil at a depth of 30 cm to prevent the movement of surface and ground water among the adjacent plots.

The nitrogen fertilization treatments were (1) N0, no nitrogen fertilizer applied; (2) N270, applied 270 kg N ha^{-1} ; (3) N300, applied 300 kg N ha^{-1} ; (4) N375 + O, applied 375 kg N ha^{-1} plus organic fertilizer (rapeseed cake fertilizer after fermentation, 2.25 t ha^{-1}). For all the treatments, 90 kg diphosphorus pentoxide (P_2O_5) ha^{-1} and 120 kg potassium oxide (K_2O) ha^{-1} were applied as basal fertilizers. Nitrogen fertilizers were applied as urea (N, 46%), phosphorus fertilizers were applied as superphosphate (P_2O_5 , 13.5%), and potassium fertilizers were applied as potassium sulfate (K_2O , 60%). For all the treatments, 50% urea-N was applied as basal fertilization, 10% as tillering topdressing, 20% as anthesis topdressing, and 20% as heading topdressing.

The basal fertilizer was manually broadcast onto the surface soil and integrated by plowing and harrowing before transplantation. The topdressing fertilizers were homogeneously broadcast onto the surface water.

Water management

The field water regime was conducted under a cycle of flooding-drainage-reflooding-moist mode. The soil was submerged before rice seedlings were transplanted until tillering, and during this period, the surface water was maintained at a depth of 3–5 cm. At the end of the tillering stage, a 10-day drainage was conducted to control the tiller number, which was followed by a reflooding. The flood water was maintained until 40 days before harvest. After that, a final intermittent irrigation was carried out.

Sample collection

Rice root and soil sampling was conducted from rice seedling beds and paddy fields before transplantation. Sampling of

roots and soil was also conducted after transplantation, at tillering, booting, flowering, filling, ripening, and 15 days after harvest. Rice roots and soil were collected from surface soil layer (0–20 cm depth). Samples were immediately placed in a cooler in the field. All live roots were carefully collected from the soils. The live roots were selected visually based on color and turgescence. Roots collected from soils were used to estimate the colonization of AM fungi within roots. Soil was used for NO_3^- -N and NH_4^+ -N concentration analyses.

Undisturbed soil cores were sampled on the 10th day of the first drainage and the 15th day after rice harvest. The reason was that during these two periods, the soil was not completely covered by water or plants and more vulnerable to splash erosion. During these two periods, soil ring samplers (diameter: 10 cm; height: 2.5 cm) were used to collect intact soil cores. All the intact soil cores with ring samplers were immediately placed in aluminum boxes to prevent any possible disturbance during transportation.

Splash erosion tests

Rainfall simulator used in our experiment was NLJY-09-1 provided by Nanjing south forest electronic technology co. LTD. Rainfall height was 4.75 m, and the medium raindrop diameter was 2.4 mm and the pressure was 0.08 MPa. The uniformity index of rainfall was 90% and accuracy of adjustment was 5%. Tap water was used for all tests. The duration of rainfall was 5 min and the rainfall intensity was set at 130 mm h^{-1} .

At the end of each rainfall event, sedimentation was conducted for 5 h. The sediment in the splash cups was air-dried and moved gently with a brush into aluminum boxes. Soil loss was calculated by dividing the air-dried sediment weight by the air-dried soil core weight before splash erosion tests.

Root and soil analysis

Roots collected from soils were used to estimate the colonization of AM fungi within roots. The roots were washed with tap water and cut into 1–2-cm pieces. These root pieces were cleared with 10% KOH in boiling water for 30 min and neutralized with 0.2% HCl. Then, after the roots were washed three times, they were stained with acid fuchsin for 30 min in water kept at 90°C . The percentage of root length colonization (RLC) by AM fungi was estimated with these stained roots under a microscope using the grid line intersect method (Giovannetti and Mosse 1980). Around 100 pieces were measured for each replicate.

Soil samples were air-dried before being analyzed for extraradical hyphal length of AM fungi as a measure of fungal abundance in the soil. Hyphae were extracted from 4.0 g of dried soil using a protocol adapted from Jakobsen et al. (1992) and then stained with Trypan Blue. Hyphae density was

measured according to Rillig et al. (1999). Spores of AM fungi were separated from 50 g of air-dried soils by wet sieving and sucrose centrifugation (Brundrett et al. 1994).

Soil samples were extracted with 2 M KCl at a soil/KCl ratio of 1:10, shaken for 1 h, and filtered for NO_3^- -N and NH_4^+ -N analyses with an automatic chemical analyzer (Smartchem140, AMS).

Soil samples from the 1-cm surface of paddy field were collected at the same time of intact core sampling. The water-stable aggregate (WSA) distribution at 2–4, 1–2, 0.5–1, and 0.25–0.5 mm size was determined using the wet-sieving method [modified from Leifheit et al. (2015)]. Determination of mean weight diameter (MWD, an indicator of aggregate stability) was as follows: $\text{MWD} = \sum_{i=1}^n X_i W_i$, where X_i is the mean diameter of the sieves opening (mm), W_i is the proportion of the size fraction in the total sample mass, and n is the number of size fractions.

Statistical analysis

Two-way analysis of variance (ANOVA) was used to distinguish the difference in AM colonization, soil loss, N availability, and soil aggregate stability. Spearman correlation analyses were performed to investigate the relationships among AM colonization, soil loss, N availability, and soil aggregate stability. The statistics and graphic visualization were carried out with software R (RCoreTeam 2017).

Results

AM colonization

At the end of seedling, percentage of AM root colonization was 6%. It varied from 15 to 73% across the whole investigation period and the four nitrogen (N) fertilization levels (Fig. 1). To estimate the effect of rice growth, N fertilization, and their interaction on AM colonization, we conducted a two-way ANOVA test. We found that they all played significant roles in varying AM colonization (Table 1).

In the control (N0), AM colonization increased from 26% at tillering to 54% at booting, decreased to 36% at flowering and filling. After that, there was a slight increase to 40% at ripening, followed by a decrease to 25% during the fallow period after rice harvest. For the two fallow periods, AM colonization before rice transplantation (46%) was much higher than that after rice harvest (25%).

During the fallow period, before rice transplantation and tillering, proper dosage of N fertilization (N270) increased AM colonization while more N fertilization resulted in smaller AM colonization. At booting and ripening, N addition lowered AM colonization. During flowering, filling and

fallow after rice harvest, there was no significant effect of N fertilization on AM colonization (Fig. 1).

In addition to percentage of AM root colonization, we also investigated spore density and density of extraradical hyphae for AM fungi. In terms of spore density, we found that the impact of N fertilization was not significant while it was greater after rice harvest than that at tillering. For extraradical hyphae, its seasonal variation and responses to N fertilization were similar with percentage of AM root colonization (Tables 1 and 2).

Soil erosion

Soil loss due to splash erosion was significantly altered by N fertilization, rice growth, and their interaction (Table 1). Compared with the control (N0), it was greater at high inorganic N fertilization (N300) during tillering while it was lower in treatment with organic N fertilization (N375 + O) after rice harvest. Soil loss after rice harvest was higher than the tillering (Fig. 2a).

Availability of soil N

Soil NH_4^+ -N concentration was significantly altered by N fertilization, rice growth, and their interaction (Table 1). It was much lower at tillering than those after rice harvest. At tillering, N270 had higher value while after rice harvest, N0 had lower value (Table 2).

Rice growth had significant effects on soil NO_3^- -N concentration while N fertilization and their interaction had no significant effect (Table 1). Specifically, soil NO_3^- -N concentration was much lower at tillering than those after rice growth (Table 2).

Soil aggregate stability

N fertilization only had significant effect on water-stable aggregate (WSA) in 2–4 mm size fraction and had no significant effect on other WSA fractions (Table 1). Compared to the non-fertilization control (N0), organic N fertilization increased this size fraction (Table 2).

Rice growth had significant effect on all WSA fractions (Table 1). Specifically, WSA in 2–4 and 0.5–1 mm size fractions were higher at tillering than those after rice harvest. By contrast, 1–2 and 0.25–0.5 mm size fractions were lower at tillering than those after rice harvest (Table 2).

The effect of interaction between N fertilization and rice growth was only significant on 0.5–1 mm size fraction (Table 1). At tillering, organic N fertilization increased this size fraction but did not impact on this after rice harvest. This size fraction was greater at tillering than that after rice harvest (Table 2).

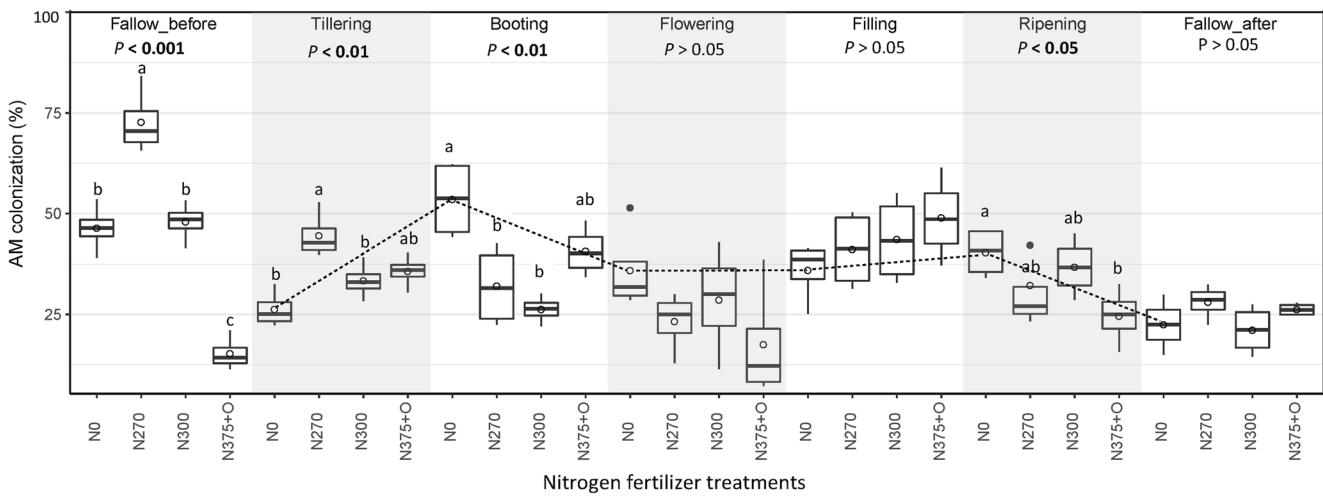


Fig. 1 Variance in AM colonization indicated by percentage of root length colonization. Circles in the boxplots shown are the means calculated using four replicates for each treatment; points in black color were outliers; fallow_before: at the fallow period before rice transplantation; fallow_after: at the fallow period after rice harvest (postharvest); N0: no nitrogen fertilizer treatment; N270: nitrogen

fertilizer dosage was 270 kg N ha⁻¹; N300: nitrogen fertilizer dosage was 300 kg N ha⁻¹; N375 + O: nitrogen fertilizer dosage was 375 kg N ha⁻¹ plus organic fertilizer. Dotted line shows the seasonal variance of AM colonization for N0. Different lowercase letters indicate differences (*P* < 0.05) among the nitrogen fertilizer treatments

The mean weight diameter (MWD) of WSA was significantly altered by N fertilization, rice growth, and their interaction (Table 1). It was increased by organic N fertilization at tillering but did not change after rice harvest. This parameter was significantly greater at tillering than that after rice harvest (Table 2).

All in all, organic N fertilization (not inorganic N fertilization) mainly increased 2–4 mm size fraction of WSA and then MWD. At tillering, 2–4 and 0.5–1 mm size fractions of WSA and MWD were higher than those after rice harvest.

Relationships

Combining the two stages, both soil NH₄⁺-N and NO₃⁻-N concentration negatively correlated with soil loss (Figs. 2b, c and 3). WSA in 2–4 and 0.5–1 mm size fractions and MWD negatively correlated with soil loss (Figs. 2d, f, h and 3); those

in 1–2 and 0.25–0.5 mm size fractions were positively correlated with soil loss (Fig. 2e, g and 3).

We found that AM colonization negatively correlated with soil loss and soil N availability (Figs. 3 and 4a–c). Among the sizes of WSA, AM colonization positively correlated with 2–4 and 0.5–1 mm WSA and MWD (Figs. 3 and 4d, f, h), but negatively correlated with 1–2 and 0.25–0.5 mm WSA (Figs. 3 and 4e, g).

Discussion

Building on past studies focused on the effects of AM fungi on crop yields (Bakhshandeh et al. 2017; Sisaphaithong et al. 2017; Zhang et al. 2017; Zhu et al. 2017) and nutrient loss to water environment (Asghari and Cavagnaro 2012; Cavagnaro et al. 2015), our study investigated: (i) Does N

Table 1 Effects of nitrogen fertilization, rice growth, and their interaction on AM colonization, spore density, density of extraradical hyphae, and soil loss due to splash erosion, soil nitrogen availability, and soil aggregate stability. WSA: water-stable aggregate; MWD: mean weight diameter; *F* values are shown

| | Nitrogen fertilization (N) | Stages (S) | Interaction between N and S |
|--------------------------------------|----------------------------|------------|-----------------------------|
| AM colonization | 16.172*** | 7.187*** | 8.427*** |
| Spore density | 0.791 | 11.720*** | 1.22 |
| Density of extraradical hyphae | 4.32* | 3.59* | 4.488* |
| Soil loss | 6.854** | 44.698*** | 6.129** |
| Soil NH ₄ ⁺ -N | 29.83*** | 227.89*** | 16.52*** |
| Soil NO ₃ ⁻ -N | 0.484 | 215.516*** | 0.476 |
| 2–4 mm WSA | 3.191* | 38.718*** | 2.885 |
| 1–2 mm WSA | 2.630 | 7.627* | 2.709 |
| 0.5–1 mm WSA | 2.296 | 18.295*** | 3.127* |
| 0.25–0.5 mm WSA | 1.898 | 4.603* | 0.491 |
| MWD | 2.372 | 29.550*** | 3.542* |

Table 2 Effects of nitrogen fertilization, rice growth stages, and their interaction on soil spore density, density of extraradical hyphae, and physical characteristics. Mean values are shown (\pm sd) calculated using four replicates for each treatment

| Nitrogen fertilization | Tillering | | | | After rice harvest | | | |
|--|------------------------------|-------------------------------|-------------------------------|------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| | N0 | N270 | N300 | N375 + O | N0 | N270 | N300 | N375 + O |
| Spore density (spore 100 g^{-1}) | 63.9 \pm 8.2 ^a | 59.1 \pm 6.9 ^a | 61.6 \pm 5.5 ^a | 71.5 \pm 9.8 ^a | 78.0 \pm 4.9 ^A | 80.9 \pm 8.3 ^A | 75.7 \pm 6.9 ^A | 83.6 \pm 7.1 ^A |
| Density of extraradical hyphae (cm g^{-1}) | 35.9 \pm 0.6 ^b | 42.7 \pm 4.0 ^a | 34.3 \pm 1.9 ^b | 37.7 \pm 5.2 ^{ab} | 24.0 \pm 7.0 ^a | 27.4 \pm 4.3 ^a | 30.0 \pm 6.8 ^a | 27.6 \pm 6.1 ^a |
| Soil NH_4^+ -N (mg kg^{-1}) | 1.90 \pm 0.40 ^b | 5.71 \pm 1.00 ^a | 2.90 \pm 1.26 ^b | 2.01 \pm 1.04 ^b | 5.74 \pm 1.06 ^B | 9.34 \pm 0.96 ^A | 8.80 \pm 1.34 ^A | 10.92 \pm 0.29 ^A |
| Soil NO_3^- -N (mg kg^{-1}) | 0.10 \pm 0.01 ^a | 0.10 \pm 0.02 ^a | 0.10 \pm 0.04 ^a | 0.10 \pm 0.01 ^a | 2.93 \pm 0.53 ^A | 3.70 \pm 0.94 ^A | 3.50 \pm 0.86 ^A | 3.61 \pm 1.14 ^A |
| 2–4 mm WSA (%) | 2.97 \pm 0.51 ^b | 4.80 \pm 0.96 ^a | 3.87 \pm 1.79 ^{ab} | 5.41 \pm 0.82 ^a | 2.21 \pm 0.91 ^A | 2.02 \pm 0.95 ^A | 2.13 \pm 0.82 ^A | 1.98 \pm 0.93 ^A |
| 1–2 mm WSA (%) | 2.21 \pm 0.06 ^a | 2.00 \pm 0.07 ^a | 1.86 \pm 0.05 ^a | 1.76 \pm 0.03 ^a | 2.29 \pm 1.14 ^{AB} | 2.60 \pm 0.53 ^{AB} | 3.16 \pm 0.27 ^A | 1.91 \pm 0.48 ^B |
| 0.5–1 mm WSA (%) | 3.79 \pm 1.13 ^b | 5.92 \pm 1.01 ^{ab} | 4.23 \pm 2.42 ^{ab} | 7.90 \pm 2.34 ^a | 3.20 \pm 1.31 ^A | 2.91 \pm 1.37 ^A | 3.07 \pm 1.18 ^A | 2.86 \pm 1.35 ^A |
| 0.25–0.5 mm WSA (%) | 2.14 \pm 0.14 ^b | 2.94 \pm 0.84 ^{ab} | 2.10 \pm 0.11 ^b | 3.09 \pm 2.06 ^a | 2.48 \pm 0.71 ^B | 3.80 \pm 1.91 ^{AB} | 3.16 \pm 0.80 ^{AB} | 4.98 \pm 2.05 ^A |
| MWD (mm) | 0.16 \pm 0.02 ^b | 0.23 \pm 0.03 ^{ab} | 0.18 \pm 0.06 ^{ab} | 0.26 \pm 0.04 ^a | 0.13 \pm 0.03 ^A | 0.14 \pm 0.04 ^A | 0.15 \pm 0.03 ^A | 0.13 \pm 0.04 ^A |

WSA water-stable aggregate, MWD mean weight diameter, N0 no nitrogen fertilizer treatment, N270 nitrogen fertilizer dosage was 270 kg N ha⁻¹, N300 nitrogen fertilizer dosage was 300 kg N ha⁻¹, N375 + O nitrogen fertilizer dosage was 375 kg N ha⁻¹ plus organic fertilizer. Different lowercase and capital letters indicate differences ($P < 0.05$) among the nitrogen fertilizer treatments

fertilization impact on seasonal variation in AM colonization and soil erosion? (ii) What are the relationships among AM colonization, soil erosion, soil N availability, and soil aggregate stability? Our results highlighted the potential role of AM colonization in decreasing soil erosion.

Impact of N fertilization on seasonal variance in AM colonization

As expected, AM colonization varied seasonally and N fertilization had different impacts on this seasonal variation in the Taihu Lake region. The increase in AM colonization from tillering to booting might be due to the 10-day drainage. This drainage created an aerobic environment and the oxygen limitation to AM fungi was removed, leading to better growth of AM fungi (Lumini et al. 2011; Unger et al. 2009). The decrease in AM colonization during flowering and filling might be attributed to the flooding inhibitory effect (Auge 2001). The slight increase at ripening likely resulted from the moist mode of water management where oxygen availability and redox potential were improved (Lumini et al. 2011; Unger et al. 2009). The possible reason of the final decrease during the fallow period after rice harvest might be that there was no lipid sources for AM fungi growth after rice was harvested (Jiang et al. 2017). The significant difference in AM colonization before rice transplantation (wheat roots remained in soil) and after rice harvest (rice roots remained in soil) could be explained by the difference in compatibility between wheat and rice (Smith and Read 2008). Taken together, this indicated that future field research on investigating AM abundance should pay more attention on this seasonal variation and the impact of previous crop.

Besides water management mode, soil temperature and plant carbon-gain-related factors (e.g., leaf area index and canopy photosynthesis rate) might also vary AM colonization. In our experimental site, soil temperature decreased gradually from the mean value of 29 °C to 14 °C during our experimental period. The low soil temperature inhibited photosynthate transferring from plants to AM fungi and AM fungi growth was carbon-limited, leading to decreasing AM colonization with rice growth (Hawkes et al. 2008). Additionally, it was known that the leaf area index increased fast during the vegetative growth period, reached the peak at the end of tillering, and then decreased gradually in the reproductive growth period (Fang et al. 2014). Similarly, rice canopy photosynthesis rate reached the peak before heading and got lower during the reproductive growth period (Sasaki et al. 2005). As AM fungi only obtain carbon from their host plants (Jiang et al. 2017), these plant carbon-gain-related factors might play a role in altering AM colonization. Further study, however, is required to confirm the effect of soil temperature and plant carbon-gain-related factors.

Researchers highlighted that AM fungi should be considered as a Daerwin species, rather than an extension of plant roots (Brunns et al. 2017). This suggested that AM fungi also require other nutrients (e.g., N) for their own growth so that AM colonization was expected to be lower in soils with lower N availability (Hodge et al. 2010). In contrast, higher N availability might have an inhibitory effect on AM fungi development as AM fungi might be limited by carbon (Johnson et al. 2015). Based on the functional equilibrium theory, plants tended to allocate less resources to AM fungi where mineral nutrient (and/or water) was ample than in nutrient (and/or water)-stress conditions (Johnson 2010). Therefore, we hypothesized that higher AM colonization would be observed

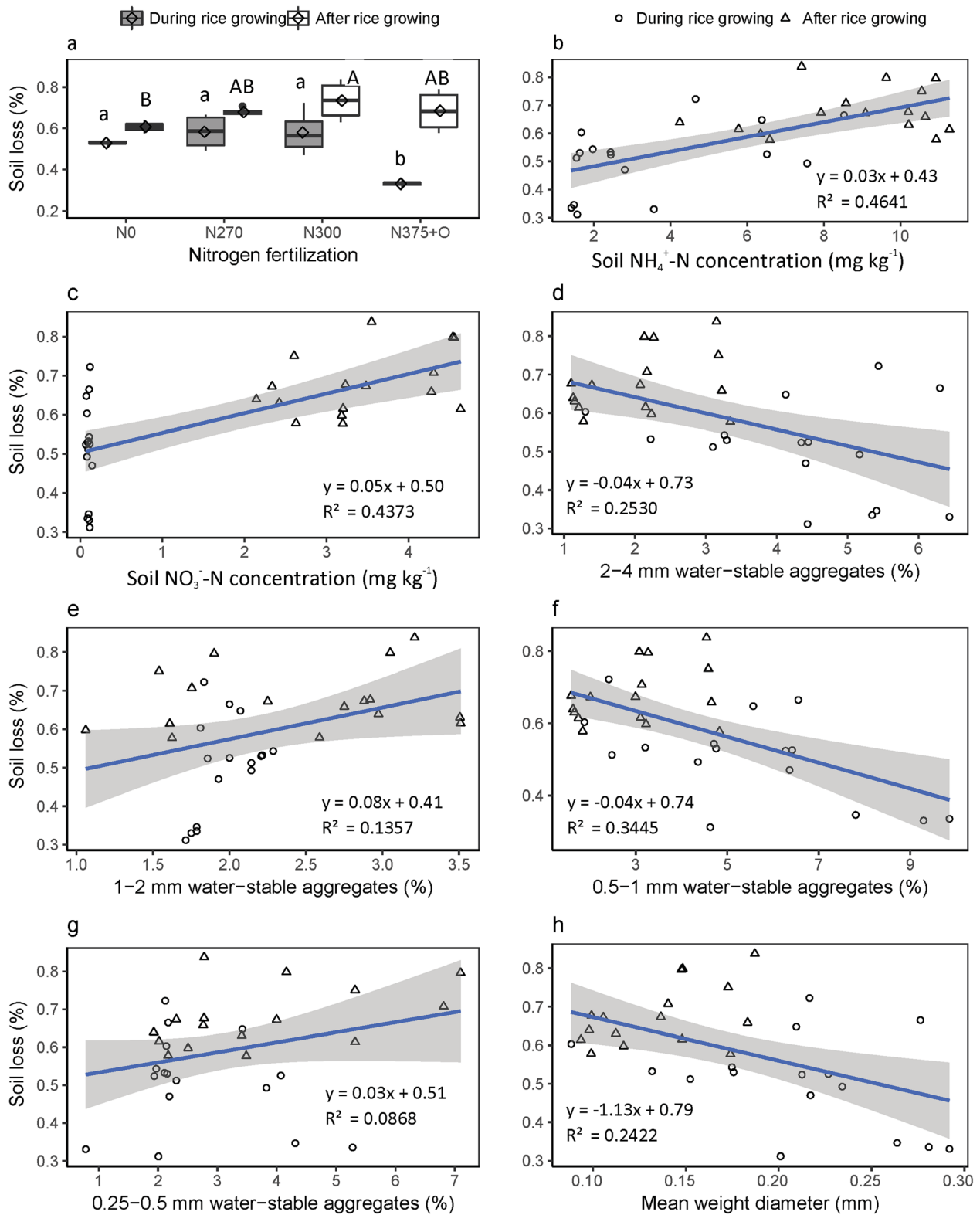


Fig. 2 Soil loss and its relationship with soil N availability and aggregate stability. **a** Diamonds in the boxplots are the means calculated using four replicates for each treatment; filled and non-filled boxes are for tillering and fallow after rice harvest, respectively; N0: No nitrogen fertilizer treatment; N270: nitrogen fertilizer dosage was 270 kg N ha^{-1} ; N300: nitrogen

fertilizer dosage was 300 kg N ha^{-1} ; N375 + O: nitrogen fertilizer dosage was 375 kg N ha^{-1} plus organic fertilizer. Different lowercase and capital letters indicate differences ($P < 0.05$) among nitrogen fertilizer treatments. For others, circles and triangles are for the data collected during tillering and fallow after rice harvest (postharvest), respectively

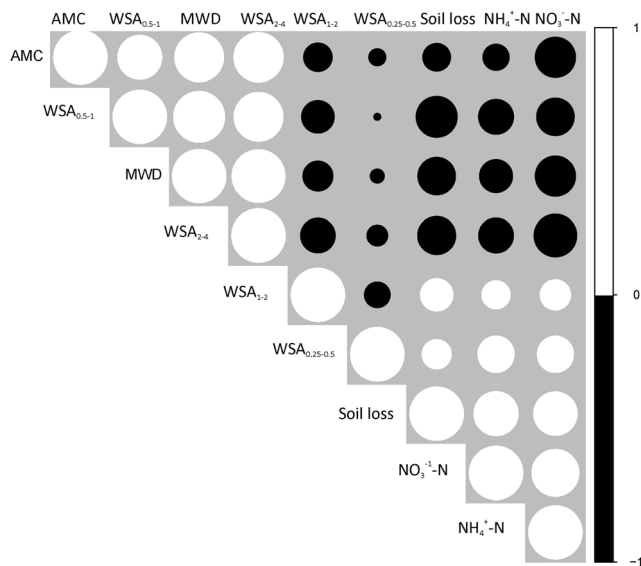


Fig. 3 Correlation matrix of AM colonization, soil loss, N availability, and aggregate stability. AMC, AM colonization; MWD, mean weight diameter; WSA_{0.25–0.5}, WSA_{0.5–1}, WSA_{1–2}, and WSA_{2–4} are short for 0.25–0.5, 0.5–1, 1–2, 2–4 mm size fractions of water stable aggregate. Circles with bigger sizes indicated greater absolute values of the Spearman correlation coefficient (only significant results were shown; $P < 0.05$). Circles filled with black indicate that the coefficients are negative; circles filled with white color indicate that the coefficients are positive, respectively

under lower N fertilization while lower AM colonization under highest N fertilizer levels.

Our results, collected during fallow period before rice planted and tillering stages, supported our hypothesis. This pattern was not observed at other stages. One of the likely reasons was that N fertilizers were applied four times, 50% applied before transplantation as basal fertilization, 10, 20, and 20% at tillering, flowering, and heading as topdressings. Therefore, the impact of N fertilizers was also changing seasonally. Another possible reason was that after application, the amount of soil N nutrients from fertilizers decreased with rice growing due to uptake by plants or soil microorganisms, ammonia volatilization (Zhao et al. 2015), denitrification (Wang et al. 2017), loss with leachate (Zhao et al. 2009), and runoff water (Zhao et al. 2012). Our analysis on the seasonal change of soil NH_4^+ concentration supported this hypothesis (Table 2). However, whether N fertilization pattern and N loss with rice growing contributed to the seasonal variation in AM colonization needs further research.

Impact of N fertilization on seasonal variance in soil erosion

Vegetation was reported to play a significant role in reducing soil erosion (Kervročdan et al. 2018). In our study, intact soil cores were used for the erosion test experiment, which excluded the effect of the above-ground part on soil erosion. So, only

the effect of roots on soil erosion was considered in our study. After rice harvest, the microorganism-induced decomposition of roots started under field condition (Zhu et al. 2016). Therefore, we hypothesized that soil erosion was less serious at tillering than those during the fallow period after rice harvest. As expected, we found that soil loss was smaller at tillering than the fallow after rice harvest. Importantly, soil NH_4^+ -N and NO_3^- -N concentrations were remarkably higher at fallow than tillering (Table 2), supporting our hypothesis that microorganism-induced decomposition of roots contributed less than viable roots.

We expected that high inorganic N fertilization would aggravate soil erosion while organic N fertilization would decrease soil erosion. Surprisingly, the negative effect of high inorganic N fertilization was only observed during the fallow period after rice harvest, not at tillering (Fig. 2a). The explanation might be that high inorganic N fertilization did not aggravate soil erosion directly but indirectly via decreasing resources allocated to AM fungi (functional equilibrium hypothesis) (Johnson 2010). The negative relationship between AM colonization and soil loss provided some support for this indirect role of N fertilization (Fig. 3). Additionally, the positive effect of organic N fertilization was only detectable at tillering (Fig. 2a). The possible reason might be that organic fertilizers not only provide N but also organic carbon which increased soil organic matter content and then reduced soil loss due to splash erosion (Wuddivira et al. 2009). Taken together, more attention should be paid on the period after rice harvest, rather than tillering stage, to effectively reduce soil erosion in rice production.

Potential role of AM colonization in reducing soil erosion

Soil erosion was reported to be related to soil cohesion (Prosser et al. 1995) and aggregate stability. We hypothesized that AM fungi might reduce soil erosion directly via enhanced soil cohesion and indirectly via improving soil aggregate stability. Firstly, we tested this direct effect of AM fungi on soil loss by plotting soil loss against AM fungi and we found a negative relationship between AM colonization and soil loss due to splash erosion. One of the reasons is the network of extraradical mycelium of AM fungi-enhanced soil cohesion. Additionally, compared with other soil fungi, the hyphae of AM fungi were more persistent, coarser, and thicker, playing a greater role in reducing soil erosion (Mardhiah et al. 2016).

The indirect role of AM fungi in reducing soil loss was based on the improvement in soil aggregate stability. As a soil structure and function unit, soil aggregate is considered an influential factor governing the biological, chemical, and physical characteristics of soils (Falson et al. 2012). Topsoil aggregate stability is often acknowledged for their resistance

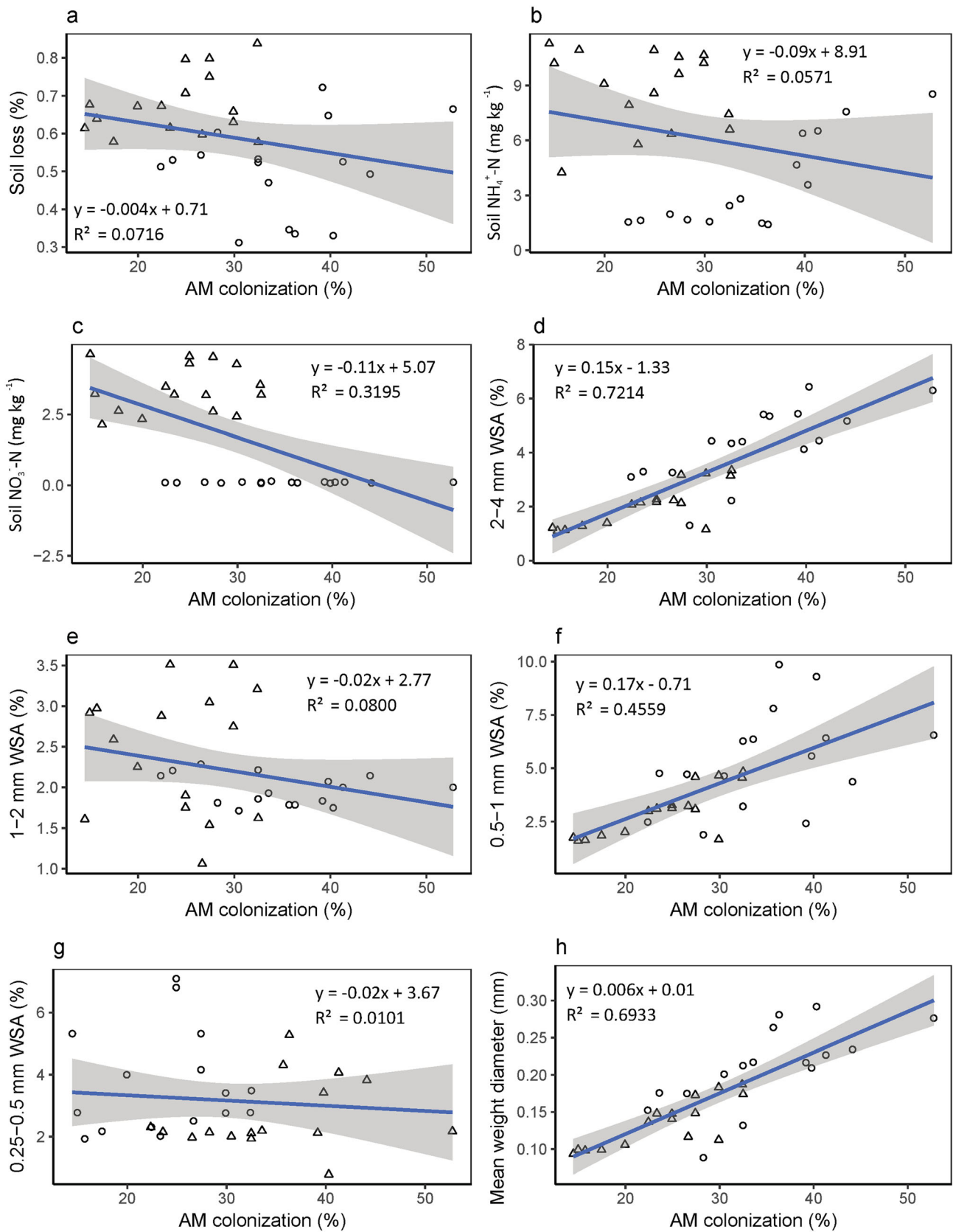


Fig. 4 Relationships between AM colonization and soil N availability and aggregate stability. Circles and triangles are for the data collected during tillering and fallow after rice harvest, respectively

to soil erosion (Barthès and Roose 2002). Stable aggregates can reduce detachment caused by raindrop impact under natural and simulated rainfall (Vermang et al. 2009). We tested this indirect role by plotting soil loss and AM colonization with aggregate stability. We found a negative relationship between soil loss and aggregate stability, but positive relationships between AM colonization and aggregate stability, supporting our hypothesis.

Soil aggregate stability might be enhanced by AM fungi via increasing glomalin (Driver et al. 2005) or soil carbon accumulation (Mardhiah et al. 2016). The glomalin was much more persistent than other soil proteins and was positively related to soil aggregate stability (Wright and Upadhyaya 1998; Wu et al. 2014a). In addition, the glomalin could also increase soil organic matter with AM hyphae rapid turnover (Staddon et al. 2003; Wilson et al. 2009) functioning as a rapid pathway of carbon flux from aboveground to the belowground (Johnson et al. 2002). Furthermore, differently from other soil fungi, AM fungi did not produce enzymes degrading soil carbon but decreased soil erosion indirectly by increasing soil carbon accumulation (Mardhiah et al. 2016). These could explain the indirect role of AM fungi in reducing soil loss due to splash erosion. All in all, agricultural practices that have harmful effects on AM fungi, such as intercropping or rotated with non-host plants, intensive tillage, fallow, etc. should be limited to reduce soil loss via AM fungi (Rillig et al. 2019).

Conclusion

Arbuscular mycorrhizal (AM) fungi had great potential in promoting crop yields and controlling nutrient loss (Cavagnaro et al. 2015; Zhang et al. 2014). We investigated the seasonal variance of AM colonization across four nitrogen (N) fertilizer levels and tested the direct and indirect role of AM fungi in controlling soil loss due to splash erosion. We found that AM colonization varied from 15 to 73% across the whole investigation period in the delta region Taihu Lake. The impact of N fertilization depended on rice growth. We also found that soil loss due to splash erosion was greater during the fallow period than that during rice growing season (i.e., tillering). High inorganic N fertilization increased soil erosion after rice harvest and organic N fertilization decreased soil erosion at tillering. The negative relationship between AM colonization and soil loss indicated the direct role of AM fungi in reducing soil erosion. We proposed the indirect role of AM fungi via the negative relationship of soil loss to aggregate stability and the positive relationship between AM colonization and aggregate stability. Our study highlighted that more consideration should be paid on the role of AM colonization in reducing soil erosion when nitrogen fertilization increased.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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