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Fertilizer regime changes the competitive uptake of organic nitrogen by wheat and soil microorganisms: An *in-situ* uptake test using ^{13}C, ^{15}N labelling, and ^{13}C-PLFA analysis

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ABSTRACT

Fertilizer regime affects plant growth and soil microbial community composition, however, its impact on organic nitrogen (N) uptake by plants remains poorly understood. To address this, we undertook an in-situ, short-term uptake experiment based on ^{13}C, ^{15}N labelling, and ^{13}C-PLFA analysis at two long-term (6 year) fertilizer trial sites (Jintan and Changshu). Each site had five treatments: a control without fertilizers, NPK fertilizers, 50% NPK fertilizer +6 t/ha pig manure, 100% NPK fertilizer + cereal straw, and 50% NPK fertilizer +6 t/ha pig manure and cereal straw. Overall, we found that 6–21% and 6–11% of the added ^{13}C-^{15}N-glycine was taken up intact by wheat, while 18–35% and 8–20% was captured by soil microorganisms in Jintan and Changshu locations, respectively. These results indicate that wheat has an appreciable capacity to utilize organic N, even in fertile agricultural soils. Organic N uptake by wheat correlated positively with ammonium and nitrate soil contents, indicating that inorganic N may enhance organic N capture by increasing plant biomass. The ^{13}C:^{15}N ratio in the microbial biomass showed that 32–71% and 13–71% of the ^{15}N was absorbed through a direct uptake route in Jintan and Changshu soils. Chemical fertilizer reduced microbial biomass and increased the proportion of intact glycine uptake by wheat. Gram-positive bacteria accounted for 18–23%, and 13–15% of the total ^{13}C labelled PLFA in Jintan and Changshu, respectively, while Gram-negative bacteria accounted for 43–48% and 66–72% indicating that they are the dominant competitors with plants for soil nutrients. Total ^{15}N uptake by wheat and microorganisms was highest in the 50% NPK fertilizer + pig manure and cereal straw treatment at both sites, indicating that it represents the best fertilizer practice for sustainable food production, as it not only reduced chemical fertilizer application, improved wheat growth and microbial biomass, but also increased wheat utilization of soil organic N.

1. Introduction

Plants uptake soluble organic nitrogen (ON) to partially fulfil their growth and development demands (Näsholm et al., 2009). Small ON compounds, including amino acids and oligopeptides, are abundant in soils (Ganeteg et al., 2017; Inselsbacher and Näsholm, 2012), with many studies demonstrating that both non-mycorrhizal and mycorrhizal plant species use such compounds (Jörgen and Näsholm, 2001; Kaštovská and Šantrůčková, 2011; Ma et al., 2017). The use of dual (^{13}C or ^{14}C, ^{15}N) labelled amino acids injected into the soil has clearly demonstrated the ability of plants to exploit this potential ON source in the field, providing evidence that plants can circumvent the need to rely on the microbial production of inorganic N. Amino acid transporters (such as lysine histidine transporter 1 and amino acid

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permease 5) in nonmycorrhizal plants have also been identified that allow plants to take advantage of amino acids present in the soil (Näsholm et al., 2009), showing that ON may be a potentially important N source for plant N nutrition in some situations (Jones et al., 2005; Kuzyakov and Xu, 2013).

The contribution of amino acids to soil N pool differs greatly between ecosystems and plant species, potentially accounting for over half of plant N uptake in some N-limited, low-temperature ecosystems, such as the arctic, alpine tundra, boreal forest, and heathland ecosystems (Näsholm et al., 1998; Ohlund and Näsholm, 2001; Warren, 2009). Nevertheless, ON is traditionally regarded as a negligible fraction of the plant N supply in agricultural systems, where fertilization ensures the availability of high levels of inorganic N (IN) (Kaštovská and Šantrůčková, 2011). However, ON is important for the N nutrition of non-mycorrhizal weeds, even in fertile agricultural soils, as demonstrated by recent studies combining the traditional dual labelling of plant genotypes with distinct differences in amino acid uptake capacity and the miniaturized *in-situ* soil N compound dialysis systems (Ganeteg et al., 2017). In addition, amino acids represent a significant part of soluble and exchangeable N pools in agricultural soils, except during the initial period after N fertilizer application, when IN concentrations in the soil are high (Holst et al., 2012; Jämtgård et al., 2010). The recent detection of N availability at the root scale (rather than bulk soil) has shown that plants absorbed more ON than IN, even in a fertile agricultural soil, except for a short period immediately after IN fertilizer application (Brackin et al., 2015). Furthermore, ON uptake increases the efficiency in N use by promoting N productivity and root growth (Broughton et al., 2015). Therefore, it is important to study ON plant nutrition in agricultural soils.

Both directly and indirectly, fertilizer regime can strongly influence plant growth, soil properties, and microorganism composition, and thus ON uptake. In arable systems, fertilizers are typically added in inorganic form, and crop residues may be burnt or removed, ultimately leading to soil degradation, pollution, and reduced crop yields (Cui et al., 2013). In comparison, organic amendments enhance the health of agricultural soils by reducing bulk density, promoting soil structural stability, biological activity and nutrient levels as well as providing nutrients in an organic form (Chen et al., 2016). Consequently, the combined application of organic amendments and inorganic fertilizers is likely to represent a more appropriate fertilizer practice for sustainable food production. Several authors have suggested that plants do not absorb significant amounts of ON, as plant roots are regarded as weaker competitors for ON than soil microbes (Jones et al., 2005, 2013; Kuzyakov and Xu, 2013). However, recent research showed that wild-type plants acquire similar ^{15}N labelling from ammonium and L-glutamine, indicating similar N uptake from the two N sources and, hence, a similar competitive ability against microbes for these two N forms. Such evidence does not support the notion that plants are weaker competitors for organic N than soil microbes (Ganeteg et al., 2017).

The long-term application of fertilizers affects the microbial community of agricultural soils (Chen et al., 2016). For example, chemical fertilizers reduce the size of the microbial biomass (Ramirez et al., 2012) and reduce both fungal and bacterial diversity (Kamaa et al., 2011); consequently, the growth and activity of pathogenic fungal genera may be enhanced (Paungfoolonhienne et al., 2015). In contrast, organic fertilizers tend to maintain a higher soil microbial biomass, fungal and bacterial diversity, mesofaunal abundance and enzyme activity (Ge et al., 2010). Phospholipid fatty acid (PLFA) analysis is an effective non-culture-based method used to identify the microbial community living in the soil. In parallel, ^{13}C-PLFA is a useful method for detecting which component of the microbial cmommunity competes for soil-borne amino acids with plants (Yao et al., 2015). This approach is widely used to trace C flux in soil-plant systems, but has not been used extensively to study plant ON nutrition. Using ^{13}C-PLFA, Broughton et al. (2015) demonstrated the functional role of the soil microbial community in the Antarctic with respect to the uptake of amino acids and oligopeptides. The authors showed that gram-positive (G^+) bacteria are the primary competitors for L-enantiomeric forms of amino acids and their peptides, even though both D- and L-enantiomers are available C and N sources for fungi and bacteria (Broughton et al., 2015). In addition, the results suggested that ^{13}C-PLFA is a good tool for studying which part of the microbe community actively utilizes free amino acids in soil.

Fertilizer regimes cause significant changes to the composition and activity of soil microbes, as well as soil ON composition, which in turn alter the comparative uptake of ON by plants and soil microorganisms. However, the effects of long-term fertilization on the uptake of amino acids by plants and soil microorganisms have not been well documented. The aim of this study was to explore: 1) the ability of field-grown wheat to uptake ON, 2) the effect of fertilizer regime on the competition of plant and microorganisms for ON, and 3) to determine which key groups of microorganisms are active in amino acids uptake under various fertilizer regimes. We firstly hypothesized that the addition of chemical fertilizer with pig manure and cereal straw will reduce plant N limitation and promote microbial growth which in turn will increase plant-microbial competition, reducing the ability of wheat to capture amino acids intact from the soil. Secondly, we hypothesized that wheat roots can acquire amino acids intact even under long-term chemical fertilizer application.

2. Materials and methods

2.1. Field description and experimental design

Microbial communities vary significantly between soils with different properties (Delmont et al., 2014). Therefore, we selected two long-term fertilization sites. One site was located in Jintan City (JT), Jiangsu Province, China (31°39′ N, 119°28′E, 3 m asl). The second site was located at Changshu City (CS), Jiangsu Province, China (31°35′ N, 120°55′ E, 6 m asl). Soils at the two sites have a clay loam texture (Fe-leachic-gleyic-stagnic-anthrosol) but differ in the size of their microbial biomass. The two sites are located 150 km apart, with both falling within a northern subtropical monsoon climate with a mean annual temperature and precipitation of 15.3 °C and 1063.6 mm, respectively. The long-term fertilizer regime treatments at both sites started in 2010, with each plot measuring 5 m × 8 m. All plots are long-term annual rotations of summer rice (*Oryza sativa* L. cv. Changyou 5), sown in June and harvested in October and winter wheat (*Triticum aestivum* L. cv. Yangmai 16), sown in November and harvested in June, which is the typical cropping system in the study region (Zhao et al., 2014a,b).

The fertilization experiment was set up in a randomized block design, including five treatments and four replicates. Treatments included a control without any fertilizer (Control), 100% NPK fertilizer (F), 50% NPK fertilizer + 6 t/ha pig manure (F + M), 100% NPK fertilizer + crop straw (F + S), and 50% NPK fertilizer + 6 t/ha pig manure and crop straw (F + MS). The F and F + S plots received 150 kg/ha N, 80 kg/ha P_2O_5, and 90 kg/ha K_2O in the wheat cropping season, and received 240 kg/ha N, 70 kg/ha P_2O_5, and 100 kg/ha K_2O during the rice cropping season. The F + M and F + MS treatments received half of the NPK provided in the F treatment. All P, K, and manure fertilizers were applied as basal fertilizers before planting. For rice, N fertilizer (urea) was used, with 40% as basal fertilizer before planting, 20% as supplementary fertilizer at the tillering stage, and 40% for panicle stage. For wheat, N fertilizer (urea) was used, with 40% as basal fertilizer, 30% as striking root fertilizer, and 30% as panicle fertilizer. Crop straw was returned to the soil after harvesting (F + S and F + MS). Soil properties in May 2016 are shown in Table S1.

2.2. In-situ detection of amino acid uptake by wheat and soil microorganisms

The short-term amino acid (AA) uptake test by wheat and soil

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