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Long-term agricultural management maximizing hay production can significantly reduce belowground C storage

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ABSTRACT

Liming and fertilization of grasslands have been used for centuries to sustain hay production. Besides improving hay yields, these practices induce compositional shifts in plant and soil microbial communities, including symbiotic arbuscular mycorrhizal (AM) fungi. However, in spite of increasing interest in soil carbon (C) sequestration to offset anthropogenic CO_2 emissions, little is known about the long-term effects of these agronomic interventions on soil C stocks. We examined how plants, AM fungi, and soil C respond to more than seven decades of annual applications of lime, mineral nitrogen (N), and mineral phosphorus (P) to test the hypotheses that (1) management practices increasing aboveground plant production decrease C allocation to roots, AM fungi and the soil; and (2) the relative availability of N and P predicts belowground C allocation in a consistent manner. Our study was conducted at the Rengen Grassland Experiment, established in 1941. Lime combined with N increased hay yields and promoted development of AM fungal hyphae in soil, while reducing relative C allocation to roots. Simultaneous enrichment of soil with lime, N, and P further boosted hay production, promoted grasses and suppressed other plant functional groups. This treatment also decreased soil organic C and strongly suppressed AM fungi in the soil, although the response to P varied among different AM fungal taxa. Our results indicate that agricultural management practices aimed at maximization of hay production may, in the long run, significantly (−20%) reduce belowground C storage. This is a great concern with respect to the intended use of grasslands as anthropogenic CO_2 sinks because the fertilization-induced decrease in soil C stocks can partly or fully negate the C sequestration potential of the grassland ecosystems as a whole.

1. Introduction

Grasslands cover about 40% of the terrestrial surface of the planet and about half of this area is currently used in agricultural production (Lal, 2007). Because soils contain more organic carbon (C) than both the atmosphere and biota combined and because grassland soils generally have much larger C storage capacity than annually cropped soils, grasslands are extremely important for global soil C sequestration (Conant et al., 2001; Lal, 2013). Long-term productivity of grasslands is influenced by many factors including climate, geographic location, and management practices, and particularly by the level of fertilization (Sala et al., 1988; Conant et al., 2001). For sustainable hay production, soil organic matter is critical because it supplies plants with nutrients, helps to reduce soil erosion, and increases cation exchange and water holding capacity (Schulten and Schnitzer, 1997; Daynes et al., 2013). Consequently, management practices that restore and/or maintain high levels of soil organic matter are desirable. This in combination with recent interest in soil C sequestration, as a means to offset rising CO_2 levels in the atmosphere, has led to a keen interest in optimizing grassland management for C storage

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(Conant and Paustian, 2002; Lal, 2008). An earlier review of 115 studies from around the world demonstrated that grasslands fertilization, especially with nitrogen (N), tends to be associated with increased soil C (Conant et al., 2001; van Groenigen et al., 2006), suggesting that fertilization is potentially an important driver of soil C sequestration. However, the relationship is difficult to predict because it may critically depend on the type of fertilizer, and is likely to be nonlinear (Wander et al., 1994). One reason for this is that belowground C allocation by the plants and subsequent C transformations within soils likely depend on plant and microbial responses to relative, not absolute nutrient limitations (Cleveland and Liptzin, 2007; Kaiser et al., 2014).

The soils and roots of plants in natural and managed grasslands are abundantly colonized by arbuscular mycorrhizal (AM) fungi. These fungi, belonging to the phylum Glomeromycota, form symbiotic relationships with plants that are often mutually beneficial for both partners. Plant hosts supply carbohydrates in exchange for fungal provisioning of mineral nutrients, especially phosphorus (P) and zinc, some of which would otherwise be unavailable for plants (Allen, 1991; Jansa et al., 2003). Besides facilitating nutrient uptake, AM fungi can provide benefits to colonized plants, such as resistance against pathogens and drought tolerance (Newsham et al., 1995; Smith et al., 2010). High densities of AM fungal hyphae in soil form underground networks that contribute to creation and stability of soil aggregates and reduce soil losses through erosion (Chaudhary et al., 2009). Because many of these features are considered beneficial for the sustainability of agricultural production, there is a great interest in increasing mycorrhizal symbioses through agricultural management (Gianinazzi, 2010; Fitter et al., 2011).

Mycorrhizal fungi are key components of grassland C sequestration (Treseder and Allen, 2000; Zhu and Miller, 2003; Johnson et al., 2006; Wilson et al., 2009). Hyphae of AM fungi may comprise a large fraction (estimates go up to a half) of microbial biomass in grassland soil (Olsson et al., 1999), and therefore their responses to fertilization are highly relevant to soil C dynamics. Although AM fungi are expected to rapidly channel and immobilize a significant portion of plant-derived C through the soil, there is an on-going debate about the importance of this C highway in the buildup of stable soil organic matter and soil C sequestration (Staddon et al., 2003; Phillips et al., 2013; Averill et al., 2014; Balasooriya et al., 2014). Density of AM fungal hyphae in the soil was previously found to be positively correlated with the responses of soil organic C to long-term N enrichment and burning in a North American tall-grass prairie, while application of fungicides suppressed AM fungal hyphae and reduced soil organic carbon (Wilson et al., 2009). Responses of AM fungi to N fertilization have been shown to vary with availability of soil P. For example, N enrichment of P deficient grasslands often increases AM fungal biomass but N enrichment of P rich grasslands often decreases it (Johnson et al., 2003; Wilson et al., 2009; Liu et al., 2012).

The functional equilibrium model can help explain why N enrichment may either increase or decrease AM fungal biomass. This conceptual model states that plants should preferentially allocate photosynthates to structures that acquire the most limiting resources; plants growing in infertile soil should allocate more to roots and mycorrhizas and plants growing in nutrient rich soil should allocate more to shoots and leaves (Brouwer, 1983; Johnson et al., 2003). Increasing soil N availability in P-limited soils exacerbates P limitation and enhances the importance of symbiotically acquired P; thus plants are expected to increase allocation of photosynthates belowground to AM fungi. In contrast, N enrichment of P-rich soils is likely to remove limitation by any belowground resource and, in accordance with the functional equilibrium model, plants are expected to shift allocation of photosynthates aboveground to shoots and away from AM fungi (Johnson, 2010).

Changes in nutrient availabilities and consequent shifts in C allocation by plants can have large effects on AM fungal communities (Egerton-Warburton et al., 2001, 2007; Liu et al., 2012). Application of fertilizers systematically increases plant productivity, but also reduces plant diversity (Silvertown et al., 2006; Hejcman et al., 2007; Semelová et al., 2008). Generally, the most discussed nutrients in relation to the management of grasslands are N, P, and calcium (Ca), of which the last mentioned is most often provided in carbonate form (lime) not to primarily correct for plant nutrient deficiencies, but to reverse soil acidification, developing mainly due to application of N fertilizers (Johnston et al., 1986). Soil acidification is recognized as one of the main limits of agricultural production and provision of ecosystem services on a wide range of soils (e.g., Scott et al., 2000). The effect of liming on AM fungi is not easy to predict, in some cases the application of Ca promoted AM fungal colonization of roots (Johnson et al., 2005), whereas in others it had no effect (Kennedy et al., 2005). Recent unconstrained monitoring of AM fungal communities in a number of agricultural soils (including grasslands) in Switzerland pointed to a particular importance of soil pH in structuring indigenous AM fungal communities (Jansa et al., 2014), which provides some mechanistic explanation on how could induced soil pH shifts (due to liming of acidic soils) affect the indigenous AM fungi. The effects of fertilization on individual AM fungal taxa are highly context-dependent and are often confounded with the effects of soil disturbance and crop rotation (Jansa et al., 2006 and references therein). Individual taxa of AM fungi differ in their responses to fertilization; some species increase and others decrease in abundance in response to nutrient enrichment (Douds and Schenck, 1990; Johnson, 1993; Egerton-Warburton et al., 2001).

The aim of this study was to analyze the responses of soil C and AM fungi to 70 years of annual applications of lime and mineral fertilizers at one of the oldest agricultural experiments worldwide—the Rengen Grassland Experiment. Our goal was to test the ability of the functional equilibrium model to predict responses of soil C stocks to grassland inputs. We examined the abundance of AM fungi inside and outside plant roots and used molecular techniques to determine the abundance of a few individual AM fungal taxa. This allowed us to test the hypothesis that lime and fertilizers would reduce plant allocation of photosynthates to belowground structures including the mycorrhizas. We predicted that the differences of lime and fertilizer inputs among treatments would have consequences for the long-term buildup of soil C stocks, co-incident with the effects on AM fungi: N enrichment will increase allocation to AM fungi due to increasing relative demand for limiting P, while fertilization with both N and P will decrease allocation to AM fungi, consequently reducing the soil C sequestration.

2. Material and methods

2.1. Study site description and experimental design

This study was conducted at the Rengen Grassland Experiment established in 1941 by the University of Bonn in low productivity *Nardetum* grassland in the Eifel Mountains, Germany (50°13′N, 6°51′E). The site is 475 m above sea level, average annual precipitation is 811 mm and the mean annual temperature is 6.9 °C. Soil type is a pseudogley. The experimental plots (3 m × 5 m) received annual amendments of lime (in the form of $Ca(OH)_2$, obtained by combination of CaO with water) and fertilizers for more than seven decades, reaching levels considered sufficient for sustainable hay production in that area (Wendland et al., 2012). We