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Arbuscular mycorrhizal spore composition and diversity associated with different land uses in a tropical savanna landscape, Tanzania

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ABSTRACT

Understanding the diversity and community structure of arbuscular mycorrhizal fungi (AMF) is important for potentially optimizing their role in the functioning of terrestrial ecosystems. Land use can have profound effects on AMF abundance, productivity, and species composition, but such effects have been explored less in tropical landscapes where agriculture is often less intensive and wildlife conservation can be predominant. Here, we conducted a landscape-scale investigation to quantify the effects of land uses on the AMF diversity in the Greater Serengeti Ecosystem, Tanzania. Abundance, productivity, and diversity of the spores of AM fungal species were determined from field soils by morphological techniques. A total of 315 AM fungal spores belonging 9 species and four families were recorded. Land use had a significant ($P < 0.05$) effect on AM fungal spore density and biomass production of AM hyphae in in-growth mesh bags. The AM fungal spore density was statistically significant ($P < 0.05$) and positively correlated with soil N, organic carbon content and sand contents, but negatively correlated with increasing soil P and pH. After accounting for soil N, Organic carbon, P and pH, wildlife grazed areas had nearly double the spore densities compared to livestock grazed and crop agriculture areas. Likewise, wildlife grazed soils had a higher Shannon-Wiener diversity index (2.13 ± 0.05) than either livestock grazed soils (1.76 ± 0.10) or cultivated soils (1.59 ± 0.09).

AM fungal families exhibited significant differences in their abundance among land use types. While Glomeraceae had high abundance under all land uses, Gigasporaceae and Scutellosporaceae exhibited the highest abundance in wildlife grazed sites and Acaulosporaceae had high abundance in livestock-grazed and crop agriculture sites. Species composition within families was mostly similar across land uses, with the exception of *Scutellospora sinuosum* and *Acaulospora denticulata*, which exhibited much greater abundance in wildlife grazed sites than in livestock-grazed or crop agriculture sites. These results suggest that protected area grassland sites subject to wildlife grazing held a more abundant, diverse, and compositionally distinct AM fungal community than both livestock-grazed and crop agriculture sites, even after accounting for the influence of land use on soil N, Organic carbon, P and pH that affect AM fungi. From the perspective of sustainable production, it is very important to ascertain tillage practices and moderate grazing that can promote mycorrhizal diversity and, therefore, contribute to the long-term sustainability of agro-pastoral ecosystems under tropical conditions.

1. Introduction

Arbuscular mycorrhizal fungi are widely distributed and knowledge of how spatial factors affect their diversity in a specific area or a specific soil type is essential for sustainable management (Beauregard et al., 2013; Moll et al., 2016). AMF are a major component of the soil microbial community and form symbiotic associations with roots (Brundrett, 1991, 2009; Wang and Qiu, 2006). These mutualistic plant-fungal relationships are driven by exchanges of plant-derived carbon in return for several potential benefits (Smith and Read, 1997; Smith et al., 2009), including enhanced plant uptake of poorly mobile soil nutrients such as phosphorus (P), improved water relations and soil structure (Barea et al., 2005), and reduced root pathogenic infections (Smith and Read, 1997; Schweiger and Jakobsen, 2000; Tkacz and Poole, 2015; Berruti et al., 2016). Through their impacts on plants, AM fungi affect multiple ecosystem functions and processes including nutrient cycling, plant productivity, and competition (Hartnett and Wilson, 1999; van der Heijden et al., 2003; Scheublin et al., 2007), and plant diversity (van der Heijden et al., 1998; Klironomos et al., 2000; O'Connor et al., 2002; Lee et al., 2013).

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Beneficial effects of AM fungi plants may depend on the abundance and diversity of particular AM species, such as those with large hyphal networks (e.g., Gigaspoaceae) versus other species that may confer protection against pathogens or even be parasitic (Tkacz and Poole, 2015; Berruti et al., 2016). Soil microbial communities are strongly influenced by the local environment (Hazard et al., 2013; Smith et al., 2014). A key question is what factors, including edaphic factors, climate and land use, influence AM fungal species composition and diversity. AM fungal individual species have been shown to vary in their potential to promote plant growth and adaptation to biotic and abiotic factors (Stutz and Morton, 1996; Lekberg et al., 2007; Oehl et al., 2010; Tahat and Sijam, 2012; Parkash and Saikia, 2015). Several factors that may influence AM fungal species composition have been identified, including abiotic (e.g., soil physico-chemical properties) and biotic (e.g., host plant) factors (van der Heijden et al., 1998; Fierer and Jackson, 2006; Chaudhary et al., 2008; Lauber et al., 2008). Land use, such as conservation of protected areas, cultivation and livestock grazing, is thought to be a key driver of AM fungal species composition and diversity (Douds and Millner, 1999; Oehl et al., 2003; Klironomos et al., 2004; Renker et al., 2005) through the effects of such uses on soil disturbance, reduction or increases in plant biomass and carbon assimilation due to grazing and fertilization. For example, disturbance of vegetation, soils and associated microflora from conversion of grassland or woodland to agriculture may deplete AM fungal populations and alter AM fungal composition (Daniell et al., 1999, 2001; Allen et al., 2003; Alguacil et al., 2008; van der Gast et al., 2011; Schechter and Bruns, 2013). These influences are often superimposed on soil and climate gradients, and a key question is how and whether land use influences are distinct from edaphic and climate drivers.

While there are many studies on the effect of land use on the diversity and structure of AM fungal communities in temperate grasslands (Jansa et al., 2002, 2003; Oehl et al., 2003; Kivlin et al., 2011; Dai et al., 2013), such effects in tropical ecosystems are poorly studied. Even in temperate biomes, most data are from a single site, and relatively few studies have compared AM fungal communities among sites that varied in soils and plant species composition at a landscape scale and among sites that differ in their land use (Dai et al., 2013; Xiang et al., 2014; Moora et al., 2014). Tropical ecosystems have several distinguishing features that may yield different land use impacts on AM fungi species composition and diversity. Tropical grasslands are often dominated by C_4 grasses, which can support greater AM fungal diversity and strong AM fungi associations (Antoninka et al., 2011) and may be obligate mycotrophs (Wilson and Hartnett, 1998; Hartnett and Wilson, 2002). Land use in the developing tropics also may involve less intensive practices in croplands, and different patterns of forage use by livestock in pastoral lands, and wildlife conservation may occur on a greater portion of the landscape (Darr et al., 2014).

In this study, we tested the hypothesis that, given variation in soil pH, N and P, AMF spore diversity is lower and species composition is different from that found in areas with either pastoral livestock grazing or crop agriculture as compared with wildlife conservation areas. Furthermore, carbon loss and soil disturbance would be expected to preferentially reduce AM taxa that exhibit low colonization and sporulation rates but build large hyphal networks such as Gigasporaceae. We also expected that AM fungal families would exhibit significant differences in their abundance among land use types; protected areas devoted to wildlife conservation, human-dominated areas devoted to livestock grazing, and to subsistence agriculture.

2. Material and methods

2.1. Study site description

Soil samples were collected inside (wildlife grazed) Serengeti National Park (SNP), Tanzania in East Africa (34°49′55.75″E longitude and 2°19′57.27″S latitude, 240 km south of the equator) and on adjacent open lands that were either used for livestock grazing (livestock grazed) or for cultivated crops (croplands). Major soil types of Serengeti National Park include Chromi-Luvic Phaeozems, Eutric Leptosols, Eutric-Pellic Vertisols, Mollic Solonetz and Vitric Andisols (FAO, 1998). Climatically, mean maximum temperatures in the Serengeti are between 24° and 27 °C, and mean minimum temperatures between 15° and 21 °C. Mean annual rainfall varies from 1050 mm in the northwest to 550 mm in the southeast (Sinclair et al., 2000; Fryxell et al., 2005). This rainfall is strongly seasonal, with peaks between March and May, and between November and December (Sinclair, 1979a). Rainfall is the main determinant of vegetation growth, and hence ungulate food supply (Sinclair, 1977; McNaughton, 1983). The southeastern Serengeti consists of C_4-grass dominated grasslands that shift from short pure grasslands to medium to tall grass-dominated *Acacia* savannas plains towards the north and west (McNaughton, 1985). The Serengeti supports over 30 species of ungulates numbering close to 3 million individuals (Sinclair, 1979b), including 2 million migratory wildebeest (*Connochaetes taurinus*), Zebra (*Equus burchelli*), and Thomson's gazelle (*Gazella thomsoni*) that remove 63% of the aboveground biomass each year (McNaughton, 1985). The Serengeti plains have fine nutrient rich volcanic sands that make up the soils (vertisol) which supports many plant communities (Jager, 1982). Areas outside the western park boundary feature mixed ethnic communities including Ikizu, Sukuma, Tatuturu, Ikoma, Kuryia, Natta and Issenye that practice agro-pastoralism in the form of cultivation of a maize (*Zea mays*) – bean (*Phaseolus vulgaris*) crop rotation and livestock husbandry (mostly cattle but with some sheep and goats). Agriculture is dominated by smallholder farmers with an average farm size of 0.9–3 ha (Estes et al., 2012). The majority of farmers cultivate by hand hoe or ox-plough. Cultivated fields are typically top dressed with calcium ammonium nitrate (CAN) fertilizer at a uniform rate of 30 kg N/ha diammonium phosphate (DAP), Minjingu rock phosphate (MRP) fertilizers are applied at 60 kg/ha P_2O_5 and farmyard manure (Meertens et al., 2003). Livestock are maintained at relatively high densities sufficient to consume 70–90% of aboveground biomass (McSherry, 2015).

2.2. Field soil sampling

We studied the effects of current land use (sampling sites were in place for > 40 years) on AM fungal spore density and species composition in relation to soil properties across eighteen (18) sites (Fig. 1). Transect samples were taken and evaluated in the each of three pre-established land use categories: wildlife grazed system inside SNP, livestock grazed system in uncultivated open areas outside the park, and agriculture (maize-bean intercropping) in cultivated open areas. Wildlife grazed sites were chosen to represent grassland communities that span the Serengeti's gradient of soil properties. Sampling sites were chosen from a much larger set of 112 sites that had been selected at random from across the landscape to survey associations between AM fungi, land use, and soil properties (Soka et al., 2015). Sites in SNP were chosen for a park-wide study of grazing impacts (Anderson et al., 2007) and included a wide range of textures and nutrient concentrations (Ritchie, 2014) and were used only if they had not burned in the previous 12 months. Livestock-grazed and agriculture sites were selected randomly from the larger pool of sites of the same soil types in a previous survey (Soka et al., 2015) and also included a range of soil textures and nutrient concentrations.

Soil samples were taken at each site at the end of the longer wet season in June 2013 by collecting 4 soil cores randomly to a depth of 15 cm, the rooting zone and main organic layer. Cores were then pooled into a single sample per field site and analyzed for physicochemical characteristics. Soil samples were mixed by breaking up clods, mix thoroughly and spread the total sample evenly on a clean surface. From a mixture of field site sample, a sub-sample of 250 g was used to propagate slow and also non-sporulating fungi that may not have sporulated at the time of sampling. The pooled cores and 250 g sub-sample

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