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Influence of current land use and edaphic factors on arbuscular mycorrhizal (AM) hyphal abundance and soil organic matter in and near Serengeti National Park

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Arbuscular mycorrhizal fungi (AMF) are important microbial symbionts for plants especially when soil phosphorus (P) and nitrogen (N) are limited. Little is known about the distribution of AM hyphae in natural systems of tropical soils across landscapes and their association with different land uses. We studied mycorrhizal hyphal abundance in a wildlife grazed system, a livestock grazed system and under cultivated soils in and near Serengeti National Park, Tanzania. Samples of the upper 15 cm of soil beneath locally dominant plant species were collected. Hyphae were preserved on permanent slides and the length of hyphae per cubic centimeter of soil was calculated. Significant differences ($p<0.001$) in AM hyphal densities were observed across land use systems, as mean hyphal densities were 61.03±22.02, 52.89±16.41 and 47.9±22.65 m/cm^3 for wildlife grazed system, livestock grazed system and croplands, respectively. There were significant correlations between soil P and N on AM hyphal densities that reflected a pattern of decreasing hyphal densities with increasing soil P and N across sites. These results are congruent with the functional equilibrium hypothesis, which predicts that plants allocate relatively more to belowground structures when they are more limited by belowground resources than by aboveground resources, because AMF densities were highest at the sites with the lowest soil resources.

Key words: Land use, mycorrhizal, hyphal, abundance, soil, Serengeti, Tanzania.

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) are associated with a broad range of plant species and are more widely distributed than other types of mycorrhizal associations (Sieverding, 1991; Bedini et al., 2007; Smith and Read, 2008). AMF are often important for plant nutrition and soil fertility (Smith and Read, 1997; Jeffries et al., 2003) and represent a living bridge for the translocation of nutrients from the soil to the plant roots and of carbon from the plant roots to the soil (Miller and Jastrow, 2000; Zhu and Miller, 2003; Smith et al., 2009; Johnson et al., 2010). They can be significant in plant community development, nutrient uptake and aboveground productivity

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(George et al., 1995; Smith and Read, 1997; van der Heijden et al., 1998; Klironomos et al., 2000; Wardle et al., 2004; van der Heijden et al., 2008). AMF can also enhance tolerance of or resistance to root pathogens (Smith and Read, 1997; Gorissen and Cotrufo, 2000) or abiotic stresses, such as drought and metal toxicity (Meharg and Cairney, 2000).

In mycorrhizal biology, much research has been focused on the phase of the fungus inside the root; in the root, fungal abundance is relatively easily assessed by measuring percent root colonization. However, it is the extra-radical mycelium that must take on a central role in a discussion of the contribution of AMF to plant fitness and productivity and soil quality. AMF can efficiently absorb mineral nutrients from the soil and deliver them to their host plants in exchange for carbohydrates (Miller and Jastrow, 1992; Oehl et al., 2003). The mycelial network of AM fungi extends into the soil volume and greatly increases the surface area for uptake of immobile nutrients, particularly P, N and Cu (George et al., 1995; Brundrett, 2004; Johnson et al., 2010; Nouri et al., 2014). Studies have shown that total hyphal length (Hunt and Fogel, 1983), root infection and spore numbers vary with soil conditions (Bever et al., 1996, 2001; Sheng et al., 2013). A study by Leake et al. (2004) estimated that one gram of soil can contain up to 200 m of fungal hyphae. Also, soil densities of AMF hyphae in temperate grasslands have been shown to decline with precipitation, which may be associated with greater potential C assimilation by plants and inputs to AMF (Johnson et al., 2003) and land use (Oehl et al., 2003).

In agro-ecosystems, AMF are an important component of soil fungal communities, accounting for about 30% of the whole microbial biomass (Olsson et al., 1999; Bainard et al., 2013). Land use practices, such as ploughing, chemical fertilization and pesticide application, generally decrease the density of AMF hyphae and spores (Douds and Millner, 1999; Oehl et al., 2003), and modify AMF taxonomic composition (Allen, 1991; Schnoor et al., 2011). Most of these patterns have been reported for temperate natural and agricultural systems (Daniell et al., 2001), but not for tropical ones. Given the potential critical role of AMF for ecosystem function, a greater understanding of how AMF abundance changes with different land uses in tropical systems seems critical.

With the global increase in the extent and intensity of human domination of terrestrial ecosystems, it is vital to establish how land use influences AMF abundance and its impact on ecosystem services (Jefwa et al., 2009; Dai et al., 2013). Despite their ubiquity and potential importance for ecosystem structure and function (Hawksworth, 2001), surprisingly little is known about how AMF abundance, land use and soil properties are associated with tropical soils. Investigating how AMF abundance and diversity vary with changing levels of soil pH, N, and P in the tropics will further advance our understanding of the factors controlling mycorrhizas in soils (McNaughton and Oesterheld, 1990; Gai et al., 2012). In this study, we used a grid line intersection method to quantify AM hyphal density in soils across three land-use types and related these differences to measured edaphic properties. We hypothesized that AM hyphal abundance would increase along a gradient from cultivated lands with high human influence through livestock grazed system (public land) to wildlife grazed system (Serengeti National Park). The objective was to examine how AM hyphal densities may respond to land use practices and how shifts in the abundance of AM hyphae correspond to changes in soil edaphic properties such as soil P, N and pH.

MATERIALS AND METHODS

Site description

Serengeti National Park (SNP) covers about 14,000 km^2 in the north-western part of Tanzania, East Africa and immediately below the Tanzania-Kenya border (Figure 1). The park straddles between 34 and 36°E longitude and 1 and 2° S latitude and is surrounded by wildlife management and game control areas. There is little variation in the mean monthly temperatures, only a 4-6°C change throughout the year, with January tending to be the warmest month and July the coolest (McNaughton, 1983). The region is controlled by rainfall gradient with the short rains starting in November, and the long rains starting in March, and a dry season from June to October. The south-eastern part of the Serengeti is dominated by short grass plains with the transition from medium to tall grass plains in the north and west. In the Serengeti grasslands, 90% of the total biomass of grasses consists of C_4 grass species (McNaughton, 1983) and are considered to be obligate mycotrophs because they cannot survive without mycorrhizas (Wilson and Hartnett, 1998; Hartnett and Wilson, 2002). The northern and western parts of the Serengeti are dominated by *Acacia* woodlands with large patches of open grassland inhabited by various ethnic communities practicing agriculture, pastoralism or more typically, a combination of the two. There are nearly 2.5 million ungulates in the Serengeti, comprising over 30 species whereby migratory herds of wildebeest dominate (Sinclair, 1979; Sinclair et al., 2008).

The experimental design

AM hyphal abundance was compared in three land use types in and near the SNP. The study sites selected for this research included livestock grazed systems (public lands), regarded as having no conservation status, cultivated lands and wildlife grazed systems (in SNP), which were fully protected with strict conservation measures. In cultivated soil, a maize-bean intercropping system was characterized by low inorganic inputs (an estimate of 30 kg P and N/ha) combined with farm yard manure. We selected sampling sites at random intervals and recorded their location with a Global Positioning System (GPS). A total of 112 soil samples were collected along a gradient of human use influence from cultivated land through livestock grazed system into SNP, which had not burned in the previous 12 months. At least 20 sampling sites, spaced about 10 km apart were established in each land cover types. Percentage (%) ground cover was estimated visually in plots measuring 20 x 20 m using a Braun-Blanquet (Mueller-Dombois and Ellenberg, 1974) scale, whereby ground cover <25% scored 1; cover 25-50% = 2; 50-75% = 3 and above 75 = 4 (Stohlgen et al., 1995; Murphy and Lodge, 2002). We identified

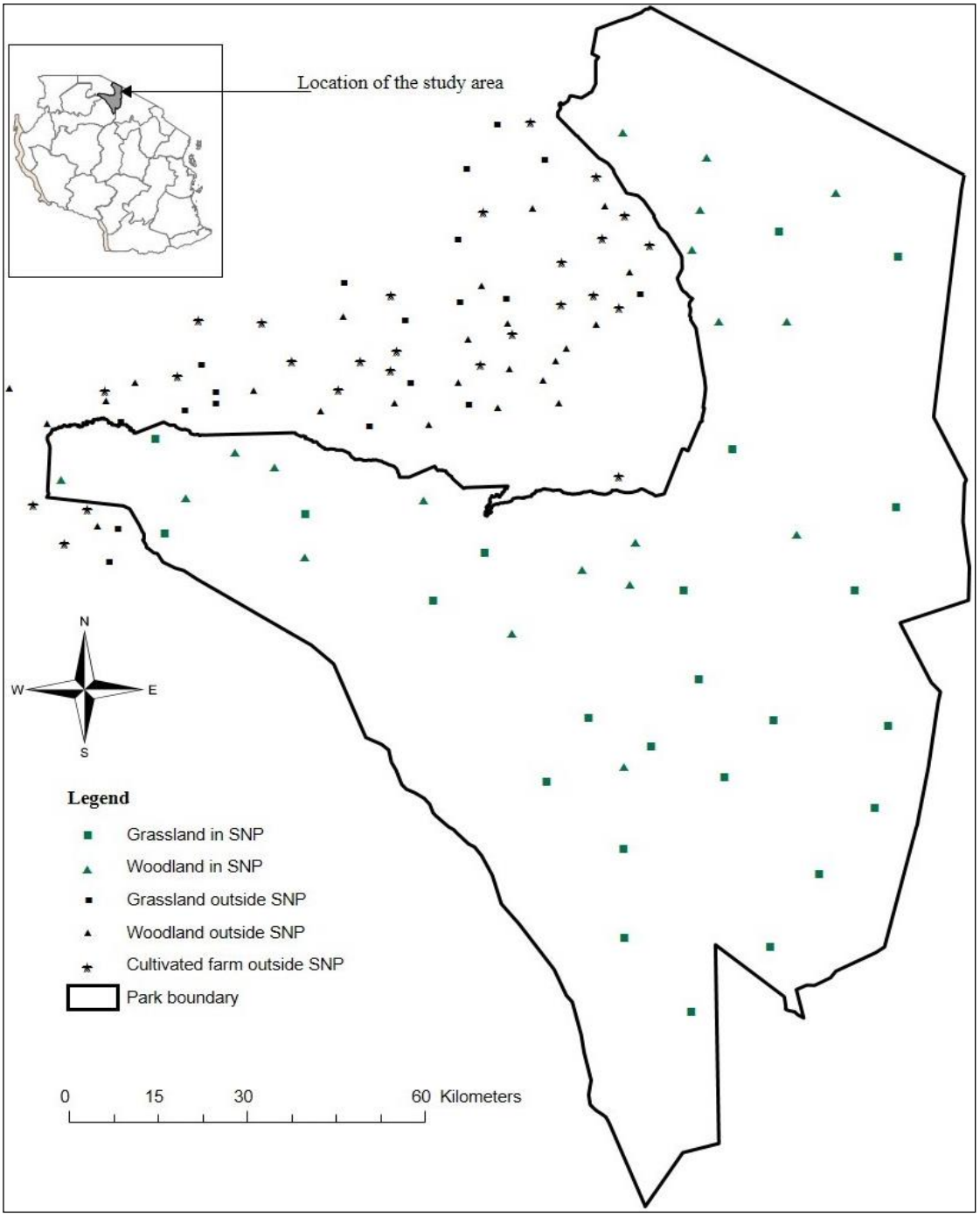

Figure 1. Map of study sites and location of study area within Tanzania.

the dominant plant species in the plots. Species which were difficult to identify in the field were collected, pressed and dried and taken to the Herbarium of Serengeti Wildlife Research Center for proper identification by matching with dried herbarium specimens or by using available floras. The nomenclature used follows that of the Exell and Wild (1960). Farm age was established following discussions with the land owners, presence/absence of sisal on the boundaries of the farms and distance from the park boundary (new farms were close to the park boundary).

Soil sampling

Soils were sampled from 112 sites in the five designated land cover categories; 26 in cultivated lands, 24 in livestock-grazed woodlands, 21 in livestock grazed grasslands in public land, 21 in wildlife grazed woodlands inside the park and 20 in wildlife grazed grasslands inside the park. Soil samples (plot sizes, 20 x 20 m) were taken in June 2012. This date corresponds to the end of the growing season in the region. At each plot, four 0 - 15 cm deep (8

cm diameter) soil core samples were collected. Soil samples from each plot were pooled together to make a composite sample of 1 kg. The soils were stored in sealed bags in a cooler maintained at 4°C and then immediately transported to Sokoine University of Agriculture laboratory for isolation of AMF spores and soil physicochemical analysis. Sub-samples of collected soil samples were analyzed for total N, carbon, available P and pH at Sokoine University of Agriculture soil laboratory following standard methods for tropical soils (Anderson and Ingram, 1993). These analyses included extraction of hyphae and determination of several chemical soil parameters, such as pH, total N and the available phosphorus. Soil pH was determined on a soil/water paste ($^1/_2$) and the available P as described by Olsen and Sommers (1982) by extraction with a 0.5 M $NaHCO_3$ solution at pH 8.5. The samples were dried, weighed and grounded and then analyzed for total nitrogen and total soil organic carbon using the Walkley Black benchtop wet chemistry method. A conversion factor of 1.72 (Nelson and Sommers, 1996) was used to convert organic carbon to organic matter:

Organic matter (%) = Total organic carbon (%) x 1.72

In addition, bulk density (g cm^{-3}) of the soil was determined following Gee and Banders (1986). After drying at 105°C to a constant mass, soil moisture content was calculated as water (%) by mass = (wet mass - dry mass / dry mass) x 100%. Soil texture was determined according to the standard soil textural triangle by analyzing and calculating the percentages of sand, silt and clay (Whiting et al., 2011).

Extraction and quantification of extraradical hyphae

Abundance of AM fungi was measured from hyphal densities (Bardgett, 1991; Schweiger and Jakobsen, 2000; Hart and Reader, 2002). Hyphal densities of AM fungi in the soils (standing crop) were analyzed for a 1.4 g sub-sample of the pooled cores from each sampling plot stored at 4°C until extraction of the hyphae. Also, soil sub-samples were used to determine the dry weight to wet weight ratio. The dry weight was determined by weighing 5 g of soil and placed into the drying oven for three days at 105°C. The soil sub-sample was blended in a 1.5 L blender with 500 mL deionized water for 8 s to produce a homogenized soil suspension. This suspension was then poured through a 180 µm sieve and washed through with water. The filtrate (containing hyphae) was further filtered (pore size 20 µm) under vacuum and was mounted on microscope slides with polyvinyl-lactic acid-glycerol. Hyphae were preserved on permanent slides, examined with a compound microscope (200x magnification using a 10 x 10 grid eyepiece graticule) and 50 microscopic fields were observed per slide for morphology that is characteristic of AM fungi (e.g., absence of regular septae) (Plate 1). Hyphal abundance (hyphal length x bulk density) was measured using the line intersect method (Tennant, 1975) and calculated using the following equation:

$$H = [(\text{sum c}) \times (11/14) \times a] \times [3.142 \times r^2] / [(\text{sum s}/100) \times 2g \text{ 1 mm slide}^{-1})]$$

Where, Sum *c* = sum of the number of counts; *a* = the size of a small square at 200x magnification (0.5814 mm); *r* = the radius of the membrane catchment area (7 mm); *g* = the size of one side of the 10 x 10 grid (0.5 mm); Sum *s* = the number of small squares that fell across the membrane filter catchment area (100 squares x views).

Statistical analysis

Mycorrhizal hyphal abundance was compared among different land use and cover types using analysis of covariance (ANCOVA). This approach tests whether AMF abundance differed among different land use and cover types after controlling for relationships between AM hyphal abundance response and the different covariates. ANCOVA was performed to compare the influence of a random factor (land use/cover type) and the influence of various sample site-specific variables (soil P, N, pH, N:P, texture and moisture) on AM hyphal densities and soil organic matter (SOM) as covariates. Soil P was log transformed prior to the analysis to ensure normality. ANCOVA also was conducted to compare AM hyphal densities in the soil samples from old (continuously cultivated for more than 10 years) and new farms (continuously cultivated for less than 10 years) after controlling for the soil variables. Pair wise comparisons of treatment means associated with different land uses were made by using Fisher's protected least significant difference (LSD) at $p < 0.05$ confidence level. All statistical analyses were performed using SPSS 17.0 (IBM Corp., Chicago IL, USA).

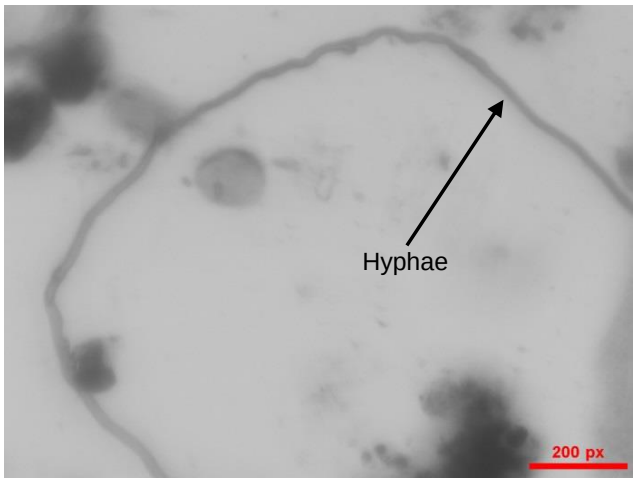

Plate 1. Image showing extracted AM hyphal magnified 200x.

RESULTS

Land-use and edaphic soil properties

Soil texture and moisture, SOM, extractable P and bulk density differed significantly among land use types ($p < 0.05$ in all cases), while soil pH, soil N : P ratio and soil C : N ratio did not vary significantly across the landscape ($p > 0.05$ in all cases) but did vary considerably across the sampling sites (Table 1). SOM, moisture and available P in the wildlife grazed plots were approximately twice those of cultivated soils. The agricultural (cultivated) soils had the lowest N as compared to livestock and wildlife grazed soils. Likewise, the extractable P varied significantly between wildlife and agricultural soils, with wildlife grazed soils having approximately two times greater extractable P than cultivated and livestock grazed soils. Soil N and available P were positively and significantly correlated ($r = 0.26$, $p = 0.006$). Soil pH was not different among land uses, but varied considerably (5.5 - 7.5) across all sites.

Table 1. Soil characteristics of the three land use types in and near SNP.

Soil parameter	Agriculture	Livestock grazed system	Wildlife grazed system	p-value
pH	6.22±0.15	6.27±0.10	6.39±0.08	0.505
P (mg kg^{-1})	11.28±2.89	10.46±2.91	19.03±3.82	0.009*
Total N (%)	0.11±0.01	0.14±0.00	0.18±0.11	0.001*
N:P	0.02±0.005	0.10±0.04	0.03±0.005	0.189
C:N	1.84±0.54	2.06±0.19	1.76±0.203	0.686
Organic matter (%)	1.46±0.11	2.12±0.23	2.74±0.17	0.001*
Soil moisture (% mass)	4.77±0.77	6.17±0.56	8.68±1.18	0.019*
Bulk density (g cm^{-3})	1.16±0.07	1.00±0.03	1.05±0.07	0.025*
Clay (%)	18.81±2.03	25.89±1.89	32.34±1.87	0.001*
Silt (%)	7.73±0.84	11.24±0.80	15.44±1.09	0.001*
Sand (%)	73.12±2.61	62.62±2.41	52.22±2.69	0.001*

Mean values (± SE) in 0-15 cm soil profile, within land use for measured soil properties. Variables that were significantly ($p < 0.05$) related to land use are indicated with an asterisk.

Linking edaphic properties and AM hyphal abundance

The relationships between the abundances of AM hyphal and edaphic soil properties were examined by ANCOVA to determine the overall patterns of AM hyphal abundance in soils across different land use types. Our results show that AM hyphal abundance in and near SNP varied with soil nutrients. We found a significant negative correlation between AM hyphal densities and soil P ($r = -0.31$, $p = 0.002$) (Figure 2A). AM hyphal densities were also negatively correlated with soil N ($r = -0.32$, $p = 0.04$) among soil samples across land use types (Figure 2B). AMF abundance increased significantly with increasing soil C : N ($r = 0.41$, $p = 0.01$). AM hyphal densities were significantly non-linearly related to soil pH, as fitted by a polynomial quadratic function (Table 2 and Figure 2C). The polynomial regression fit the data much better ($R^2 = 0.26$, $p = 0.06$) than a simple linear regression ($R^2 = 0.08$, $p = 0.38$). The greatest AM hyphal abundance occurred at neutral pH and declined at pH above or below 7 (Figure 2C). AM hyphal abundance decreased more weakly, but still significantly with soil clay content ($F_{1, 99} = 1.62$, $p = 0.04$). As expected from the relationship vs. clay content, AM hyphal abundance also exhibited a significant ($F_{1, 99} = 1.97$, $p = 0.03$) positive association with increasing sand content (Figure 2D). Finally, AM hyphal abundance was negatively correlated with SOM ($r = 0.21$, $p = 0.03$).

Linking land use/cover and AM hyphal abundance

AM hyphal abundance varied substantially and significantly across land use types in and near SNP ($F_{2, 106} = 15.885$, $p < 0.001$) after controlling for the soil covariates (soil P, N and pH). There was a main effect of soil P ($F_{1, 106} = 12.08$, $p = 0.01$) on AM hyphal abundance across land uses. There was also a main effect of soil N ($F_{1, 106} = 27.29$, $p < 0.001$) on AM hyphal abundance across land uses. No main effect of soil pH ($F_{1, 106} = 1.49$, $p = 0.22$) on AM hyphal abundance across land uses was found. The average AM hyphal densities were 61.03±22.02, 52.89±16.41 and 47.9±22.65 m/cm^3 for wildlife grazed system; livestock grazed system and cultivated soils, respectively (Figure 3). No significant difference was observed in AM hyphal abundance in relation to farm age ($F_{1, 24} = 0.28$, $p = 0.59$). Based on *post hoc* LSD multiple comparisons AM hyphal densities were greater for wildlife-grazed soils than soils of the other two land uses and AM hyphal densities were the same for livestock-grazed and agriculture soils ($p = 0.31$, Figure 3).

There was a significant difference ($F_{4, 99} = 2.75$, $p = 0.03$) in AM hyphal abundance in different land cover types after controlling for soil properties. Wildlife-grazed grasslands had the highest AM hyphal abundance (66.89 ± 18.34 m/cm^3) while croplands had the lowest AM hyphal abundance (47.89 ± 22.65 m/cm^3) (Figure 4). A *post hoc* LSD multiple comparisons between land cover types revealed a significant difference between AM hyphal abundance in wildlife grazed grasslands and cultivated soils ($p = 0.002$), livestock grazed grasslands ($p = 0.01$) and livestock grazed woodlands ($p = 0.03$). No significant difference in AM hyphal abundance was observed between wildlife grazed grasslands and wildlife grazed woodlands ($p = 0.07$).

Whilst the estimated ground cover was generally low during field data collection, it was significantly lower in livestock grazed plots, showing that habitat type has a significant influence. The sparse vegetation was also of short stature, with the majority of plants having a height below 20 cm. Also, there was a significant positive correlation between AM hyphal densities and ground cover ($r = 0.6$, $p = 0.01$). We observed that extensive bare ground was common in livestock grazed plots with

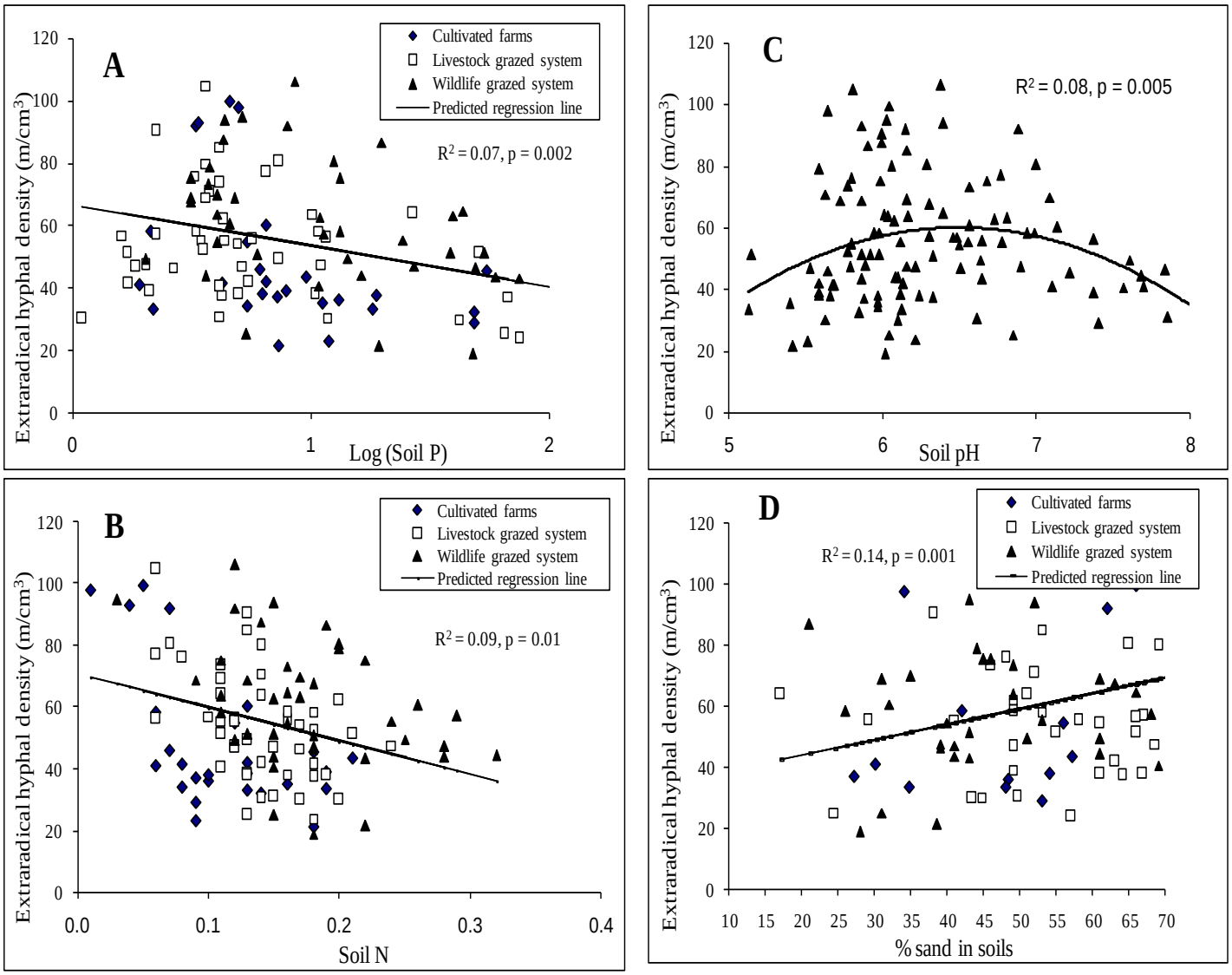

Figure 2. Associations between AM hyphal abundance and soil properties: soil P (**A**), soil N (**B**), pH (**C**) and sand content (**D**) in soils in and near Serengeti.

Table 2. Correlation coefficients between AM hyphal density (m/cm^3) and soil properties across land uses.

Soil variable	AM hyphal density (m/cm^3) in cultivated soils	AM hyphal density (m/cm^3) in livestock grazed soils	AM hyphal density (m/cm^3) in wildlife grazed soils
pH	-0.18	-0.24	-0.10
(% Clay	-0.15	-0.16	-0.23
% Silt	-0.14	-0.01	-0.29
% Sand	0.19	0.12	0.28
Total N (%)	-0.58	-0.50	-0.37
P (mg/kg)	-0.41	-0.30	-0.39
Organic matter (%)	-0.34	-0.18	-0.24
Soil moisture (% mass)	0.69	0.56	0.68
N:P	-0.32	-0.21	-0.01
C:N	0.62	0.25	0.36

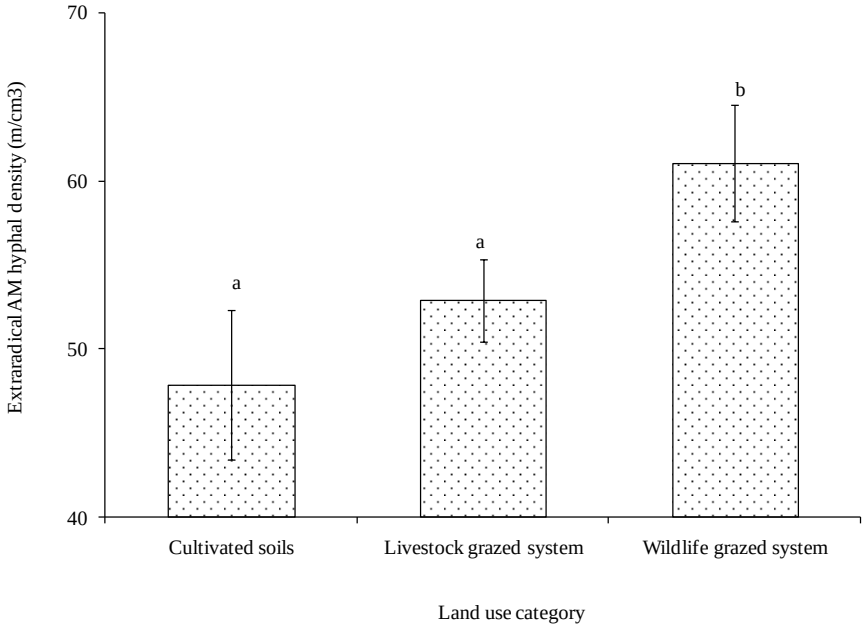

Figure 3. Land use effects on AM hyphal abundance in and near SNP. Values are means and error bars represent SE. Different letters indicate significant differences at $p<0.05$.

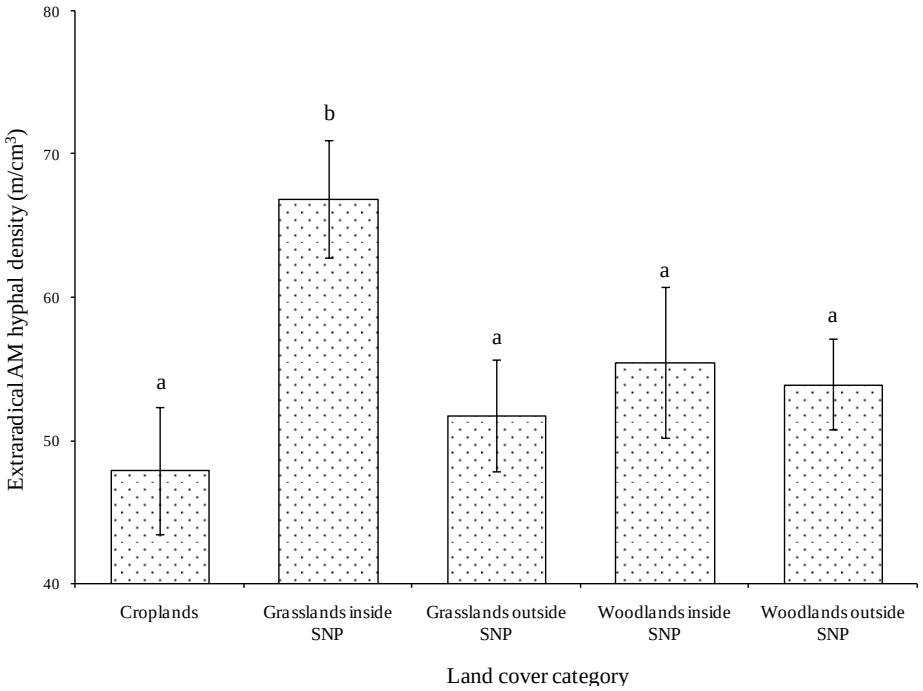

Figure 4. AM hyphal abundance in different land cover types in and near SNP. Values are means and error bars represent SE. Different letters indicate significant differences at $p<0.05$.

less than 25% ground cover. Wildlife-grazed plots had a ground cover ranging between 50 and 75%. We observed that moderately-grazed sites were mostly dominated by *Themeda triandra, Panicum coloratum,*

Table 3. Organic matter (%) and soil properties correlation coefficients across land uses.

Soil variable	Agriculture	Livestock grazed system	Wildlife grazed system	p-value
Bulk density (g/cm^3)	-0.40	-0.24	-0.32	0.11
Soil pH	-0.41	-0.14	-0.06	0.41
Clay (%)	0.01	0.04	0.03	0.21
Silt (%)	0.18	0.08	0.06	0.09
Sand (%)	-0.36	-0.22	-0.18	0.08
Total N (%)	0.12	0.17	0.06	0.02
P (mg/kg)	0.28	0.07	0.09	0.07
Soil moisture (%) by mass	0.11	0.43	0.37	0.03
N : P	0.01	0.00	0.06	0.46
C : N	0.12	0.56	0.38	0.01

Penicetum mezianum, Chloris pysnolix, Bothrichloa insculpta, Chloris gayana, Cynodon dactylon and *Harpathelia disoluta. Digitaria macroblephara, Chrysochloa orientalis, Cymbopogon excavatus, Chloris pycnothrix, Sporobolus africana, Sporobolus ioclados* and *Eragrostis tenuifolia* were the most encountered grass species on heavily-grazed sites in the park and in livestock-grazed sites.

Variations of soil organic matter with soil properties

The relationships between soil organic matter and edaphic soil properties were examined to determine the overall patterns of soil organic matter with land use types. Organic matter was positively correlated with some soil variables. As expected, SOM was significantly correlated with soil N across land use types ($p = 0.01$). SOM was also significantly correlated with soil P across land use types ($p = 0.05$). SOM was negatively but not significantly correlated with soil pH ($p = 0.26$). Soil organic matter was strongly influenced by soil moisture ($p = 0.005$), which demonstrates that organic matter fluctuates with changes in soil moisture. This indicates that soils with greater soil organic matter have greater water-holding capacity and therefore greater soil moisture contents. SOM was significantly correlated with C : N ratio ($p = 0.001$), but not significantly correlated with N : P ratio ($p = 0.58$). SOM was positively but not significantly correlated with percent clay content in soils ($p = 0.11$). As shown in Table 3, SOM increased significantly ($p = 0.04$) with an increase in the percentage of silt in the soils across land use types. SOM was also negatively but not significantly correlated with percent sand content in soils ($p = 0.06$), suggesting a decrease in SOM with an increase in the percentage of sand in the soils. As expected, SOM was negatively and significantly correlated with bulk density ($p = 0.02$). SOM varied substantially and significantly across land use types in and near Serengeti ($F_{2, 106} = 9.78$, $p < 0.001$) after controlling for the soil covariates. There were no main effects of soil P, N and pH on soil organic matter across land uses ($p > 0.05$ all cases).

DISCUSSION

Variations of AM hyphal abundance with land use/cover

In this study, variation in densities of AM hyphal abundance was observed across different land use systems. Land use practices can stress the plant-mycorrhizal symbiosis and may be a threat to AMF (Siddiqui and Pichtel, 2008). For example, soil tillage has been found to reduce AM fungi in agricultural ecosystems by changing the abundance and distribution of mycorrhizal fungi in several ways (Jasper et al., 1989; Abbott and Robson, 1991). First, it may change the physical, chemical or biological environment of soil leading to either direct effects on AM fungi (Abbott and Murphy, 2003) or indirect effects on plant growth (Verma and Jayakumar, 2012). Secondly, the disturbance may eliminate host plants leading to changes in the distribution and abundance of AM fungi (Abbott and Robson, 1991).

We found that cultivated soils contained the lowest AM hyphal densities, suggesting that tillage physically damages AM hyphal network. The observed low AM hyphal densities in cultivated soils are consistent with the previous observations that tillage damages the mycelium networks (Munyanziza et al., 1997; Mader et al., 2000; Eom et al., 2001; Allen et al., 2003; Oehl et al., 2003). Since the persistence of AM fungi in soil depends on the survival of their active propagules (e.g., spores, hyphae and colonized roots), tillage can negatively affect AM fungi (Alguacil et al., 2008) by damaging the mycelium networks. Roldan et al. (2007) observed the highest levels of mycorrhizal propagules in maize and bean intercropped soil under no-tillage as compared to tillage soils. Soil tillage alters the ability of AMF to colonize roots, breaking up their hyphal network. As a consequence, there is a significant reduction in root colonization and, in turn, in the nutrient absorption from the soil (McGonigle and Miller, 1996; Peng et al., 2013). With an increase in soil disturbance, loss of fungi that form hyphae in soils is expected. Also, damage to the soil

hyphal network by soil disturbance may contribute to the losses in mycorrhizal infectivity. It may be that they are physically damaged, or that redistribution in the soil exposes them to soil conditions which are unfavourable for germination or colonization.

Variations of AM hyphal abundance with grazing

Mycorrhizal symbioses also can be influenced by aboveground organisms such as herbivores (Vicari et al., 2002; Gehring et al., 2002). In addition, overgrazing may alter plant community structure and in return cause a shift in AMF species composition (O'Connor et al., 2002) as well as the reduction in AM hyphal abundance (McNaughton and Oesterheld, 1990). Livestock grazed soils had lower AM hyphal densities than corresponding wildlife grazed soils. This suggests that grazing intensities and temporal patterns of grazing which are associated with typical livestock husbandry practices in the Serengeti ecosystem may reduce hyphal densities. Reduced AM hyphal abundance in livestock grazed system may cause reduction in host plant biomass and potentially carbon inputs in livestock grazed plots (Ritchie, 2014). There are many possible mechanisms for decreasing carbon inputs in livestock grazed system. For example, it was observed that plants were exposed to intensive grazing by livestock for the extended periods of time, without sufficient recovery periods (Ritchie, 2014). High grazing intensities (> 60% removal of biomass) by cattle caused soil compaction, loss of carbon inputs and alteration of nutrient inputs through recycling of urine and dung under intense grazing (Ritchie, 2014). This may negatively impact AM hyphal density through limited natural regeneration potential of host plant species. Overgrazing may attribute to continual removal of soil N and P within the ecosystem, and decrease photosynthetic source for mycorrhizal fungi and associated microbes (Eom et al., 2001; Gange et al., 2002). In contrast, wildlife grazed grasslands were observed to support the highest AM hyphal abundance possibly due to the presence of high plant biomass and diversity of host plants. Moderate grazing may reduce fuel loads, it may also return a significant fraction of aboveground plant production to the soil as the organic matter in dung (Dungait et al., 2009; Davies et al., 2010; Strand et al., 2014). Our results are in agreement with earlier findings that environmental factors in the tropics influence AMF propagules (Dandan and Zhiwei, 2007), demonstrating that there is a need for proper management of public grassland and woodland as well as a need for alternative measures to reduce the level of overgrazing around Serengeti.

Variations of AM hyphal abundance with soil properties

This study found that soil characteristics (here soil N, P, pH and moisture) played an important role in determining AM hyphal abundance. Previous research by McNaughton and Oesterheld (1990) also found that soil properties had a significant effect on AM hyphal abundance and soil organic matter composition. Our results suggest that similar controls at the site scale may be influencing AM hyphal abundance because of land use. We found that soils differ in chemical and physical characteristics, and the question is whether or not the abundance of AMF was influenced by those properties. Indeed, the results of this investigation show that soil properties are a major determinant of the abundance of AM hyphal densities in the soils (Kahiluoto et al., 2001; Allison and Goldberg, 2002; Mathimaran et al., 2007). This dependence of fungal spatial distributions on edaphic factors is consistent with observations in other communities, including tall grass prairie (Johnson et al., 1992) and sand dunes (Koske, 1981). This study found that site-specific differences in soil N, P and moisture are important factors in explaining the variation in AM hyphal densities. We found that AMF hyphal densities were negatively correlated with available P and soil N (Figure 2A and B). Earlier work showed that pH (Wang et al., 1993; Giovannetti, 2000), organic matter content (Sieverding, 1991; Al-Karaki and Al-Raddad, 1997) and soil N and P availability (Johansen et al., 1996; Olsson and Tyler, 2004; Uhlmann et al., 2004; Jin et al., 2005; Bashan et al., 2007; Oehl et al., 2010; Sheng et al., 2013) influence the composition of AMF communities and the abundance and occurrence of specific AMF species. We observed that AMF hyphal densities were positively correlated with soil moisture. Several studies have reported that soil moisture may be an important control on microbial community structure, especially bacterial and fungal abundance and biomass (Frey et al., 1999; Gehring and Whitham, 2002; Dandan and Zhiwei, 2007). Reduced soil AM hyphal density and viability are predicted to hamper soil moisture retention properties and could lead to faster soil water depletion in heavily grazed sites. Soil moisture may play an important control in the decomposition of soil organic matter.

In this study, a weak and negative correlation between AM hyphal densities and soil organic matter was observed. Organic matter has been reported to be a critical factor in determining the potential of tropical soils and is highly dependent on land use system and farming practice (Craswell and Lefroy, 2001). It influences the structure of the soil and thereby affects water infiltration and storage, aeration and root penetration (Paul and Clark, 1989; Smith et al., 2014). In the humid tropics, with their abundant rainfall and highly weathered soils, organic matter has been reported to be a major source of nutrients and cation exchange capacity (Lathwell and Bouldin, 1981). Changes in the soil chemical properties reported in this study could have also caused a shift in AMF composition and subsequently influenced AM hyphal abundance in the soils. The sustainability of

mycorrhizae in the soil is thus, important to maintain in order to promote productivity of croplands and natural systems, and may be critical to the maintenance of biodiversity (Allen et al., 1995; Klironomos et al., 2000). As a result, loss of this relationship can have serious consequences in terms of plant community degradation or productivity.

Variations of AM hyphal abundance with plant cover

Positive correlations have been reported between plant species richness and AMF abundance (McNaughton and Oesterheld, 1990; Johnson et al., 1992) indicating high mycorrhizal species richness in areas with high plant diversity (Sieverding, 1991). We observed that moderately wildlife-grazed grasslands supported the highest AM hyphal densities of all the other land cover types. This indicates that high plant cover and diversity of host plants (Chiarello et al., 1982; McNaughton and Oesterheld, 1990) has a positive effect on AMF hyphal densities. AMF form networks through which materials can be transferred between individuals of the same or different plant species and therefore have the potential to affect such ecosystem and community processes as energy flow, nutrient cycling, competition and species diversity (Grime et al., 1987; Waring et al., 2013).

A study by Oehl et al. (2010) demonstrated that AMF com-munities of grasslands colonized the plant roots faster than the AMF communities of the tilled arable lands. Similarly, woodlands or grasslands that include highly mycorrhiza-dependent or responsive plants can increase AMF populations and consequently improve colonization and AMF functioning for subsequent plant species (Smith et al., 1999). Burrows and Pfleger (2002) also observed an increase in AMF species richness with an increase in plant species diversity. Johnson et al. (1992) hypothesized that soil factors and plant species may be of equal importance for the diversity of AMF species communities. Plants may support a given biomass of mycorrhizae according to the availability of nutrients which may be only loosely related to the total amount of nutrients in the soil (McNaughton and Oesterheld, 1990).

Conclusion

Greater mycorrhizal abundance was associated with lower soil nutrients (soil N, P and soil organic matter) and an attenuation of the translation of soil nutrient variations. This implies that AM hyphal densities could serve as an indicator in assessing biological soil quality and fertility if soil properties are adequately considered. The results suggest that AM hyphal density's response to land use and soil characteristics can vary widely between cultivated, livestock and wildlife grazing sites. This study shows also that AM hyphal densities varied broadly across land uses. Livestock grazed system had lower AM hyphal densities than the corresponding wildlife grazed system, suggesting that overgrazing by livestock led to the reduction in AM hyphal densities in the soils by decreasing carbon inputs. We found that cultivated soils contained the lowest AM hyphal densities, suggesting that tillage physically damages AM hyphal network. In general, both land use and soil properties have a greater impact on the AM hyphal densities and have to be taken into consideration in the conservation of AMF. Future studies should explore how different soils properties and land use affect AMF species composition. The promotion of non-tillage farming and diversification of crops may enhance soil chemical properties, mycorrhizal symbiosis and in return improve plant productivity in tropical poor soils.

Conflict of interests

The authors did not declare any conflict of interest.

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