SITE CHARACTERISTICS AND VEGETATION DRIVE THE ABUNDANCE AND DIVERSITY OF ARBUSCULAR MYCORRHIZA FUNGI IN SELECTED LAND DEGRADATION SURVEILLANCE FRAMEWORK STUDY SITES IN KENYA †

[LAS CARACTERÍSTICAS DEL SITIO Y LA VEGETACIÓN DETERMINAN LA ABUNDANCIA Y DIVERSIDAD DE HONGOS MICORRÍCICOS ARBUSCULARES EN SITIOS SELECCIONADOS DEL MARCO DE ESTUDIO DEL ESQUEMA DE VIGILANCIA DE LA DEGRADACIÓN DE LA TIERRA EN KENIA]

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SUMMARY

Background: In tropical agroecosystems, arbuscular mycorrhizal fungi (AMF) is an essential component of soil fertility. Limited number of studies have emphasized the effects of vegetation type and soil physico-chemical characteristics on AMF communities, although several studies have stressed the importance of AMF in agroecosystems. **Objective:** To evaluate how specific vegetation types and site affect the physico-chemical properties of the soil and the abundance and diversity of AMF spores. **Methodology:** Three specific locations from the ongoing Kenya Cereal Enhancement Programme Climate Resilient Agricultural Livelihoods (KCEP-CRAL) initiative were chosen to carry out the study. Kubo South in Kwale County, Muminji in Embu County, and Thange in Makueni County were chosen as the study's site areas. The sites were selected based on the implementation of a land degradation surveillance framework (LDSF), comprising both cultivated and uncultivated plots. In each study site, four vegetation types namely bushland, grassland, cropland, and shrubland were selected. **Results:** The results showed significant variations in soil physicochemical properties among different sites. Thange exhibited the highest carbon (C) content, pH, and exchangeable bases compared to Muminji and Kubo South. Sand content was higher (57%) in soils from Kubo South compared to that obtained in Muminji (41%) and Thange (27.8%). In contrast, the clay content was higher in Thange (58%) and Muminji (41%) than in Kubo South (27%). Vegetation type had a significant effect on soil pH and C only in Muminji. A higher abundance of AMF spores was recorded in soil from the Muminji site (385.0 spores kg^{-1} soil) followed by Kubo south (226.0 spores kg^{-1} soil) and lowest in Thange (67.0 spores kg^{-1} soil). Muminji had the highest mean taxonomic richness (3.21 species) compared to Kubo South and Thange (2.96 and 1.98 species respectively). Taxonomic diversity as shown by the Shannon diversity index (H′) had a similar trend as richness. However, vegetation type only had a significant effect on AMF richness and diversity. **Implication:** The findings of this study may especially be important in agroecosystems since AMF play a key role in soil fertility and productivity through soil aggregation process, nutrient cycling, water relations, and in plant nutrition and health which contribute to the overall ecosystem functioning. **Conclusion:** These findings show that vegetation type and site influence AMF sporulation and diversity and hence may influence the AMF functions in contributing to the reclamation of degraded soil ecosystems.

Key words: Vegetation type; Soil physicochemical properties; Land use change; Spore abundance.

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RESUMEN

Antecedentes: En agroecosistemas tropicales, los hongos micorrízicos arbusculares (HMA) son un componente esencial de la fertilidad del suelo. Un número limitado de estudios han enfatizado los efectos del tipo de vegetación y las características físico-químicas del suelo en las comunidades de HMA, aunque varios estudios han enfatizado la importancia de los HMA en los agroecosistemas **Objetivo**: Evaluar cómo los tipos específicos de vegetación y el sitio afectan las propiedades físico-químicas del suelo y la abundancia y diversidad de esporas de HMA. **Metodología**: Se eligieron tres ubicaciones específicas de la iniciativa en curso del Programa de Mejora de Cereales de Kenia para Medios de Vida Agrícolas Resilientes al Clima (KCEP-CRAL, por sus siglas en inglés) para llevar a cabo el estudio. Kubo South en el condado de Kwale, Muminji en el condado de Embu y Thange en el condado de Makueni fueron elegidas como las áreas del sitio del estudio. Los sitios se seleccionaron sobre la base de la aplicación de un marco de vigilancia de la degradación de la tierra (LDSF, por sus siglas en inglés), que comprende parcelas cultivadas y no cultivadas. En cada sitio de estudio, se seleccionaron cuatro tipos de vegetación, a saber, matorrales, pastizales, tierras de cultivo y matorrales. **Resultados**: Los resultados mostraron variaciones significativas en las propiedades fisicoquímicas del suelo entre diferentes sitios. Thange exhibió el mayor contenido de carbono (C) (12.6 g kg^{-1}) y bases intercambiables a (13.8 cmol kg^{-1}). Por el contrario, Muminji tenía un contenido de C ligeramente inferior (8.3 g kg^{-1}) y bases intercambiables (9.2 cmol kg^{-1}). Kubo South, por su parte, registró el menor contenido de C (4.7 g kg^{-1}) y bases intercambiables (3.6 cmol kg^{-1}). El pH del suelo en Thange fue ligeramente más alto (6.7) en comparación con Kubo Sur y Muminji (6.1 y 6.0 unidades, respectivamente). El contenido de arena fue mayor (57%) en los suelos de Kubo Sur en comparación con el obtenido en Muminji (41%) y Thange (27,8%). Por el contrario, el contenido de arcilla fue mayor en Thange (58%) y Muminji (41%) que en Kubo Sur (27%). En Muminji, el pH del suelo se vio afectado significativamente por el tipo de vegetación y fue alto en los matorrales, pastizales y tierras de cultivo en comparación con los matorrales. Por otro lado, el contenido de C fue mayor en los matorrales que en los matorrales y pastizales de Thange. Se registró una mayor abundancia de esporas de HMA en el suelo del sitio de Muminji (385.0 esporas kg-1 de suelo), seguido de Kubo al sur (226.0 esporas kg^{-1} de suelo) y más bajo en Thange (67.0 esporas kg^{-1} de suelo). Muminji tuvo la mayor riqueza taxonómica media (3.21 especies) en comparación con Kubo South y Thange (2.96 y 1.98 especies respectivamente). La diversidad taxonómica, como lo muestra el índice de diversidad de Shannon (H), tuvo una tendencia similar a la de la riqueza, con el número más alto registrado en Muminji (0.97 especies), intermedio en Kubo Sur (0.89 especies) y más bajo en Thange (0.46 especies). Sin embargo, el tipo de vegetación solo tuvo un efecto significativo en la riqueza y diversidad de HMA. **Implicaciones:** Los hallazgos de este estudio pueden ser especialmente importantes en los agroecosistemas, ya que los HMA desempeñan un papel clave en la fertilidad y productividad del suelo a través del proceso de agregación del suelo, el ciclo de nutrientes y la relación con el agua, y en la nutrición y la salud de las plantas, que contribuyen al funcionamiento general del ecosistema. **Conclusión:** Estos hallazgos muestran que el tipo de vegetación y el sitio influyen en la esporulación y diversidad de HMA y, por lo tanto, pueden influir en las funciones de HMA para contribuir a la recuperación de ecosistemas de suelo degradados

Palabras llave: Tipo de vegetación; Propiedades químicas del suelo; Cambio de uso de la tierra; Diversidad de AMF; Abundancia de esporas.

INTRODUCTION

Over 80% of plants establish symbiotic associations with arbuscular mycorrhizal fungi (AMF) (Bernatchez *et al.*, 2008). The fungi benefit from the plants by getting carbohydrates while the plants benefit from AMF through enhanced water and nutrient uptake (Bauer, 2020). The establishment of such a symbiotic relationship is crucial for the plant-limiting soil nutrients such as phosphorous (P) and other micronutrients since AMF hyphae can grow beyond the nutrient-depleted zones around the roots of most crops and trees and hence explore greater soil volumes that are beyond the plant's reach. This is made possible through the fungal hyphae, which can access small soil pores that the plant roots cannot explore, increasing the plant's nutrient uptake (Treseder and Allen, 2000). AMF also contributes to enhancing plants' tolerance to pathogens, pests, salinity, drought, and heavy metals (Cardoso and Kuyper, 2006; Kahiluoto *et al.*, 2009; Wu *et al.*, 2013). These interventions enhance the performance of plant's growth, and this is especially amplified in water stress areas (Seleiman *et al.*, 2021; Zarea *et al.*, 2009). Therefore, AMF comprises a very critical component of soil biodiversity in natural and human-managed systems.

Growth and development of AMF are influenced by soil properties, climatic conditions, and the way the land is managed (Oehl *et al.*, 2010; Melo *et al.*, 2019). For instance, land use change from forest to practices such as crop cultivation particularly annual monocropping leads to alterations in plant cover and the quality and characteristics of the soil (Oruru and Njeru, 2016). Plant cover change may lead to differences in organic matter addition as well as alter the microclimatic conditions around the individual plants, thus affecting soil chemical properties which can consequently influence AMF spore development (Ohsowski *et al.*, 2018). Additionally, removing or introducing non-mycorrhizal plants through land use change may influence AMF communities (Oehl *et al.*, 2010). Soil properties like pH, impacts the mobility of ions within the soil, thus affecting their absorption by plants and soil microorganisms (Jamiołkowska *et al.*, 2018). For example, acidic soils may cause unfavorable conditions for plant's growth and AMF activities though this may depend on certain species; some studies have shown that certain AMF species like *Acaulospora* tend to thrive in acidic soils (Clark, 1997; Clark *et al*., 1999).

Furthermore, climatic factors such as fluctuations in precipitation and temperature affect the development and proliferation of the fungus hence impacting and influencing the growth, and development of the host plants (Kamau *et al.*, 2020; Melo *et al.*, 2019). Past research has identified a positive association between spores abundance and plant root colonization showing that AMF sporulation increases with enhanced growth of mycorrhiza plants (Khakpour and Khara, 2012; Zarea *et al.*, 2009). Nonetheless, there is limited scope of scientific evidence on the influence of soil characteristics and vegetation type on AMF spore abundance (Jansa *et al.*, 2002; Alguacil *et al.*, 2016). Many previous studies have shown that spore production and root colonization mostly occur on the soil surface (0-20 cm depth) where the concentration of root hairs is greatest and soil properties are greatly altered (Querejeta, *et al.*, 2009; Shukla *et al.*, 2013; Schreiner, 2020). Therefore, the objectives of this study were to evaluate how vegetation type and site characteristics affected; (i) soil physicochemical properties, (ii) diversity and abundance of AMF, and (iii) relationship between AMF diversity, abundance, and soil properties.

MATERIALS AND METHODS

Description of the study sites

Data was collected from three sites, Muminji, Thange, and Kubo South in Kenya, each covering 100 km^2 (Figure 1). Kubo South is located in the south coast in Kwale County and receives about 1250 mm annual rainfall. On the other hand, Thange is situated in Makueni County and is drier than the other study sites, receiving about 610 mm annual rainfall, while Muminji is located in Embu County at the lower edge of the Central Highlands of Kenya and is at the highest elevation, receiving an annual rainfall of about 920 mm (Table 1). The study sites were chosen from a pool of project sites for Kenya Cereals Enhancement Programme - Climate Resilient Agricultural Livelihoods Window (KCEP-CRAL) using the Land Degradation Surveillance Framework (LDSF) which was established by Center for International Forestry Research - World Agroforestry (CIFOR-ICRAF). The LDSF emphasizes the importance of establishing a biophysical reference point as a basis for monitoring landscape degradation and evaluating the success of restoration efforts in the tropical regions (Winowiecki *et al*., 2021).

Study sites were classified according to vegetation type into bushland, cropland, grassland, and shrubland (Table 2). Crops cultivated in the study areas were maize (*Zea mays* L.), cowpea (*Vigna unguiculata* L. Walp), green grams (*Vigna radiata* L. Wilczek), cashew (*Anacardium occidentale* L.), and khat (*Catha edulis* Forsk). Farmers rarely apply inorganic fertilizers, and more frequently use farmyard manure for cultivation of these crops. Most plots in cropland have been cultivated on average for over 25 years. The prevalent bushland species were *Erythrophloeum suaveolens* (Guill. et Perr), *Grewia plagiophyla* K. Schum, *Annona senegalensis* Pers., and *Albizia versicolor* Welwitsch ex Oliver. The dominant shrubland species present were *Ozoroa insignis* R. Delile, *Aloe barbadensis* Philip Miller, and *Boscia coriacea* Johann Friedrich. Within the subset of plots not allocated to cultivation, a significant proportion was designated as extensive grazing land and used for grazing for 30 to 40 years, or they laid fallow. Remarkably, private land ownership emerged as the predominant tenure arrangement uniformly observed across all three LDSF study sites. The agroecological zones in the three sites are different ranging from zone IV (semi-humid to semi-arid) to zone V (semi-arid).

Table 1. Characteristics of the study sites.

Site	GPS Coordinates	Average elevation (m)	Average annual temperature (°C)	Average annual rainfall (mm)	Predominant soil type
Kubo South	4.1816° S, 39.4606° E	90.5	27.63	1255.6	Luvisols
Muminji	0.6185° S, 37.7131° E	1117.5	23	922.9	Nitisols
Thange	2.2559° S, 37.8937° E	919.5	24.1	609.8	Lithosols

‡Based on Jaetzold *et al*. (2006).

Table 2. Description of classes for vegetation type in Land Degradation Surveillance Framework dataset.

Type	Description
Grassland	Land covered with grasses and other herbs. Woody vegetation ≤ 10%
Shrubland	Open or closed stand of shrubs ≤3 m tall.
Cropland	Cultivated land with annual or perennial crops
Bushland	A mix of trees and shrubs with a canopy cover of ≥ 40%

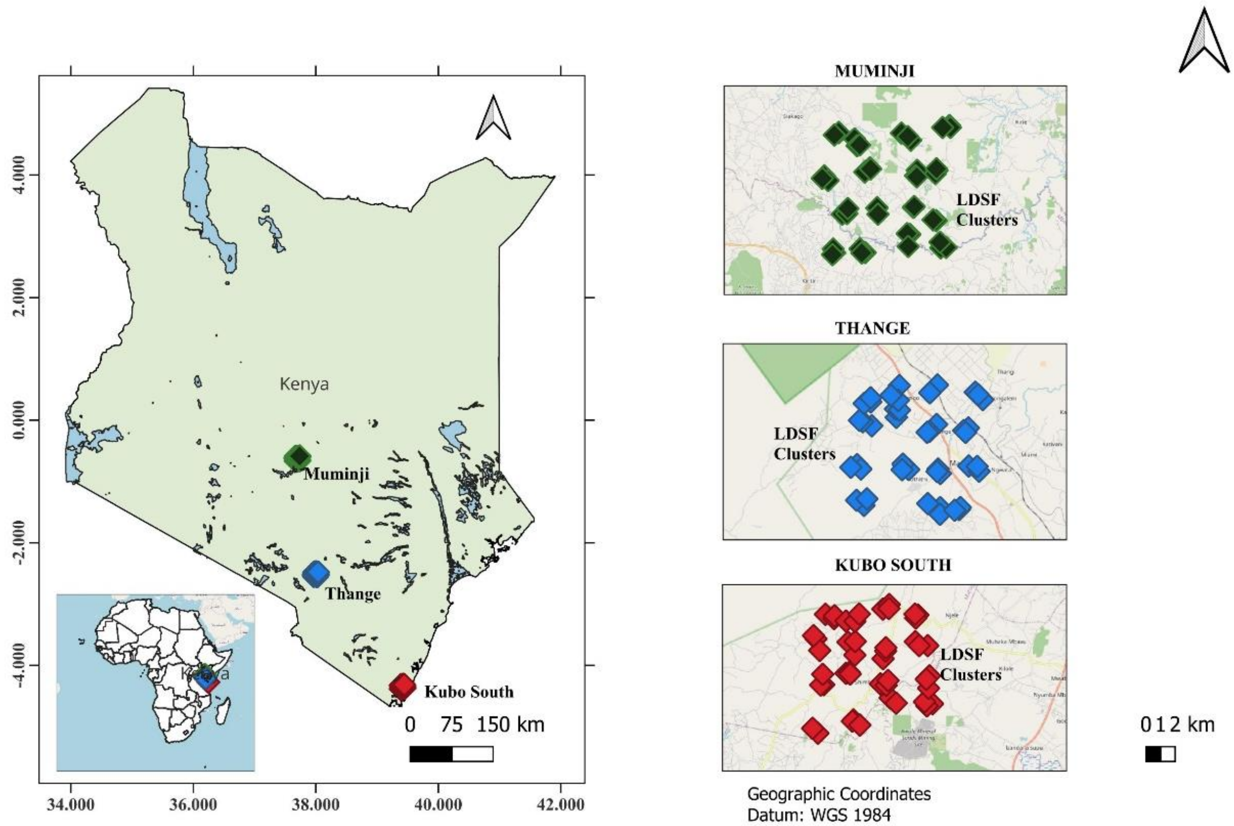

Figure 1. Location of the three study sites; Muminji in Embu County, Thange in Makueni County and Kubo South in Kwale County. The inverted squares represent the LDSF cluster sites where sampling was done.

Soil sampling and vegetation type survey

Soil samples were collected in 2019, with Thange and Kubo South being sampled during the long rainy season (March-April) and Muminji being sampled in June which is a transition month between the end of rains and the beginning of dry season. Sampling was done following a hierarchical design described in LDSF. The sites measured 100 km^2 (10 × 10 km) and each site was divided into 16 grid cells (2.5 km × 2.5 km each) (Figure 2). Each grid cell has cluster plots allocated and the centroid locations within the clusters were marked and randomized. Each cluster consisted of 10 plots which measured 1 km^2 each, with randomized center points pinned out within a 5.64 m radius from the centroid of the cluster to minimize local biases that may arise from convenience sampling. The plots were further subdivided into four (100 m^2) subplots. Soil sampling for this study was done at the center of three plots within each cluster for the three sites. A soil auger was used to sample soil from a depth of 0-50 cm. The total number of samples collected from each of the three sites was 48 (16 grid cells × 3 plots) soil samples. Soil sample weighing 500 g was obtained and placed into labelled sampling bags for laboratory analysis.

Arbuscular mycorrhizal fungi (AMF) trap culture

AMF spores were extracted from soil using the trap culture method. Twenty grams of field soil was mixed with autoclave coarse sand in a 1:1 ratio and placed in a 10 cm diameter pots. Sorghum seeds were sown into individual pots and the cultures were grown in a soil ecology facility at ICRAF nursery for four months. The pots were then left to dry undisturbed in a room with fairly stable temperature.

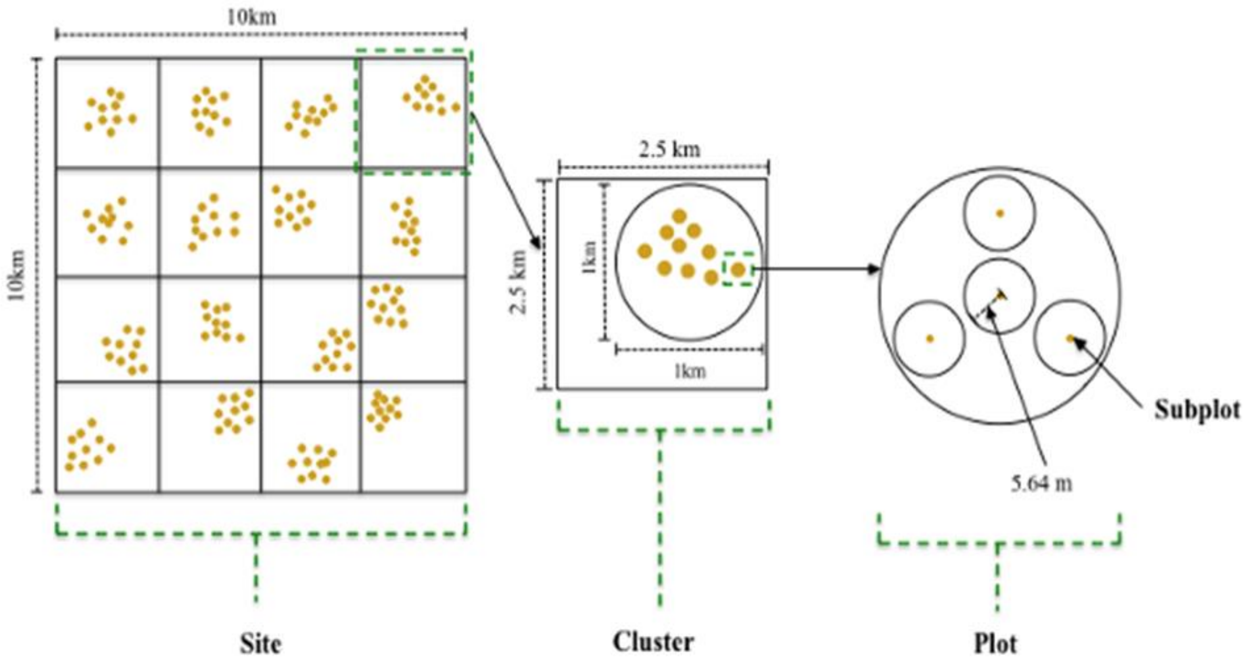

Figure 2. Land Degradation Surveillance Framework hierarchical sampling design. In each site, an area measuring 10 × 10 km (100 km^2) is divided into 16 grid cells where each cell contains 1 km^2 cluster. There are ten plots (1000 m^2) within each cluster. Each plot is laid out with radial arms and further contains four (100 m^2) sub-plots. This is called nested sampling design because of the different spatial scales at which sampling is done.

Analysis of mycorrhiza spores

The enumeration and isolation of AMF spores from the pot cultures were conducted using the procedure outlined by Gerdemann and Nicolson (1963). Each soil sample was mixed thoroughly, and 50 g was taken for spore extraction using wet sieving and sucrose density centrifugation procedure. Spores were counted using grid-line intersect method, and isolated using fine glass Pasteur pipettes under a compound microscope for further analysis. Spores were categorized to different types based on morphological characteristics namely size, pigmentation, wall thickness, presence of internal structures and appendages, presence of hyphae, and attachment points (Cheruto *et al.*, 2023). Spores were preserved and archived at the World Agroforestry laboratories (ICRAF).

Soil physicochemical properties

Whole soil samples from the field were air-dried at room temperature and then ground to pass through a 2 mm sieve. The soil properties assessed included pH, total carbon, total nitrogen, exchangeable bases, as well as sand and clay contents. Soil pH was determined using a 1:2.5 soil/water ratio. Exchangeable bases were determined using the Mehlich-3 procedure (Mehlich 1984) and their concentrations were measured using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP OES). The analysis of total carbon and nitrogen was done using FLASH 2000 NC Analyser (ThermoFisher Scientific, Cambridge, UK). Sand and clay contents were estimated using a Laser diffraction particle size analyzer (LDPSA).

Statistical analysis

In this study, generalized linear mixed models (GLMM) were utilized to test the influence of vegetation type and site on the abundance and diversity of AMF spores. The statistical analysis was performed using the lme4 package (Bates *et al.*, 2015) in R software (R Core Team 2021). These models were selected based on the deviation from normality observed in the AMF spores' data as indicated by the results of the Shapiro-Wilk test, and the presence of heterogeneity in variance as confirmed in Levene's test. In contrast, generalized linear models (GLMs) were employed to investigate the effect of vegetation type and site on soil physico-chemical properties. The selection of the models was based on Akaike Information Criterion (AIC), where models with the lowest value of AIC were chosen to be the best models. Detailed procedure on selection process is given in Kamau *et al.* (2020). Where significant effects of the variables were observed, Tukey's Honest Significant Difference (HSD) test was performed at a 5% level of significance. Redundancy Analysis (RDA) was used to test for relationship between AMF genera, abundance, richness, and diversity according to vegetation type.

RESULTS

Effects of Site and vegetation type on soil properties

Soil properties were significantly influenced more by site than vegetation type in general (Table 3). For instance, soils in Thange were slightly higher in pH compared to Kubo South and Muminji. Soils in Thange had significantly higher total carbon (C) content by more than 70% compared to those in Muminji and Kubo South. Similarly, exchangeable bases were more than three times higher in Thange and Muminji in comparison to Kubo South. Sand content was higher in soils from Kubo South compared to Muminji and Thange sites. In contrast, the clay content was higher in Thange and Muminji than in Kubo South. Site and vegetation type showed significant interaction effect on soil pH and total C.

Effects of site and vegetation type on AMF spore abundance and diversity

Similar to soil chemical properties, AMF spore count, diversity and taxonomic richness were significantly affected more by the site than the vegetation type. We recorded significantly higher spore count in soils obtained from Muminji and Kubo South compared to soil obtained from Thange (Table 4). The dominant AMF genus was *Glomus*, contributing almost 40% of the total AMF spore counts in each of the three sites. Genera *Acaulospora* and *Enterophospora* were significantly higher in Muminji site compared to Kubo South and Thange sites. Genera *Scutellospora* was higher in Kubo South compared to Muminji and Thange. The population of genera *Diversispora, Gigaspora*, *Glomus*, *Pacispora,* and *Paraglomus* from Muminji site was more than double the number obtained from Kubo South and Thange sites. Diversity and taxonomic richness also differed based on the site. Muminji had the highest mean taxonomic richness compared to Kubo South and Thange. Shannon diversity index showed the same trend as species richness, with the highest number recorded in Muminji, intermediate in Kubo South and low in Thange. However, the influence of vegetation type on total AMF abundance was only observed in Kubo South, where cropland and shrubland showed significantly higher AMF abundance compared to grassland and bushland. For individual genera, only *Diversispora, Pacispora,* and *Paraglomus* were significantly affected by vegetation type (Table 4). In Kubo South, genera *Diversispora* and *paraglomus* were more than four times higher in cropland compared with the number obtained from the other three vegetation types. However, in Muminji *Diversispora*, *Paraglomus*, and *Pacispora* were more than double in grassland compared to bushland, shrubland, and cropland. Significant differences in species richness based on vegetation type were observed only in Muminji, where grassland recorded higher richness compared to that obtained in bushland, cropland and shrubland. Differences in Shannon diversity index based on vegetation type were observed only in Thange, where significantly higher diversity was observed in bushland compared to the lowest value in shrubland.

Correlation between soil physicochemical properties and AMF abundance and diversity

The Redundancy Analysis (RDA) biplot between soil physicochemical properties and AMF abundance showed strong and positive relationship between sand content and majority of the AMF genera (Figure 3). This could be as a result of their higher presence in sandier soils than clayey soils, a characteristic which was predominant in Muminji and Kubo South. There was also a strong but negative relationship between most of these genera with soil pH. Here, the genera were found to be low in soils with lower soil pH, which was also a common feature in Muminji and Kubo South. There were no other unique patterns that could be drawn for the other soil chemical properties. Besides, the variation explained by the two axes (axis 1 and 2) was low, with axis 1 explaining about 18% of the variation and axis 2 about 15%, for a combined value of about 33%.

DISCUSSION

Effects of vegetation type and site on soil physicochemical properties

We found a strong significant effect of site characteristics on soil properties as opposed to vegetation type. This is contrary to our assumption that vegetation type would have a higher influence on soil properties due to differences in vegetation composition and structure, management practices (e.g., tillage operations, animal grazing), and intensity of disturbance. The dominant influence of sites could be due to differences in their characteristics. For instance, parent material, climate, topography, and land use history can all play key roles in determining soil properties of a given site (Fu *et al.*, 2018). Average rainfall, for instance, is higher in Kubo South than in Muminji and Thange. High rainfall may contribute to low soil chemical properties due to leaching of soil elements such as exchangeable bases and N (Gachimbi, 2002; Fatubarin and Olojugba, 2014). However, the low rainfall in Thange could mean reduced leaching hence the higher amounts of soil chemical elements. Soil texture affect infiltration rate, nutrient storage, water holding capacity and erosion. Therefore, soils with high content of sand like those

Table 3. Soil chemical properties, sand, and clay content as affected by site and vegetation type.

Site	Vegetation type	Soil properties					
		pH (water)	Total C (g kg^{-1})	Total N (g kg^{-1})	exchangeable bases (cmol (+) kg^{-1})	% sand	% clay
Kubo South	Bushland	6.1 (0.5)	4.7 (0.3)	2.9 (2.5)	3.4 (0.5)	61.0 (2.7)	23.7 (2.3)
	Cropland	6.1 (0.1)	4.4 (0.2)	0.4 (0.0)	3.5 (0.4)	57.8 (2.7)	26.1 (2.2)
	Grassland	5.9 (0.1)	4.9 (0.4)	0.5 (0.1)	3.2 (0.2)	52.6 (4.5)	31.2 (4.4)
	Shrubland	6.1 (0.1)	4.9 (0.7)	0.4 (0.1)	4.1 (0.8)	56.5 (4.3)	27.8 (3.0)
	***Mean*†**	**6.1 (0.2)^{B}**	**4.7 (0.2)^{B}**	1.3 (0.5)	**3.6 (0.3)^{C}**	**57.0 (1.7)^{A}**	**27.2 (1.4)^{C}**
Muminji	Bushland	**5.4 (0.4)^{b}**	7.9 (0.8)	0.7 (0.1)	9.7 (3.2)	43.6 (2.7)	38.1 (2.7)
	Cropland	**6.4 (0.1)^{a}**	6.8 (0.6)	0.6 (0.1)	8.6 (1.4)	45.5 (3.2)	36.1 (3.5)
	Grassland	**5.9 (0.4)^{ab}**	8.9 (0.5)	0.8 (0.1)	7.3 (3.4)	32.6 (12.3)	51.0 (12.0)
	Shrubland	**6.4 (0.1)^{a}**	9.4 (1.5)	0.8 (0.1)	11.2 (2.3)	42.4 (3.8)	39.6 (3.6)
	***Mean*†**	**6.0 (0.2)^{B}**	**8.3 (0.6)^{B}**	0.7 (0.1)	**9.2 (1.4)^{B}**	**41.0 (1.9)^{B}**	**41.2 (1.9)^{B}**
Thange	Bushland	6.7 (0.1)	**22.0 (3.7)^{a}**	1.6 (0.4)	18.4 (4.1)	30.3 (3.5)	54.7 (3.7)
	Cropland	6.7 (0.1)	**11.2 (1.5)^{ab}**	2.9 (1.9)	12.6 (1.1)	26.8 (2.0)	63.2 (2.5)
	Grassland	6.7 (0.0)	**9.5 (1.8)^{b}**	0.9 (0.2)	11.6 (1.8)	28.5 (10.3)	53.2 (10.0)
	Shrubland	6.8 (0.3)	**7.5 (1.0)^{b}**	0.8 (0.1)	12.7 (2.6)	25.5 (3.6)	60.7 (4.3)
	***Mean*†**	**6.7 (0.1)^{A}**	**12.6 (2.0)^{A}**	1.6 (1.1)	**13.8 (1.3)^{A}**	**27.8 (1.6)^{C}**	**58.0 (1.9)^{A}**
***p*-value**	Site	**<0.001*****	**<0.001*****	0.4651	**<0.001*****	**<0.001*****	**<0.001*****
	Vegetation type	0.1882	0.1377	0.8782	0.4049	0.3323	0.3144
	S*V	**0. 0500***	**0.0232***	0.8836	0.6063	0.8716	0.3025

Abbreviations; C = carbon, N = nitrogen. † This mean gives aggregate effect of site. Within columns, means in bold and followed by different letters in superscript are significantly different at $p < 0.05$. Upper case letters indicate the differences based on site while lower case letters indicate differences based on vegetation type. Means were separated based on Tukey's honest significant difference (HSD) test. The *p*-values marked in bold are significant: * $p < 0.05$; *** $p < 0.0$.

Table 4. Arbuscular mycorrhiza fungi spore count and diversity as affected by site and vegetation type.

Site	Vegetation type	AMF genera									Total abundance	Species richness (*S*)	Shannon diversity index (*H′*)
		Acaulospora	*Ambispora*	*Diversispora*	*Enterophospora*	*Gigaspora*	*Glomus*	*Pacispora*	*Paraglomus*	*Scutellospora*			
Kubo South	Bushland	4.0 (2.7)	0.0 (0.0)	**2.7 (1.1)**^{b}	26.6 (12.0)	12.2 (4.5)	59.6 (17.4)	15.0 (8.5)	**4.3 (2.2)**^{b}	28.8 (9.4)	**153.2 (27.2)**^{b}	2.78	0.80
	Cropland	59.5 (28.1)	0.0 (0.0)	**21.8 (8.4)**^{a}	14.8 (5.8)	15.3 (6.4)	61.9 (18.5)	11.8 (5.8)	**23.6 (6.8)**^{a}	50.2 (17.6)	**258.9 (39.6)**^{a}	3.13	1.02
	Grassland	17.2 (10.5)	0.0 (0.0)	**4.5 (4.5)**^{b}	18.1 (8.8)	21.9 (13.6)	92.6 (56.7)	10.8 (6.9)	**7.3 (4.5)**^{b}	64.1 (37.1)	**236.5 (83.2)**^{ab}	3.60	1.06
	Shrubland	68.4 (37.7)	0.0 (0.0)	**1.1 (1.1)**^{b}	13.6 (10.0)	15.4 (10.0)	87.1 (32.8)	3.5 (3.5)	**0.0 (0.0)**^{b}	69.1 (22.4)	**258.2 (41.7)**^{a}	2.30	0.67
	Mean†	**37.3 (12.2)**^{B}	**0.0 (0.0)**^{B}	**7.5 (2.9)**^{B}	18.3 (5.3)	**16.2 (3.5)**^{B}	**75.3 (12.1)**^{B}	**10.3 (3.8)**^{A}	**8.8 (2.7)**^{B}	**53.0 (8.9)**^{A}	**226.7 (20.7)**^{B}	**2.95**^{A}	**0.89**^{A}
Muminji	Bushland	126.8 (56.2)	0.0 (0.0)	**41.2 (16.1)**^{b}	17.4 (15.4)	34.7 (14.9)	125.6 (45.6)	**4.6 (4.6)**^{b}	**46.4 (25.5)**^{ab}	75.5 (21.3)	472.1 (52.4)	**3.07**^{ab}	0.90
	Cropland	47.2 (15.3)	0.0 (0.0)	**13.3 (11.3)**^{c}	22.7 (22.7)	16.4 (7.7)	147.5 (22.5)	**0.0 (0.0)**^{b}	**11.9 (8.6)**^{b}	57.1 (17.5)	316.1 (32.2)	**2.92**^{ab}	0.88
	Grassland	0.0 (0.0)	0.0 (0.0)	**65.6 (1.5)**^{a}	0.0 (0.0)	34.2 (34.2)	167.4 (37.8)	**66.3 (1.7)**^{a}	**67.1 (1.9)**^{a}	0.0 (0.0)	400.6 (77.5)	**4.50**^{a}	1.41
	Shrubland	93.5 (41.0)	0.0 (0.0)	**18.5 (8.1)**^{c}	45.1 (24.2)	53.5 (22.3)	83.0 (32.1)	**11.1 (7.7)**^{b}	**12.8 (7.9)**^{b}	34.3 (13.6)	351.9 (45.9)	**2.38**^{b}	0.72
	Mean†	**66.9 (24.2)**^{A}	**0.0 (0.0)**^{B}	**34.7 (7.0)**^{A}	21.3 (11.6)	**34.7 (9.7)**^{A}	**130.9 (20.2)**^{A}	**20.5 (3.7)**^{A}	**34.6 (9.4)**^{A}	**41.7 (10.0)**^{A}	**385.2 (26.8)**^{A}	**3.21**^{A}	**0.97**^{A}
Thange	Bushland	10.7 (5.9)	1.5 (1.0)	0.0 (0.0)	10.4 (5.7)	3.1 (1.8)	23.9 (11.3)	**0.0 (0.0)**^{b}	10.7 (5.1)	16.7 (5.6)	76.9 (12.4)	2.50	**0.69**^{a}
	Cropland	4.6 (2.4)	2.1 (1.1)	1.4 (1.0)	4.2 (2.0)	2.6 (1.0)	34.8 (5.2)	**0.0 (0.0)**^{b}	1.4 (0.7)	11.9 (4.0)	62.9 (6.2)	2.21	**0.55**^{ab}
	Grassland	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	23.4 (19.9)	0.0 (0.0)	12.1 (12.1)	**9.0 (5.8)**^{a}	19.8 (19.8)	0.0 (0.0)	64.3 (8.1)	2.00	**0.45**^{ab}
	Shrubland	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	18.0 (11.4)	8.6 (8.6)	36.2 (29.5)	**0.0 (0.0)**^{b}	0.0 (0.0)	5.2 (5.2)	68.0 (21.7)	1.20	**0.14**^{b}
	Mean†	**3.8 (2.0)**^{C}	**0.9 (0.7)**^{A}	**0.3 (0.3)**^{C}	14.0 (2.5)	**3.6 (1.1)**^{C}	**26.8 (5.1)**^{C}	**2.3 (0.4)**^{B}	**7.5 (1.8)**^{B}	**8.5 (2.8)**^{B}	**67.9 (5.2)**^{C}	**1.98**^{B}	**0.46**^{B}
***p*-value**	Site	**<0.001*****	**0.0062****	**<0.001*****	0.1642	**<0.001*****	**<0.001*****	**0.0333***	**0.0186***	**<0.001*****	**<0.001*****	**0.0185***	**0.0011****
	Vegetation type	0.7218	0.7687	0.5445	0.6674	0.3784	0.7511	0.1407	0.1794	0.9458	0.9566	**0.0239***	**0.0471***
	S*V	0.2245	0. 8645	**0.0430***	0.7737	0.7215	0. 6245	**0.0061****	**0.0049***	0.0691	**0.0047****	0.7365	0.4882

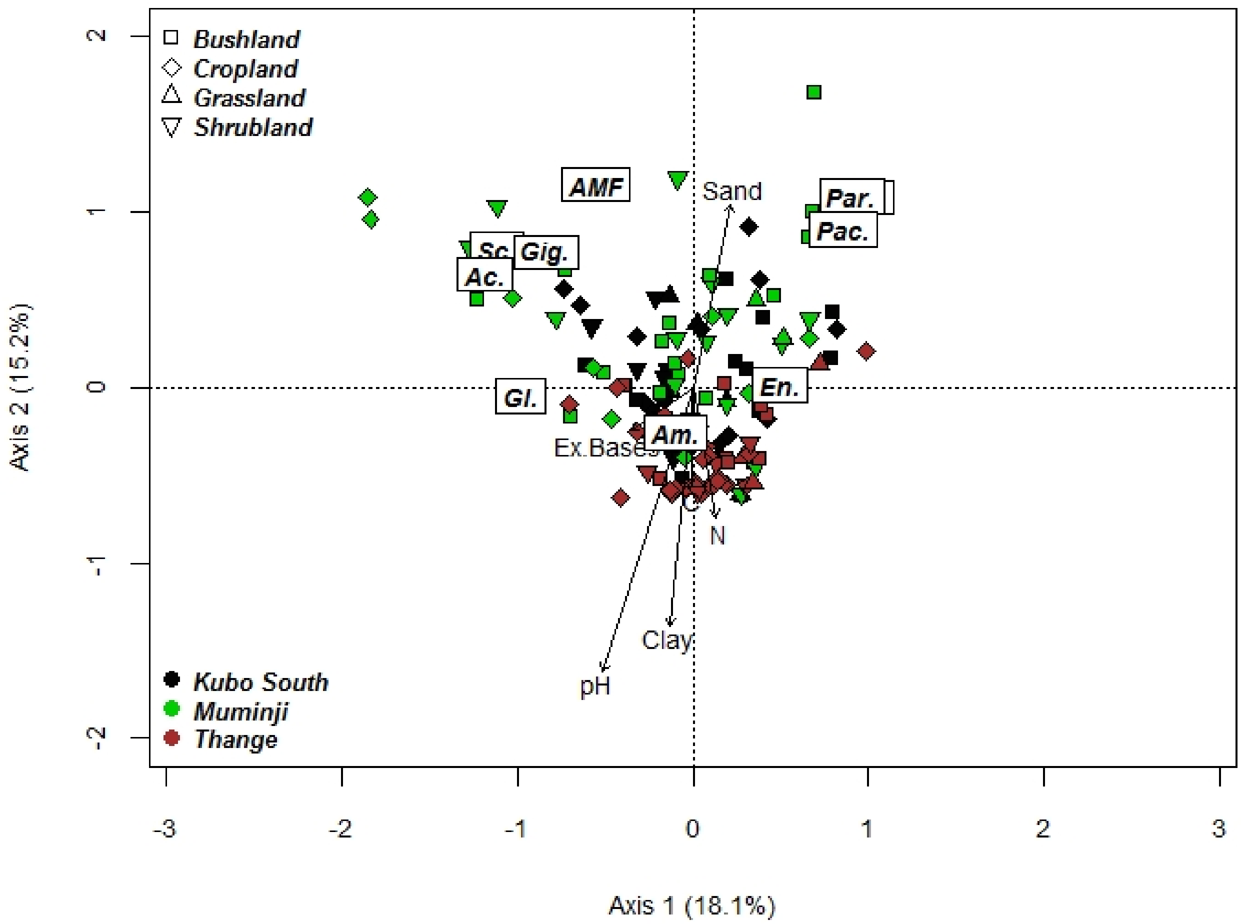

Figure 3. Redundancy Analysis (RDA) of AMF genera and soil chemical properties. Abbreviations for soil properties: C = carbon, N = nitrogen, Exc. bases = exchangeable bases. Abbreviations for AMF genera: *Ac.* = *Acaulospora*, *Am.* = *Ambispora*, *Dv.* = *Diversispora*, *En.* = *Enterospora*, *Gig.* = *Gigaspora*, *Gl.* = *Glomus*, *Pac.* = *Pacispora*, *Par.* = *Paraglomus*, *Sc.* = *Scutellospora*, AMF = Total spore count.

in Kubo South may have increased infiltration rate (and thus increased leaching of nutrients), and low retention of nutrients. It has also been demonstrated that sand content negatively affects soil properties like organic C by increasing decomposition rate of soil organic matter leading to low nutrient reserves in the soil. The results of this study are consistent with Gachimbi (2002) who reported varying soil chemical properties (pH, organic C, P, N and exchangeable bases) across agroecological zones in Embu and Mbeere Districts, showing that agro-ecological zones play an important role in determining overall soil properties. This is further supported by the findings by Falk (2021) who have reported differing soil hydrological properties attributed to inherent soil properties.

The presence of woody vegetation may also contribute to differences in soil properties across sites. Higher tree and shrub densities and tree diversity have been reported in Muminji and Kubo South compared to Thange (Winowiecki *et al.*, 2021). The high density and diversity of woody species may be attributed to better soil physical and chemical properties in Muminji owing to ecosystem services provided by trees and shrubs in conserving soil, constant addition of soil organic matter via litter input, reduced soil erosion and improved soil structure (Mohammad and Adam, 2010; Tongkaemkaew *et al.*, 2018; Kisaka *et al.*, 2023). It is reported that high tree diversity in ecosystems like natural forests lead to increased storage of soil C and N (Chen *et al.*, 2023; Cheruto *et al*., 2023). However, soil elements were lowest in Kubo South despite the high tree and shrub density (according to Winowiecki *et al.*, 2021). This disparity could be associated with tree species composition among the study sites where most of the tree species in Muminji and Thange were indigenous (e.g., *Gymnosporia buxifolia* (L.) Szyszyl., *Faurea saligna* Harv., *Commiphora spp*, *Combretum spp*, *Acacia tortillis* (Forssk.) Hayne, *Croton dichogamous* Pax) while those in Kubo South were mostly exotic woodlot species and fruit trees (e.g., *Casuarina equisetifolia* L., *Annona senegalennisis* Pers., *Margaritaria discoidea* (Baill.) G. L. Webster, *Psidium guajava* L., *Citrus sinensis* (L.) Osbeck) (Winowiecki *et al.*, 2021). Tree species composition affect the quality and quantity of litter input, soil microbial structure and activity and nutrient cycling processes which determine soil properties. For instance, Li *et al.* (2015) reported faster improvement of soil properties (soil N and microbial biomass and activity) where indigenous trees were planted compared to exotic ones. Vegetation type only had significant effect on soil pH in Muminji, and total C in Thange showing that vegetation may still impact soil properties across different agro-ecological zones. This may suggest that site characteristics and vegetation type interactively shape soil properties since the interaction between site and vegetation showed significant effect on some soil properties like pH and total C. The results of this study build upon other studies (e.g., White *et al.*, 2009; Fu *et al.*, 2010; Jansa *et al.*, 2014; Munnaf *et al.*, 2020) which have highlighted the importance of site characteristics in determining changes in soil properties.

Effects of site and vegetation type on AMF spore abundance and diversity

The general strong effect of site on arbuscular mycorrhiza fungi abundance, richness and diversity point out the greater importance of site on AMF community over vegetation type across different agroecological zones. For instance, altitude has been mentioned to significantly influence AMF abundance, where an increase in altitude lead to a decrease in the abundance of certain species (e.g., *Rhizophagus irregularis*) but an increase in others (e.g.,*Diversispora celata* and *Claroideoglomus claroideum*) (Jansa *et al.*, 2014). In this study, *Diversispora* was also abundant in Muminji site which is at a high altitude (1117.5 m) compared to Thange (919.5 m) and Kubo South (90.5 m). Climatic conditions could also be an important driving factor in AMF community dynamics. Rainfall which affects soil moisture may influence AMF colonization and mycelial growth due to AMF sensitivity to changes in soil water (Fu *et al.*, 2022; Zhou *et al.*, 2022). Rainfall could also indirectly influence AMF root colonization, sporulation, and abundance of certain species by indirectly affecting soil pH through leaching (Cheptoek *et al.*, 2021). Staddon and Jakobsen (2004) and Yang *et al.* (2011) have reported a decrease in AMF abundance with drought persistence, and an increase with increased precipitation. Kubo South and Muminji have higher mean annual rainfall compared to Thange, implying that these two sites may have higher soil moisture contributing to high abundance and diversity of AMF. Jansa *et al.* (2014) also reported that some of the variation in AMF community they found could be attributed to local climatic conditions such as rainfall and temperature. It has also been reported that temperature may affect plant-AMF associations through effect on plant primary production where increased temperature led to increased allocation of carbon to AMF due to increased biomass accumulation (Mohan *et al.*, 2014). Mean annual temperature in Kubo South (27.6° C) is relatively higher than in Muminji and Thange (average 24° C) which may imply an increased photosynthetic rate hence more resource allocation to AMF. However, the contribution of temperature to occurrence of AMF in our study seem to have been suppressed by other factors since lower abundance and richness were found in Kubo South than in Muminji where temperatures were a bit lower.

The different soil physico-chemical properties found across the study sites may have also contributed to the difference in AMF abundance and diversity since soil properties are reported to affect AMF community (Hossain and Sugiyama, 2011; Wang *et al.*, 2015; Dobo *et al.*, 2018). For instance, plants growing in soil sufficient in nutrients may not invest their carbon and other resources to symbiotic associations hence negatively affecting growth and activities of such symbionts (Smith *et al.*, 2011; Cheruto *et al*., 2023). Soils in Thange had higher soil chemical properties hence high nutrient availability for plants, and reduced reliance on AMF for the same resources which may partly explain the low abundance and diversity of AMF in this site. However, we cannot also rule out the possibility of soil moisture being a driving factor for the lower abundance in Thange. This is because Thange receives low amounts of rainfall which is poorly distributed within and between the seasons. Soil pH was negatively correlated with some of the AMF genera (e.g., *Glomus* in grassland, *Acaulospora*, *Pacispora* and *Scutellospora* in cropland, *Diversispora*, *Gigaspora* and *Paraglomus* in bushland) showing that AMF may flourish in low pH soils than in high pH. This could partly be an indirect effect of soil pH in reducing availability of soil nutrients like phosphorus (P) through adsorption with soil minerals especially aluminium and iron (Cheptoek *et al.*, 2021), thus favoring growth and development of AMF. The significant effect that vegetation type had on AMF taxonomic richness and diversity underpins the role of vegetation in AMF community composition across agroecological zones. The positive correlation between sand content and AMF genera such as *Acaulospora*, *Glomus*, *Paraglomus*, and *Scutellospora* as well as total abundance, richness and diversity parameters may suggest that majority of AMF species thrive in sandy soil. However, high clay content may inhibit growth of AMF as indicated by the negative correlation coefficients for clay. This is further supported by the overall high abundance of AMF in Kubo South with sandy soil compared to Thange which had highly clayey soil. The dominance of the

Glomus genus in all three sites aligns with previous studies (Campos *et al.*, 2018; Dobo *et al.*, 2018; Cheruto *et al.*, 2023). *Glomus'* prevalence and widespread association with various plant species highlights its importance in AMF communities and ecosystem functioning (Smith and Read, 2008). Furthermore, the differences in AMF genera distribution among sites and vegetation types highlight the importance of understanding the ecological preferences of specific AMF taxa and their preferential association with certain plant species (Yang *et al.*, 2011; Verbruggen *et al.*, 2012; Zobel and Öpik 2014; Wang *et al.*, 2020). Local environmental conditions defined by site differences may be critical in shaping AMF community as it has been suggested by other studies (e.g., Hossain and Sugiyama, 2011; Zhou *et al.*, 2022), and as shown by the significant effect of site in this study.

CONCLUSION

The findings of this study underscore the significance of soil properties, such as pH, in shaping AMF populations and their symbiotic associations with plants. Moreover, the study highlights the variability in AMF responses to different environmental conditions, indicating the adaptability and functional diversity of AMF species. These findings contribute to our understanding of plant-microbe interactions which may have implications for sustainable land management practices aimed at enhancing nutrient cycling and plant productivity. Further research is warranted to elucidate the underlying mechanisms driving the observed patterns and to explore the ecological implications of AMF community dynamics in different ecosystems.

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Author contribution statement (CRediT). L. Mwangi – Conceptualization, writing- original draft, formal analysis; **L.-A. Winowiecki** – Conceptualization, supervision, writing – review and editing, Funding acquisition; **D. Lelei** – Conceptualization, supervision, writing-review and editing; **S. Kamau** and **T.-G. Vågen** – Formal analysis, writing -original draft; **G. Cheruto** – Formal analysis, Writing - review and editing.

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