PHOSPHORUS FRACTIONS AND ARBUSCULAR MYCORRHIZAL FUNGI AS INFLUENCED BY FOREST CONVERSION INTO OTHER LAND USE TYPES ON PLANOSOLS IN NYANDARUA COUNTY

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DECLARATION

This thesis is my original work and has not been submitted for award of a degree in any other University.

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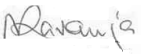
Signature: ....  Date: ...16/08/2023.....

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DEDICATION

I dedicate this work to my family who have been understanding, patient, loving and caring through this journey to its completion. To friends who extended their support, guidance and encouragement to the success of this work.

To the Department of Land Resource Management and Agricultural Technology (LARMAT), Faculty of Agriculture, University of Nairobi for training and mentorship.

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LIST OF ABBREVIATIONS AND ACRONYMS

AMF	Arbuscular mycorrhizal fungi
CAN	Calcium Ammonium Nitrate
CAVS	College of Agriculture and Veterinary Sciences
CFA	Community Forest Association
DAP	Di-ammonium Phosphate
HCL-P	Phosphorus extracted by dilute hydrochloric acid
ICRAF	International Centre for Research in Agroforestry
KEFRI	Kenya Forestry Research Institute
KFS	Kenya Forest Service
KNBS	Kenya National Bureau of Statistics
$NaHCO_3$-P	Phosphorus extracted by dilute sodium bicarbonate
NaOH-P	Phosphorus extracted by dilute sodium hydroxide
P	Phosphorus
P_i	Inorganic phosphorus
P_o	Organic phosphorus
PELIS	Plantation Establishment and Livelihood Improvement Scheme
Resin-P	Phosphorus extracted by resin strips
SOC	Soil organic carbon
SOM	Soil organic matter

ABSTRACT

Land-use conversion from natural forest to agriculture alter above and belowground biodiversity and soil properties due to reduced organic matter inputs and increased loss of topsoil through soil erosion. A study was conducted to determine the effects of forest conversion to other land uses on soil chemical properties, P fractions distribution, abundance and diversity of AMF on Planosols in South Kinangop Sub-County, Nyandarua County. Four land use types including natural forest, cypress plantation, grazed pasture and cultivated potato field were selected with natural forest considered as the reference point. Soil and plant litter samples were randomly collected from three transects and were analyzed for chemical properties (pH, organic C, total N, P, Ca, Mg, K, CEC and lignin content), Hedley P fractions and quantification of AMF spore abundance, diversity and richness and root samples for root colonization. Soil and plant data were analyzed using generalized linear models (GLMs) while spore abundance and root colonization were analyzed using generalized linear mixed models (GLMMs). AMF diversity and richness was determined using Shannon diversity and taxonomic richness indices, respectively. Whenever significant effects for land use type was observed, Tukey's Honest Significance Difference (HSD) test was used to separate means at α=0.05. All data was analyzed using R statistical software version 4.0.4.

Results showed that land use type had significant effect on all soil chemical properties. Soil pH was higher in natural forest (4.9), while potato fields had relatively acidic soils (3.8). Similarly, total C, N, Mg and Ca were significantly higher in natural forest compared to other land use types. Readily and moderately labile P were highest in potato growing fields (125.1 mg and 186.1 mg kg^{-1}, respectively) and lowest in cypress forest (36.4 mg and 82.7 mg kg^{-1}, respectively). However, non-labile P was highest in natural forest (690.1 mg kg^{-1}) and lowest in cypress forest (324.5 mg kg^{-1}). AMF spore abundance, diversity and richness and root colonization did not differ among land use types. AMF genera showed weak to strong or no correlation with soil chemical properties and P fractions. *Acaulospora* had a negative association with resin Pi, sonicate NaOH-P_o and NaHCO3-P_o (p<0.05). *Glomus* was positively correlated with exchangeable K and residual P (p<0.05) whereas *Funneliformis* had a positive correlation with exchangeable K (p<0.01), total N, sonicate NaOH-P_o and HCL-P_i (p<0.05). *Paraglomus* had a positive correlation with soil pH, exchangeable K, Ca, CEC (p<0.05), NaHCO3-P_o (p<0.05), resin P_i, $NaHCO_3$-P_i, NaOH-P_i,

sonicate NaOH-P_i, HCL-P_i and residual P (p<0.01) but was negatively correlated with sonicate NaOH-P_o (p<0.001). *Scutellospora* was positively correlated with soil total N (p<0.01) while *Enterophospora* and *Archaeospora* were positively associated with residual P (p<0.01) and NaHCO3-P_i (p<0.05), respectively. The study demonstrate that converting natural forest for other land uses may lead to alteration of soil properties and soil biodiversity with implications in nutrient availability and that soil fertility may not be maintained by other land use types.

CHAPTER ONE: INTRODUCTION

1.1 Background information

Forest conversion for agricultural production degrades soil by changing soil physicochemical and biological properties (Iwashima *et al.*, 2012; Tolimir *et al.*, 2020). The conversion is often caused by the need for more productive arable land due to increasing human population pressure and reduction in crop productivity as soil fertility declines (Benhin, 2006; Pinho *et al.*, 2012). Cultivated area rose by 500% globally within the last 5 decades, with Africa continuing to convert forests for agricultural production and other land uses (Banerjee *et al.*, 2019). Although land use intensification increases agricultural production, the negative effects on soil biodiversity and soil fertility cannot be ignored (de Graaff *et al.*, 2019; Wittwer *et al.*, 2017). Intensification could also cause loss of soil organic matter which is key driver in nutrient cycling, a collapse in soil structure and a reduction in soil microbial activity (Qiong *et al.*, 2008). A reduction in soil organic matter content weakens the capacity of soils to retain nutrients (Gatiboni *et al.*, 2017).

Soil P is considered to be the second most limiting nutrient after N and is highly unstable and easily fixed especially in acidic tropical soils. P is found both in organic and inorganic forms and differ in their availability, behavior and how they are transformed (Betencourt *et al.*, 2012). Organic P constitute a fairly large proportion of the total P in soil and exist in stable forms such as phosphonates and inositol phosphates and in active forms such as organic polyphosphates and orthophosphates. It is derived from decaying animal and plant materials including soil organisms hence organic P is more concentrated on the upper soil horizons (Condron *et al.*, 2005; Nash *et al.*, 2014). The organic P is converted to inorganic P through mineralization of the decomposed organic matter which is facilitated by soil microorganisms and the activity of plant roots (Srinivasan *et al.*, 2012). On the other hand, inorganic P is found in soluble forms as $HPO4^{2-}$ and $H_2PO_4^-$ in the soil solution and as insoluble precipitates bound to Al and Fe oxides and hydroxides or Ca and organic matter through adsorption and precipitation processes that are chemically mediated (Sato, 2003). How P behaves in the soil is influenced by soil properties such as moisture content, pH and clay content (Richardson *et al.*, 2009). P from primary sources (apatites) is released slowly into the soil solution through weathering, and the dissolution of P derived from secondary minerals (Al-, Fe- and Ca-P) may be fast or slow depending on soil pH and the size of mineral particles. For example,

increased soil pH increases dissolution of AL and Fe bound P and at pH above 8 causes Ca-P to solubilize thus releasing inorganic P into the soil solution (Shen *et al.*, 2011). However, this soluble inorganic P can be converted back to insoluble form through adsorption onto the secondary minerals and to organic P through microbial immobilization; all these constituting labile P pool. Furthermore, this labile P may be dissolved back to the soil solution or converted to more stable forms as non-labile P fraction including Ca-P and residual P (Muindi, 2019). Since P availability is strongly dependent on soil conditions, any alteration caused by land use change would significantly influence P transformation and distribution within the solution-solid P phase (Bayuelo-Jiménez *et al.*, 2020; Zhu *et al.*, 2021). This P redistribution, as a consequence of land use change, is said to take place within a shorter period of time (<50 years) which is much faster than thousands of years under natural conditions as suggested by researchers (De Schrijver *et al.*, 2012; Garcia-Montiel *et al.*, 2000; Saltali *et al.*, 2007). Use of sufficient fertilizer application may increase readily available P pool immediately after application but this may not be sustainable as more of P end up being fixed or lost through soil erosion and harvested crop (Negassa and Leinweber, 2009). Accelerated soil erosion because of insufficient crop cover, loss of organic matter and continuous nutrient mining via crop harvests without sufficient nutrient replenishment may exacerbate the loss of the only available P fraction, but also those fractions that are sparingly and non-available such as Fe and Ca phosphates and residual P (Maranguit *et al.*, 2017; Sanyal and De Datta, 1991). Other factors such as soil pH and which are sensitive to land-use change do influence P dynamics in the soil (Tanganelli, 2011; Zhu *et al.*, 2021).

Soil biodiversity is critical in nutrient cycling and availability and ecosystem functioning but is affected by land-use change (Jefwa *et al.*, 2012). Soil microorganisms such as arbuscular mycorrhizal fungi (AMF) constitute beneficial associations with plants in enhancing nutrient acquisition, and improve resistance against pathogens (Begum *et al.*, 2019; Campos *et al.*, 2018; Chandrasekeran and Mahalingam, 2014). Undisturbed natural forests are expected to have high AMF species richness and diversity compared to other land uses (Bainard *et al.*, 2011; Jefwa *et al.*, 2009). On the other hand, forest plantations show low colonization and diversity of AMF due to altered soil chemical properties contributed by litter inputs that mostly cause soil acidification and are nutrient-poor, and the presence of ectomycorrhizal-tree species (Moora *et al.*, 2014). Conversion of forests into croplands, pastures and other intensive farming practices may reduce

AMF diversity and root colonization (Faggioli *et al.*, 2019; Muchane *et al.*, 2012). The decline in AMF abundance and diversity in croplands could be linked to frequent soil disturbance, low plant diversity, changes in soil physicochemical properties and use of chemical fertilizers which suppress AMF development (Belay *et al.*, 2015; Dobo *et al.*, 2018). While there are several results, though contrasting, reported on the effects of land-use change on AMF, data on the impact of systematic change from natural forests to various land-use types especially in Africa is still limited (van der Heyde *et al.*, 2017). Therefore, the study aimed to assess the effect of land-use change on the abundance and diversity of AMF and soil P fractions.

1.2 Statement of the problem

Forest conversion for agricultural production is often carried out in search of productive land to increase agricultural productivity due to declining land productivity as a result of degradation and increasing human population growth and consequently increasing demand for food and other products. However, forest clearing lead to considerable changes in soil physicochemical properties and microbial structure as a result of changes in soil and plant structure and composition (Jefwa et al., 2012; Soka and Ritchie, 2018). Trees play a key role in soil conservation and nutrient cycling through constant organic matter addition, soil erosion control and maintenance of other soil properties hence contribute to productivity of soil (Benhin, 2006, Veldkamp *et al.*, 2020). Excluding integration of trees, which is common, in agricultural practice in crop cultivation and livestock production deprive agroecosystems of ecosystem services provided by trees such as maintenance of soil fertility and health. Most agricultural practices such as continuous monocropping, minimal crop residue incorporation into the soil, tillage operations and excessive use of agrochemicals progressively lead to degradation of soil, and consequently decline in agricultural productivity (Qiong et al., 2008; Maranguit et al., 2017). Therefore, it is crucial to prioritize maintenance of soil fertility and health if high agricultural productivity in regard to both production of crops and livestock is to be achieved and sustained. Unfortunately, there is still inadequacy in studies exploring how land use change from natural forests to croplands and pastures affect soil nutrient availability and biodiversity especially with regards to phosphorus availability and diversity of AMF. Therefore, there is need to continue evaluation of soil fertility and health under these common land uses looking at important indicators such as nutrient availability and diversity and abundance of beneficial soil microbes such as AMF. This study aimed at establishing

the effects of forest conversion into cultivated croplands, grazed pastures and forest plantation on soil P fractions and the abundance and diversity of AMF.

1.3 Justification

Sustainable land use and management is required to ensure and maintain high agricultural productivity which is crucial for majority of population who depend largely on agriculture as source of livelihood, and since agriculture is the backbone of Kenya's economy. It is widely reported in Kenya that decline in soil fertility is one of the constraints limiting crop production due to continuous utilization of soil without sufficient efforts to restore soil fertility and health. Despite the fact that soil fertility decline is known, there are still setbacks in adoption of soil conservation measures and sustainable land management practices among farmers yet soil conservation play a key role in agricultural productivity. Soil conservation in agricultural production should be prioritized especially in this era of climate change to ensure high productivity and build resilience of communities against extremes of climate change. Therefore, quantifying the effects of land use type on soil chemical properties, P distribution and soil biodiversity generates data required to identify whether agricultural land uses maintain and conserve soil fertility. The output of this study will provide information which will be valuable in identifying technologies and management practices when designing soil conservation and fertility programmes.

1.4 Objectives

1.4.1 Main objective

Demonstrate the effects of converting natural forests to selected land use systems on arbuscular mycorrhizal fungi (AMF) and soil P availability.

1.4.2 Specific objectives

1. Characterize soil and plant litter under selected land use types.
2. Evaluate effects of forest conversion on soil P fractions.
3. Evaluate effects of forest conversion on abundance and diversity of AMF.

1.5 Hypotheses

1. Soil and plant litter properties from selected land use types are similar.
2. Removal of natural forest does not affect soil P fractions.
3. Converting natural forest to agriculture does not influence the abundance and diversity of AMF.

CHAPTER TWO: LITERATURE REVIEW

2.1 Influence of forest conversion on soil properties

Forests are indispensable in soil conservation and maintenance of soil fertility particularly in tropical areas where highly weathered and low pH soils are prevalent (Benhin, 2006). Forests regulate soil moisture and temperature and promote efficient nutrient cycling partly through maintained organic matter inputs, which is uncharacteristic of agricultural ecosystems (Veldkamp *et al.*, 2020). Clearing forests to agricultural fields induces change in soil properties that is more pronounced in upper soil horizons and less significant in deeper soil layers (McGrath *et al.*, 2001), and thus may create soils that are functionally different (Scott and Messina, 2010). Change in soil properties is suggested to be among factors affecting soil organic matter loss and subsequently leading to loss of soil nutrients. This is because the soil is more exposed to higher temperatures especially between crop harvest and the next planting season where the soil is left bare thus accelerating decomposition of organic matter (Groppo *et al.*, 2015). In addition, alteration of soil properties could also be partly associated with changes in the amount and quality of organic matter inputs that not only affect composition of soil microbes but also nutrient availability (Kunlanit *et al.*, 2020; Tolimir *et al.*, 2020; Zhu *et al.*, 2021). For example, litter from broadleaved vegetation contains high amounts of nitrogen, phosphorus, potassium and calcium compared to coniferous litter with low nutrient content and high recalcitrant compounds (resin, lignin) leading to varying rates of nutrient release and availability. This will influence soil chemical properties as varying litter nutrient concentration will dictate nutrient content in the soil, turn-over rates, soil pH and base saturation. The type of litter could also determine what soil microorganisms dominate in that specific site; where soil bacteria dominate in broadleaved vegetation and fungi in coniferous (Iwashima *et al.*, 2012). Forestland conversion to agricultural land was reported to cause considerable reduction in soil organic carbon and total nitrogen (Awoonor *et al.*, 2022; Demessie *et al.*, 2013; Jafarian and Kavian, 2013; Were *et al.*, 2015; Yang *et al.*, 2009). Soil C losses occur rapidly at the initial stages of forest conversion (< 10 years) and eventually level off afterwards (> 50 years) and these losses are more pronounced in the topsoil layer (0 – 10 cm) (Murty *et al.*, 2002; Wei *et al.*, 2014). In addition, Wei et al. (2014) reported that after forest conversion, soil C and N dynamics are dominated by losses in C and N derived from the forest and that these losses are offset partially by C and N derived from crops. Similar pattern in soil nutrients decline have also

been found in conversion of natural vegetation to crop-livestock integrated systems (Groppo *et al.*, 2015; Verchot, 2010). Nonetheless, exchangeable K increases significantly and remains higher in croplands after forest conversion due to enhanced weathering of soil as a result of tillage (Chimdi *et al.*, 2014; Pulido *et al.*, 2021; Weldmichael *et al.*, 2021). The decline in soil organic matter (SOM) plays a big part in collapse of soil structure and thus a reduction in soil water availability, infiltration and hydraulic conductivity (Davari *et al.*, 2020). Nonetheless, the decrease or increase in SOM depends on management practices, type of pasture grown and the initial C content in pastures (Desjardins *et al.*, 2004). Schwendenmann and Pendall (2006) also attribute changes in soil properties in pastures established on a cleared forestland to the presence of management practices such as grazing. Different pathways by which soil organic C is replenished after forest conversion to grasslands and croplands explain differences in SOC dynamics (Don *et al.*, 2011), and thus changes in SOC depends on the new vegetation rather than the initial vegetation and its age (Eclesia *et al.*, 2012). In general, soil type, initial soil nutrient contents, changes in soil microbial community, litter properties and farming practices are suggested to drive changes observed in soil properties following forest conversion (Zajícová and Chuman, 2019). Plantation forests show lower concentrations of soil nutrients compared to grasslands or pastures (Chen *et al.*, 2000). Differences in decomposition rate of forest floor litter between pine and oak stands have been found and have been linked to differences in litter nutrient concentrations and soil microclimate regimes (Scott and Messina, 2010). Soil bulk density and porosity increases and decreases respectively after land use change owing to reduced SOM content and soil compaction arising from tillage. Soil water infiltration and hydraulic conductivity also reduces with forest conversion (Evrendilek *et al.*, 2004; Owuor *et al.*, 2018).

Soil microbial community and animals are significantly affected by shifts in land use and their response to these perturbations may not be similar to that of above-ground biodiversity. Forest conversion causes significant effects on soil microbes as well as on their attributes such as biomass, abundance, species richness and diversity (Wang *et al.*, 2021). For instance, biomass and abundance of soil macrofauna are more likely to be maintained when forests are converted to pasture than to agricultural land while soil microbes show an opposite pattern (Franco *et al.*, 2019). AMF possessing some host preference may suffer adversely from changes in plant composition and diversity associated with forest conversion leading to the loss or decline of certain species

(Faggioli *et al.*, 2019; Jefwa *et al.*, 2009). Forest conversion to pasture or croplands could cause a shift in the structure of soil microbial community with increase in diversity of certain taxa and concurrent decrease in others (Ranjan *et al.*, 2015). On the other hand, planted forests, particularly those established with conifers, have lower soil microbial activity and this is due to changes in the quality and amount of litter inputs and reduced soil pH (Chen *et al.*, 2000). The implication of a decrease in soil biological indicator parameters would be a decline in soil fertility. Nonetheless, soil biota may not show significant changes following forest conversion and thus are thought to be more resilient but it is not certain to what period of time would soil biota maintain such adaptive response. Therefore, unique soil properties characterizing different land use types are deemed important in shaping the response of soil microbial populations to forest conversions (Alele *et al.*, 2014). Thus, soil degradation following forest conversion into agricultural lands happens at different magnitudes which is attributed to inherent soil properties such as water holding capacity, and ability to accumulate and retain nutrients that cushion soils against such changes (Leminih *et al.*, 2005).

2.2 Soil management under potato cropping systems in Kenya

Potato is an important food crop as source of livelihood to most of the communities where the crop is dominant. Potato is mostly grown in the highland areas of Mt. Kenya in Embu, Meru, Kirinyaga and Laikipia; Aberdare range in Nyandarua, Nyeri, Kiambu and Muranga; Mau escarpment in Mau Narok, Nakuru and Molo; Mt. Elgon in Keiyo and Marakwet; Nandi escarpment in Tinderet, Cherangani hills and Taita Taveta region (Kaguongo *et al.*, 2008). Potato production in Kenya averages between 8-15 tons/ha which is below expected yield of 40 tons/ha (Mugo *et al.*, 2020). Poor yield has been associated with diseases, inappropriate fertilizer use, cropping systems and poor soil management practices among other factors (Muthoni and Nyamongo, 2009). Poor soil fertility management contributes significantly to this yield gap and is mostly associated with insufficient nutrient supply as farmers apply inorganic fertilizers below the recommended rate. The prevalent soil nutrient mining also contribute to the declining soil fertility especially with cultivation of high nutrient demanding crops like potato (Schulte-Geldermann, 2013). It has been reported that most nutrients are below critical nutrient levels for optimum plant growth in Nyandarua and Meru, some of the main potato growing areas and that these areas exhibit low soil fertility (Mugo *et al.*, 2020). To maintain nutrient supply to potato, most farmers apply inorganic

fertilizers (mainly DAP) to meet potato nutrient requirements. Some use organic amendments such as animal manure and composts to replenish soils (Kibunja *et al.*, 2017). However, long-term use of DAP is associated with lowering soil pH, and increased acidity limit availability of nutrients such as N, P, K, Ca, Mg while increases others like Fe, Bo and Al in soil (Janessens *et al.*, 2013; Muthoni, 2016). Similarly, continuous cultivation without longer fallow period between growing seasons also cause depletion of soil nutrients such as K (Mugo *et al.*, 2020). Although crop rotation is practiced among potato growing farmers, this is done less frequently due to small sized farms cultivated and also because potato is the main food and cash crop among those cultivating (Janessens *et al.*, 2013). As a result, potato is continuously grown on the same land for most of the seasons and thus this may prove unsustainable in maintaining soil fertility. Potato agronomic practices such as hilling may promote favorable soil conditions such as soil temperature, infiltration and water retention capacity for better crop growth but could also cause loss of soil and fluctuations in soil moisture (Nyawade *et al.*, 2018). In addition, potato does not provide enough ground cover and accumulates less residue on the soil surface thus render soils more exposed to erosion and increased heating (Nyawade, 2015). Therefore, most soils under potato production are not sustainably managed with regards to maintenance of soil fertility.

2.3 Arbuscular mycorrhizal fungi

2.3.1 Biology and distribution of arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi is the most widespread and abundant group of fungi that establishes symbiotic relationship with most terrestrial plants including agricultural crops (Chandrasekeran and Mahalingam, 2014). The fungus belongs to phylum Mucoromycota subphylum Glomeromycotina (Friberg, 2001). AMF are obligate in nature and live in the soil as spores, fragments of infected root and hyphae and in the plant root in form of arbuscules, vesicules and hyphae. The infective bodies are specifically developed for symbiotic relationship and cannot be formed by free living fungi (Tikhonovich and Provorov, 2007). AM are able to colonize different plants through their hyphal networks thus affecting more than a single plant species (Lee *et al.*, 2013). AMF infects the host plant when the spores germinate, grow and develop hyphae that extends towards the root, attach and penetrate through the root cells forming an interface for the exchange of materials between the fungus and the plant (Carbonnel and Gutjahr, 2014; Kim *et al.*, 2017). The growth of hyphae and infection on plant roots are stimulated by production of signaling

compounds such as strigolactones by plants and subsequently the fungus releases lipochito-oligosaccharides both of which initiates symbiosis (Chen *et al.*, 2018; Konieczny and Kowalska, 2017). AMF are widely distributed and found in various terrestrial ecosystems from temperate to tropical regions including forests, grasslands, swamps, dry lands, high as well as low elevation areas and in agricultural ecosystems (Kehri *et al.*, 2018).

2.3.2 Importance of AMF in plant growth and nutrient cycling

AMF are important in plant growth, nutrition and health, and protection from other environmental stresses (Chu *et al.*, 2020; Faggioli *et al.*, 2019; Taoheed *et al.*, 2018). Since plants have poor rate of P recovery (about 10-20%) from applied P fertilizers, AMF can improve this P recovery by enabling plants via the extensive mycelial network to explore more soil volume leading to additional mining for nutrients (Begum *et al.*, 2019; Campos *et al.*, 2018; Hinsinger *et al.*, 2011; Li *et al.*, 2022). AMF benefits the host plant through increasing access to nutrients and water while the AMF benefits from the energy supplied (Saharan *et al.*, 2018). AMF produce siderophores which help to mobilize P bound to metal oxides like Fe through chelation and hydrolyzing enzymes via the hyphae which releases P from organic sources as they compete with decomposers leading to increased P availability (Jansa *et al.*, 2013; Rosling *et al.*, 2016; Sanyal and De Datta, 1991). Similarly, potato colonized by AMF express StPT3 inorganic P transporter that is responsible for translocation of inorganic P from the fungus to the plant cells (Igiehon and Babalola, 2017; Johri *et al.*, 2015; Pepe *et al.*, 2020; Yang *et al.*, 2020). AMF also help in protecting host plants against root diseases and pathogens such as nematodes (Jefwa *et al.*, 2009; Lee *et al.*, 2013). This enhanced defense is attributed to improved plant health from better nutrition and acquired and induced resistance from AMF which strengthens the plant's self-protection against pathogens. AMF also enhances plant's protection through competing with other soil microbes for resources and releasing antimicrobial compounds in the rhizosphere that repel other soil microorganisms (Chen *et al.*, 2018; Delavaux *et al.*, 2017; Thirkell *et al.*, 2017). AMF can also limit plant growth when the fungus' demand for energy exceeds P supply to the host plant (Johri *et al.*, 2015). It is also possible for AMF to accumulate nutrients (especially P) to itself to the detriment of the plant when there is no benefit to the fungus or when the host plant reduces carbon supply to the fungus upon increased availability of nutrients (Hammer *et al.*, 2011). AMF also mediates nutrient cycling through their influence on the composition of other soil microorganisms particularly soil bacteria which are

thought to conduct mineralization of organic matter rather than AMF themselves (Banerjee *et al.*, 2019; Verchot, 2010). AMF also influence C cycle as increased carbon supply from host plant to the fungus leads to increased C flow to the soil. Furthermore, AMF produce glomalin which help in C storage in the soil, a proportion that exceeds that from microbial biomass (Frey, 2019; Syibli *et al.*, 2013). AMF also influence soil structure by improving soil aggregation through the extensive branching of mycelia and production of aggregate-binding glomalin thus providing better aeration and root growth (Powell and Rilling, 2018).

2.3.3 Response of arbuscular mycorrhizal fungi to forest conversion to other land use types

Diversity of AMF is partly influenced by plant community structure, soil properties and climatic factors, and root colonization by plant species (Sankaralingam *et al.*, 2016; Su and Guo, 2007; Zhang *et al.*, 2021). Soil chemical properties such as available phosphorus significantly influence the development and efficacy of AMF (Campos *et al.*, 2018). Higher plant tissue P by the virtue of increased available P in the soil suppresses AMF root colonization (Carbonnel and Gutjahr, 2014; Ratti *et al.*, 2001; Richardson *et al.*, 2009). This is because increased assimilation of P in the plant tissue leads to structural and physiological changes in the roots, which cause reduction of carbon flow to the roots for AMF nutrition as well as reduction of signal secretions that usually promote growth of hyphae. As a consequent, the colonizing fungus is starved of energy retarding hyphal growth and spore production (Sharma *et al.*, 2013). In contrast, low plant tissue P content encourages release of photosynthates to the roots stimulating root colonization and sporulation (Grant *et al.*, 2005). The percent root length colonized positively correlates with plant tissue P content (Treseder, 2013). Under irrigation systems AMF can still maintain its role in plant P and N uptake at high and low soil P concentration (Begum *et al.*, 2019).

Basically, land-use change produces a disturbance factor in the soil as well as in plant species composition, and the magnitude of this disturbance determines AMF responses (Chandrasekeran and Mahalingam, 2014; Soka and Ritchie, 2018). How mycorrhizal fungi germinate and respond to disturbance indicate their vulnerability, for instance, *Gigasporaceae spp* germinate from hyphal fragments rather than spores unlike most fungal species hence would be highly vulnerable to mechanical soil disturbance like plowing. On the other hand, high sporulation in some species such as *Glomus spp* depicts high disturbance rate (Jefwa *et al.*, 2009). Among forest ecosystems,

contrarily to indigenous forests, planted forests show lower AMF abundance and diversity caused by differences in predominant tree species and management activities. For instance, coniferous forests show low AMF richness due to lower soil pH caused by litter acidification and allelopathy, which reduces the amount of substrate available for AMF (Moora *et al.*, 2014). Similarly, forest management activities such as logging affect the structure of soil microbial communities (Mafaziya and Madawala, 2015). Grasslands, on the other hand, support higher diversity of AMF than croplands. However, management activities like grazing may interfere with species composition due to changes in the structure of plant community (Soka and Ritchie, 2018). Intense grazing decreases the ability of grassland to sequester carbon translating to low carbon flow and availability for AMF and other soil microorganisms. Disturbances may improve AMF diversity and species richness (Garcia de Leon *et al.*, 2018). Cultivated fields exhibit low diversity of AMF due to high management intensity from agronomic practices such as tillage, inorganic fertilizer use and other agrochemicals and crop harvesting (Jefwa *et al.*, 2012; Stover *et al.*, 2012). For instance, inorganic P fertilizer application by increasing plant tissue P reduces spore production and growth of external hyphae (Banerjee *et al.*, 2019; Johri *et al.*, 2015). However, in the long-term, P fertilizer use may not affect the abundance of AMF although it may reduce their spore numbers and root colonization (Grant *et al.*, 2005). Despite agricultural lands showing lower AMF abundance, differences still exist in AMF dynamics as a function of land use intensity. Subsistence farming (low input), for instance, maintain higher abundance of AMF compared with commercial farming (high input system and continuous cropping) (Muchane *et al.*, 2012). Cultivation of potato (*Solanum tuberosum* L.), common in Kenyan highlands, leads to a decline in soil fertility and lower soil pH due to continuous soil disturbance and reduced crop residue return to the soil, with possible effects on soil microbial community (Muthoni *et al.*, 2017). Diversification of cropping systems via intercropping and pasture-enrichment may mitigate the negative impact of agricultural intensification on AMF diversity (Belay *et al.*, 2015; Glaze-Corcoran *et al.*, 2020). Legume intercropping, for instance, influences rhizospheric soil pH by root exudation coupled with N fixation and uptake thus affecting mycorrhizal fungal activities (Hinsinger *et al.*, 2011; Qin *et al.*, 2017; Stomph *et al.*, 2020). Root exudates also act as communication signals stimulating growth of soil microbes and their activities (Campos *et al.*, 2018; Rochange, 2010). Increased soil microbial activities under intercropping systems is attributed to higher plant diversity and consequent higher inputs of organic matter (Bainard *et al.*, 2011).

2.4 Influence of land use type on distribution of soil phosphorus fractions

Phosphorus is one of the limiting nutrients in the soil (Solomon *et al.*, 2002) and it is involved in biochemical processes such as root development, photosynthesis, energy transfer and nitrogen fixation (Ryan *et al.*, 2012). It is found in inorganic and organic forms in the soil, and although it may be in large quantities, plants can only access a smaller fraction in inorganic form (Betencourt *et al.*, 2012). Soil organic P constitute almost half of the total P in the soil and it decreases with increasing soil depth. Phosphorus in this form is mostly influenced by soil pH, cultivation practices and soil drainage (Sanyal and De Datta, 1991). Mineralization and immobilization are the primary processes that determine soil organic P turn-over. In grazed pastures, an estimated 60 – 95 % of P assimilated by plants is returned to soil in form of root residues and litter or animal excreta which is higher than 18 – 38 % of P recycled in croplands (Condron *et al.*, 2005). Availability of P is influenced by soil physicochemical properties such as organic matter, pH, clay and presence of binding metal ions (Al, Fe, Ca) (Richardson *et al.*, 2009). For instance, P binds with Al and Fe ions at low soil pH and precipitates out with Ca at high pH (Bayuelo-Jiménez *et al.*, 2020). Soil organic matter also regulates P availability by increasing dissolution of unavailable P forms and as a source of mineralizable organic P (Zhang *et al.*, 2020). Since crops mostly deplete mineral P and unlike N which can be recycled by biological fixation of atmospheric N, P lack that ability and thus P lost from the soil can only be replenished through external sources (Sanyal and De Datta, 1991). Soil P undergoes both biological and chemical processes that regulate its transformation from one chemical form to another and they include mineralization-immobilization, weathering, precipitation-dissolution and adsorption-desorption (Prasad and Chakraborty, 2019; Thomas Sims and Pierzynski, 2005).

Since P is highly dependent on soil physicochemical properties, any land-use change that causes significant effects on soil properties would influence distribution and availability of soil P particularly in the top soil horizon where there is high presence of roots and microbial activity (Iwashima *et al.*, 2012; Soltangheisi *et al.*, 2019). Land use change determine the turnover rates of soil P with rapid turnover in resin and bicarbonate P fractions and slower in HCL-P (Helfenstein *et al.*, 2020). Furthermore, distribution of phosphorus fractions differ depending on the land use system in place (Chimdi *et al.*, 2014). Land-use change causes P losses through accelerated soil

erosion due to reduced ground cover and P redistribution by increasing available P fractions but in a short-term and ultimately to more unavailable forms in the long run (Bayuelo-Jiménez *et al.*, 2020). In comparing forested and agricultural ecosystems, forested ecosystems show sustained maintenance of high soil fertility because of considerable inputs of organic matter and conservation of soil (Qiong *et al.*, 2008). The higher amount of organic inputs in forest provides a source of P and maintains moderate levels of micronutrients indicating insignificant loss of nutrients (Nishigaki *et al.*, 2018; Rosling *et al.*, 2016). Nonetheless, continued cultivation of some tree species like pine may deplete most of non-labile P showing that this pool may provide P for plants growing in soils exhibiting low P content (Gatiboni *et al.*, 2017). The behavior of such tree species in utilization of P may promote efficient internal cycling of P and other nutrients (Zhu *et al.*, 2021). Similarly, tree establishment leads to reduction in organic P fraction. For example, soils under *Pinus*, *Cupressus* and *Eucalyptus* species were found to contain lower organic P and higher inorganic P irrespective of the tree species and association with mycorrhizae indicating that exotic tree plantations encourage increased mineralization of organic P (Chen *et al.*, 2000; Chirino-Valle *et al.*, 2016). This is possible through enhanced biologically mediated processes such as crop P uptake, increased soil exploration through mycorrhizae-plant associations and enzyme activity and changes in soil chemical properties such as soil pH (Chen *et al.*, 2008). Therefore, organic P may be lower than inorganic P in tree-based land use systems.

Grasslands or pastures consistently maintain higher contents organic P and overall soil nutrient levels and this has been associated with increased inputs from root litter (Chen *et al.*, 2003). Forest to pasture conversion causes redistribution of soil P fractions with increased accumulation of organic phosphorus in the soil (Garcia-Montiel *et al.*, 2000). In cultivated croplands, practices such as tillage, inorganic fertilizer use and cropping systems determine P transformation pathways and its availability to crops, an indication that variations in the size of soil P fractions depend on management practices and plant composition (Tanganelli, 2011). Crop cultivation has pronounced negative effect on labile organic P fractions due to reduction in SOM (Maranguit *et al.*, 2017; Saltali *et al.*, 2007). The lower levels of soil organic matter weakens soil's capacity to retain P (Aguiar *et al.*, 2013). Continued P fertilizer use elevates all soil inorganic P fractions and may increase the proportion of soil organic P but with long-term crop cultivation, this fraction decreases (Maharjan *et al.*, 2018; Mahmood *et al.*, 2020; Negassa and Leinweber, 2009; Shi *et al.*, 2013).

Conventional tillage causes even distribution of soil phosphorus in the soil thus exposes P to more sorption sites, and elevates soil organic matter mineralization (Nunes *et al.*, 2020). Soil microbial biomass, which forms part of nutrient cycling, is more sensitive to perturbations induced by land use change and thus may influence availability of nutrients, including redistribution of soil P (Sanyal and De Datta, 1991).

Methods of assessing effects of land uses on soil P dynamics have been reported by different researches such like; Hedley sequential fractionation which partitions soil P into fractions, namely; Resin-P and $NaHCO_3$-P (plant-available), NaOH-P and sonic NaOH-P (moderately available), HCL-P and Residual P (unavailable), that are relatively available to plant (Henriquez, 2002; Saltali *et al.*, 2007). These fractions may indicate effects of land use change and intensity on soil. Hedley method is advantageous in that it accounts for low labile P fractions which is undetectable by other methods.

CHAPTER THREE: MATERIALS AND METHODS

3.1 Description of the study site

The study was conducted in South Kinangop in Nyandarua County located between latitude 0.61° S and longitude 36.63° E, altitude of about 2500 m above sea level. It is in the upper highland agro-ecological zone, receives bimodal rainfall where long rains occur in March through May and short rains in October through December; with an annual rainfall amount of about 1500 mm and mean annual temperature of 20° C (Mandere *et al.*, 2011). Soils are predominantly Planosols characterized by poor drainage, low to moderate soil fertility, very dark greyish-brown to very dark grey in color, very firm clay and underlying 30-45 cm layer of silty clay loam to clay loam (Jaetzold *et al.*, 2006).

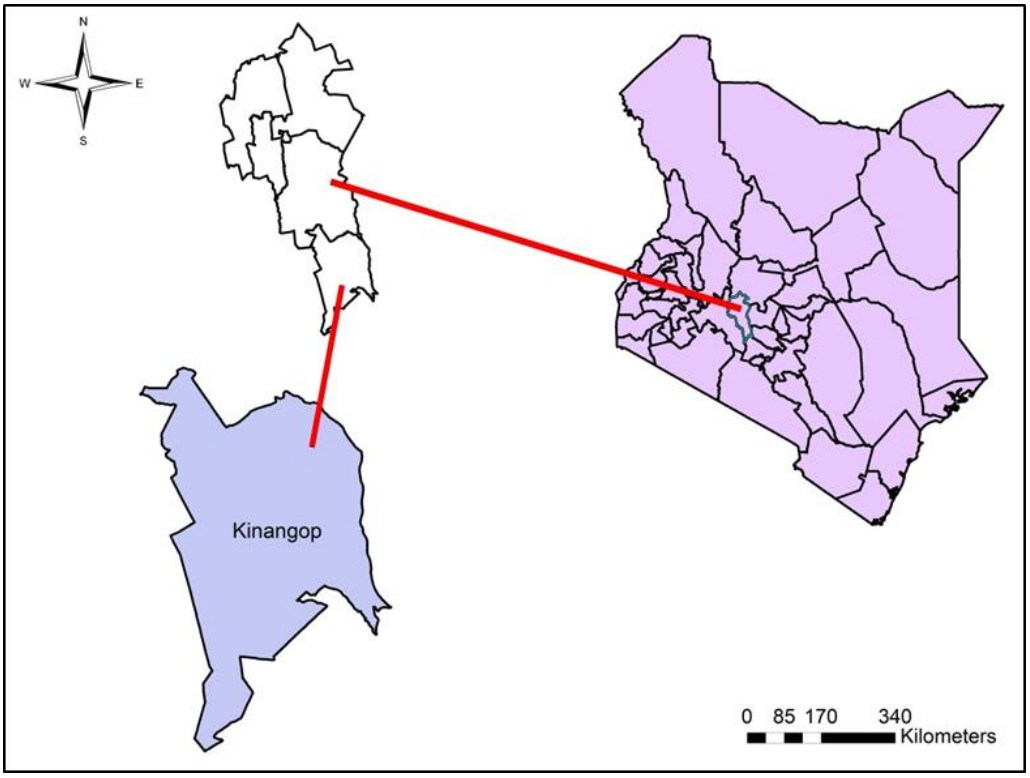

Figure 3.1: Map showing Kinangop as the study site

3.2 Historical land uses

The study area lies along the Aberdare ranges and initially the land was under natural vegetation before it was allocated to the farmers in 1963 (Rachilo, 1978). The farms have since been subdivided from the initial sizes of between 7-35 acres (then called minor plots) and 36-100 acres (chief plots) to the current sizes of less than an acre in many areas within Nyandarua County (Kamau *et al.*, 2019) .This is as a result of high population growth in the last four decades which has risen from 233,302 in 1979 to 638,289 persons in 2019 (Jaetzold and Schmidt, 1983; KNBS, 2019). Most of the farmers cultivate vegetables (cabbages, carrots and kale), potatoes and do dairy farming. Crops were cultivated without organic or inorganic fertilizers but fertilizer use (mostly Di-ammonium Phosphate (DAP) was introduced in 1980s (Jaetzold and Schmidt, 1983). *Eucalyptus spp, Cupressus lusitanica* Mill. and *Grevillea robusta* A.Cunn. ex R.Br. are the common tree species planted in woodlots or farm boundary (KFS, 2010).

3.3 Description of the selected land-use types

Natural forest, planted forest, grazed pasture and cultivated (potato fields) land were chosen as the land-use types in this study. Selection of sampling sites was based on the common land-use types, and targeted farms were to be adjacent to a forested area consisting of both natural and planted forests. The natural forest site represented the benchmark location or the reference point for comparing with disturbed soils in the farms. Five fields planted with potato and five grazed pastures were selected for the study. Diammonium Phosphate (DAP) and Calcium Ammonium Nitrate (CAN) are the common fertilizers used with maximum application being 200 $kgha^{-1}$. In potato cultivated fields, farmers rotate potato with crops like garden peas, cabbage or maize, but this is done after three consecutive seasons of potato crop. Potato residues are removed from the farm after harvesting to prevent transfer of any disease or pests from the infested potato haulms and roots to the next crop. The average farm size within the study site is approximately 0.4 ha (Kamau et al., 2019). Grazed pastures had *Pennisetum clandestinum* Hochst. ex Chiov (Kikuyu grass) as the main pasture grass. The Kenyan Holstein-Friesian (*Bos taurus taurus*) dairy cows and Corriedale (*Ovis aries*) sheep for wool are the major animals kept. The Southern Kinangop Aberdare forest covers an area of 1970 ha of indigenous trees and 2113.90 ha of exotic trees according to Aberdare Forest Management plan 2010-2019 (KFS, 2010). The natural forest where soil sampling was carried out covered an area of 9.9 ha, and *Dombeya goetzenii* K. Schum was the

common tree species. The forest plantation covered an area of 4.9 ha of pure cypress (*Cupressus lusitanica* Mill.) trees planted through Plantation Establishment and Livelihood Improvement Scheme (PELIS) in 1993.

3.4 Description of soil and plant sampling procedure

In each land-use type, the sampling of soil for analysis was done following laid out transects measuring 50 m (x3) which were laid out in a zigzag pattern in potato fields and the pastures. Along each transect, three sampling points were marked at 15 m apart. Sampling points measuring one square meter were established and were further divided into 25 grids, each grid measuring 400 cm^2. Five grids (or squares) were randomly selected in each sampling point where soil samples were collected. The soil samples were collected using soil auger at 0.3 m soil depth. In the forests (natural and planted) however, the distance of transects was increased to 150 m with the distance between sampling points being 50 m. Sampling points measured 25 m^2 divided into 25 grids, each grid measuring 1 m^2 (Figure 2). Soil sampling was done in the same way as in potato fields and grazed pastures and to the same depth. After sampling from the five grids in each sampling point, the soil was composited and a 2 kg soil sample was taken and placed in brown khaki paper bags. From each field, nine (9) samples were collected (3 transects × 3 sampling points per transect). Litter and root samples from each grid were also collected and composited. Litter samples were randomly hand-picked from the ground in natural forest and cypress plantation and were placed in brown khaki paper bags. On the other hand, root samples were collected from randomly picked plants within the sampling grids and placed in plastic zip-lock bags, sprayed with 70% ethanol and kept in a cooler box. The roots could not be collected in cypress forest due to the rooting depth of the trees and could not be reached using the common sampling tools. Soil samples were dried for 4 days at room temperature and later divided into two portions; one portion was ground using mortar and pestle and passed through 2-mm and 0.25-mm sieves for physicochemical analyses and sequential P fractionation while the other portion was kept under room temperature for spore extraction and morphotype identification. In the laboratory, the roots were fixed with 70 % ethanol and kept under refrigeration at 4° C. Plant litter was dried in the oven at 70° C for 48 hours and ground.

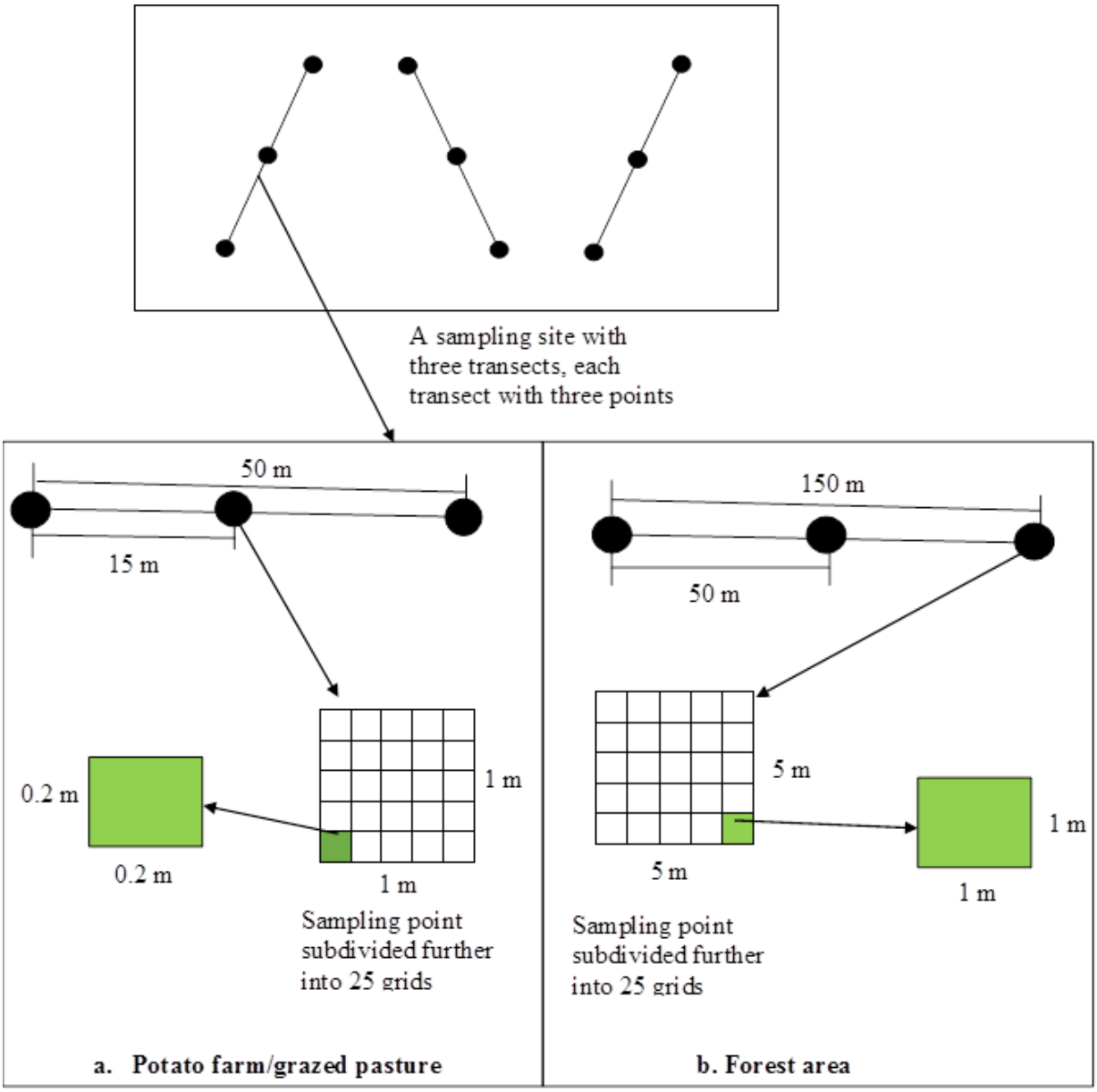

Figure 3.2: Sampling framework

3.5 Characterization of soil and plant litter samples

Soil samples were extracted for analysis of selected chemical properties. To determine soil pH, 10 g of dried soil was weighed into 50 ml centrifuge tubes and saturated with distilled water in the ratio of 1:2.5 soil to water and shaken overnight. The suspension was left to settle for 30 minutes and pH readings was taken using an electrode pH meter (Ryan *et al.*, 2001). Soil total N was determined by extracting 0.3 g of air-dried soil placed in 75 ml digestion tubes with 5 ml of mixed reagent (containing selenium powder, lithium sulphate, hydrogen peroxide and concentrated

sulphuric acid) and heated at 350° C for 3 hours. After cooling, the digest was filled up to 75 ml with distilled water and transferred to storage containers. A 10 ml aliquot of the sample digest was transferred into reaction chamber of a steam-distillation apparatus followed by 10 ml of 40 % of NaOH and immediately steam-distilled into 5 ml of 5 % boric acid containing mixed indicator up to 30 ml. The collected distillate was then titrated against dilute HCL according to Kjedhal method (Hinds and Lowe, 1980). Total N was calculated from equation (Eq. 1);

$$\text{Total N (mg Kg}-^{1}) = \frac{\text{a} \times 0.1 \times \text{v} \times 1000}{1000 \times \text{w} \times \text{al}} \quad \text{..... Eq. 1}$$

Where *a* is the corrected volume of the titrated HCL for sample, *v* is the final volume of the digested sample, *w* is the weight of the soil and *al* is the volume of the aliquot taken for analysis.

Soil total organic carbon was determined by subjecting 0.1 g of air-dried soil to complete oxidation using 5 ml of 1 M potassium dichromate and 7.5 ml of concentrated sulphuric acid and heated at 150° C for 30 minutes. The mixture was allowed to cool and then transferred to 150 ml conical flasks and 3 drops of mixed indicator was added and titrated with 0.2 M ferrous ammonium sulphate (Nelson and Sommers, 1996). The amount of total organic C was derived from Eq. 2;

$$\text{Total Organic C (mg Kg}-^{1}) = \frac{\text{t} \times 0.2 \times 0.3 \times 1000}{\text{w}} \quad \text{..... Eq. 2}$$

Where *t* is the corrected volume of the titred ferrous ammonium sulphate for the sample and *w* is the weight of the soil taken for analysis.

Soil exchangeable cations (Ca, Mg and K) were determined by extracting 2.5 g of dried soil with 50 ml of 1 M ammonium acetate. The mixture was shaken for 30 minutes and filtered using No. 42 Whatman filter papers into 150 ml conical flasks. For determination of Ca and K, an aliquot of 5 ml was taken from the soil extract and added with 1 ml of 26.8 % of lanthanum chloride and the solution was filled up with distilled water. On the other hand, Mg was determined by taking 3 ml of the extract and added with 5 ml of 5000 ppm strontium chloride and filled up to 50 ml using distilled water. The contents of Ca, Mg and K were determined by atomic absorption spectrophotometry. Concentration of these parameters was derived from Eq. 3;

$$\text{Ca, Mg, K (mg Kg}-^{1}) = \frac{\text{a} \times \text{v} \times \text{f} \times 1000}{1000 \times \text{w} \times \text{al}} \quad \text{..... Eq. 3}$$

Where *a* is the concentration of Ca, Mg and K in the extract, *v* is the volume of the sample extract, *f* is the dilution volume, *al* is the volume of the aliquot taken for analysis and *w* is the weight of the soil. Cation exchange capacity (CEC) was determined as the sum of the exchangeable bases (Eq. 4).

$$\text{CEC (cmol (+)Kg}^{-1}) = \frac{\text{Ca}}{200} + \frac{\text{K}}{390} + \frac{\text{Mg}}{120} \quad \text{..... Eq. 4}$$

Plant litter was analyzed for total N, P, Ca, Mg, K, organic C and lignin content. Total nutrient N, P and cations were determined by extracting 0.3 g of ground litter placed in 75 ml digestion tubes with 5 ml of extracting solution containing selenium powder, lithium sulphate, hydrogen peroxide and concentrated sulphuric acid and heated at 350° C for 3 hours in a heating block. The digest was allowed to cool and filled up to 75 ml and transferred to storage bottles. Total N was determined following the same procedure as was done for soil total N according to Kjedhal method (Hinds and Lowe, 1980) and calculated from Eq. 5.

$$\text{Total N (mg Kg}-^{1}) = \frac{\text{a} \times 0.2 \times \text{v} \times 1000}{1000 \times \text{w} \times \text{al}} \quad \text{..... Eq. 5}$$

Where *a* is the corrected volume of titrated HCl for sample, *v* is the final volume of the digested sample, *w* is the weight of the soil and *al* is the volume of the aliquot taken for analysis.

Plant litter total P was determined by taking 2 ml of soil digest into 50 ml volumetric flasks, added with 10 ml of ascorbic acid (containing ammonium molybdate, antimony potassium tartrate and sulphuric acid) and filled up to 50 ml with distilled water. The contents were allowed to stand for 2 hours for color development and absorbances (880 nm) were taken by UV Spectrophotometer according to Murphy and Riley (1962) method. P concentration in litter was derived as;

$$\text{Total P } \left(\text{mg Kg}^{-1}\right) = \frac{\text{a} \times \text{v} \times \text{f} \times 1000}{1000 \times \text{w} \times \text{al} \times 1000} \quad \text{..... Eq. 6}$$

Where *a* is the corrected P content in the sample, *v* is the volume of sample digest, *f* is the dilution volume, *w* is the weight of the soil tested and *al* is the volume of the sample digest taken for analysis.

Plant litter total K and Mg were determined by diluting 3 ml of sample digest with distilled water to 50 ml while for total Ca, 5 ml of sample digest was added with 10 ml of 0.15 % lanthanum

chloride and filled to 50 ml with distilled water and determined using atomic absorbance spectrophotometer. Litter cation content was derived from Eq. 7.

$$\text{Ca, Mg, K}\left(\text{mg Kg}^{-1}\right) = \frac{\text{a} \times \text{v} \times \text{f} \times 1000}{1000 \times \text{w} \times \text{al} \times 1000} \quad \text{Eq. 7}$$

Where *a* is the concentration of Ca, Mg and K in the sample digest, *v* is the volume of the sample digest, *f* is the dilution factor, *al* is the volume of the aliquot taken for analysis and *w* is the weight of the soil.

Plant litter organic matter content was determined by complete combustion method where 10 g of ground litter samples was weighed into dry crucibles and ignited in the furnace at 550° C for 3 hours, and the difference in weight loss was considered to be the amount of organic matter content, Eq. 8 (Anderson and Ingram, 1993).

$$\text{Ash content (\%)} = \left[\frac{\text{W3} - \text{W1}}{\text{W2} - \text{W1}}\right] \times 100$$

$$\text{Organic matter content (\%)} = 100 - \text{ash \%} \quad \text{E q. 8}$$

Where *W1* is the weight of an empty crucible, *W2* is the weight of crucible and ground litter sample and *W3* is the weight of crucible and litter residue after ignition.

Lignin content was determined by acid detergent fibre analysis (Van Soest and Wine, 1968). One gram (W1) of the ground plant litter sample was weighed into 250 ml round-bottom flask with a ground glass joint. Onto the flask, 100 ml of acidified cetyltrimethyl ammonium bromide (CTAB) solution was added with few drops of anti-foam reagent. The flask was connected to a reflux condenser and allowed to reflux for 1 hour. The contents were filtered through vitreosil crucible No. 1 under gentle suction. Residue remaining on the crucible was washed with three portions of 50 ml of boiling water followed by acetone to bleach. The crucible plus the contents were dried in the oven at 105° C for 2 hours and placed in a desiccator to cool. The weight of the crucible and detergent fibre contents was taken (W3). After oven-drying, the vitreosil crucible with the detergent fibre was put in a shallow cold water bath and added 25 ml of mixed permanganate buffer solution (containing potassium permanganate, silver sulphate, ferric nitrate, silver nitrate, potassium acetate, acetic acid and methanol) into the crucible. The contents remained in the water bath at 20° C for 1 ½ hours and more permanganate buffer solution was added to maintain the purple color. The contents were then filtered under suction. The crucible containing acid detergent

fibre with contents was placed in a clean pan and was filled with oxalic acid demineralizing solution (containing oxalic acid dihydrate, 95% ethanol and dilute hydrochloric acid), allowed to stand for 15 minutes and then filtered under suction. The fibre was repeatedly washed with the demineralizing solution until the fibre appeared white. The contents were filtered and again washed with 80% ethanol, after which filtering under suction was repeated twice. The contents were similarly washed with acetone. The crucible containing the fibre was then oven-dried at 105° C for 2 hours and put in a desiccator to cool. The weight of the crucible plus fibre was taken (W4) and lignin content contained in plant litter was derived from Eq. 9.

$$\text{Lignin content}\left(\text{g Kg}^{-1}\right) = \frac{\text{W3} - \text{W4}}{\text{W1}} \times 1000 \quad \cdots\cdots \text{Eq. 9}$$

3.6 Sequential soil P fractionation

Soil was extracted for determination of P fractions using Hedley sequential fractionation method and P fractions quantified in organic and inorganic forms giving rise to six main fractions; namely resin-P_i, $NaHCO_3$-P (P_i and P_o), NaOH-P (P_i and P_o), sonicate NaOH-P (P_i and P_o), HCL-P_i and Residual-P (Hedley *et al.*, 1982). One gram of dry soil (0.25 mm) was weighed and put into 50 ml centrifuge tubes and was extracted repeatedly with chemical reagents of varying dissolution strength, starting with dilute acid and alkali and eventually concentrated acid; hydrochloric acid, sodium bicarbonate, sodium hydroxide and concentrated sulphuric acid. (I.) Resin-P: Resin strips (1.5 cm x 5 cm) were first saturated with 1 M $NaHCO_3$ for 1 hour. The resin strips were first rinsed well with distilled water and then placed into the 50 ml centrifuge tubes containing the soil and 30 ml of distilled water. The contents were shaken for 16 hours and resin strips were removed using tweezers and soil was washed off using distilled water into the centrifuge tubes. Resin strips were transferred into different sets of centrifuge tubes containing 20 ml of 0.5 M L^{-1} HCl. The contents were shaken again for 1 hour and resin strips were removed and this gave resin P extract. An aliquot of 6 ml was taken for determination of resin Pi according to Murphy and Riley method and absorbance taken at 880 nm using UV Spectrophotometer. The centrifuge tubes containing soil were put in a centrifuge at 5000 rpm for 10 minutes and water decanted and discarded. (II.) $NaHCO_3$-P: 30 ml of 0.5 M L^{-1} $NaHCO_3$ was dispensed into the centrifuge tubes containing soil and was shaken for 16 hours. The soil suspension was put in a centrifuge at 5000 rpm for 10 minutes and $NaHCO_3$ extract was carefully decanted into new sets of centrifuge tubes. To

determine $NaHCO_3$-P_i, 6 ml of the extract was taken and P determined as was done in resin P fraction. A separate 6 ml of the extract was digested with 6 ml of acidified ammonium persulfate at 15 psi, 120° C for 1 hour. This digest was analyzed for P following the same procedure for resin P_i. P quantified here represented total inorganic P denoted as tP_i from which organic P ($NaHCO_3$-P_o) was derived by subtracting tP_i from P_i (Eq. 10). (III.) NaOH-P: 30 ml of 0.1 M L^{-1} NaOH was dispensed into the centrifuge tubes containing soil and shaken for 16 hours. The soil suspension was put in a centrifuge at 5000 rpm for 10 minutes and NaOH extract was decanted into new sets of tubes. NaOH P_i and P_o fractions were determined following the same procedure done for $NaHCO_3$. (IV.) Sonicated NaOH-P was determined by extracting soil in the centrifuge tubes with 20 ml of 0.1 M L^{-1} NaOH. The soil suspension was first sonicated for 15 seconds and then shaken for 16 hours, after which it was centrifuged at 5000 rpm for 10 minutes. Sonicate NaOH extract was decanted into new sets of centrifuge tubes. Inorganic and organic NaOH P fractions were determined following the steps in $NaHCO_3$ fraction. (V.) HCl-P consisting of only inorganic fraction was determined by extracting the soil in the centrifuge tubes with 30 ml of 1 M L^{-1} HCl. The soil suspension was shaken for 16 hours and thereafter centrifuged at 5000 rpm for 10 minutes. HCL extract was decanted into new sets of centrifuge tubes. Phosphorus concentration was determined according to Murphy and Riley method as was done in resin P fraction. (VI.) Residual-P: soil in the centrifuge tubes was quantitatively transferred into 75 ml digestion tubes using distilled water and put in the oven at 70° C to evaporate excess water. The soil was extracted with 5 ml of mixed digestion reagent and heated at 350° C for 3 hours. The soil digest was filled up to 75 ml with distilled water and transferred to storage bottles. Residual P was determined in the same manner as P in resin fraction. Soil P content (mg/kg) for all fractions was calculated according to Eq. 11.

$$P_o = tP_i - P_i \quad \text{..... Eq. 10}$$

Where P_o is organic phosphorus, tP_i is the total inorganic phosphorus and P_i is the inorganic phosphorus.

$$P\ (mg\ Kg^{-1}) = \frac{(a-b) \times v \times f \times 1000}{1000 \times w} \quad \text{..... Eq. 11}$$

Where *a* is the concentration of phosphorus in the extract, *b* is the concentration of phosphorus in blanks, *v* is the volume of the extract, *f* is an additional dilution volume, and *w* is the weight of the soil in grams.

3.7 Extraction and quantification of AMF spore abundance and species identification

Spores were extracted according to the wet sieving and sucrose centrifugation method described by Daniels and Skipper (1982). A 100 g of dried soil was washed through the 710 µm and 45 µm sieves with tap water repeatedly. The clear contents of 45 µm sieve were collected in 50 ml centrifuge tubes and centrifuged for 5 minutes at 1500 revolutions per minute (rpm). The supernatant was discarded; 50% sucrose solution was added to the remaining soil to the 50-ml mark and centrifuged again for 1 minute at 1500 rpm. The sucrose solution was collected in a plastic beaker and transferred to petri dishes. Spores extracted were counted under dissecting microscope and identified to genera based on spore characteristics; color, size, wall structure, hyphal attachments on spore and Melzer's reaction. The spore color was determined using Edinburgh Botanic Gardens color chart. The spores were then mounted on the glass slides using polyvinyl lactoglycerol (PVLG) and Meltzer reagent added and slightly crushed for finer details. Spore characteristics observed were marched with existing archived Voucher specimen on West Virginia International Culture Collection of Arbuscular and Vesicular-Arbuscular Endomycorrhizal Fungi website (Jefwa *et al.*, 2012).

3.8 Determination of root colonization

Roots were assessed for AMF colonization according to the presence of arbuscule, vesicle, hyphae and entry points. Before analysis, roots were thoroughly cleaned with tap water to remove ethanol (Qin *et al.,* 2017; Wang *et al.,* 2019). The roots were rinsed with 10% potassium hydroxide and autoclaved at 120˚ C for 1 hour and after cooling, they were rinsed further with tap water. They were then bleached in hydrogen peroxide + ammonium solution for 1 hour and thereafter washed with tap water to remove excess bleaching solution. Hydrochloric acid (1 %) was added to the bleached roots and left for 1 hour, after which the acid was poured off and staining solution (containing glycerol, water, 1 % HCl and 0.5 g of trypan blue) added followed by autoclaving at 120° C for 5 minutes and washing off with tap water (Philips and Hayman, 1970). Stained roots were cut into 1 cm long and 30 pieces were mounted on the glass slides for observation using grid-line intersect method under dissecting microscope as described by Giovannetti and Mosse (1980). Percent root colonization was derived from the number of root segments infected against those uninfected (Carter and Gregorich, 2007). The AMF root colonization frequency and intensity indices were derived from Eq. 3 and 4 respectively;

$$\text{Root colonization frequency} = \frac{\text{No. of infected root segments}}{\text{Total No. of roots observed}} \times 100 \quad \text{..... Eq. 3}$$

$$\text{AMF colonization intensity} = \frac{\text{Total percent root area infected}}{\text{Total percent root area uninfected}} \times 100 \quad \text{.....Eq. 4}$$

3.9 Data analysis

Generalized linear models (GLM) were used to test the effects of land-use type on soil and plant litter chemical properties using R statistical software version 4.0.4 (R Core Team, 2021). On the other hand, spore count data was analyzed using generalized linear mixed models (GLMMs), with negative binomial regression chosen as an extension of the Poisson distribution due to a significant number of zero values as described by Kamau *et al.* (2017) and Kamau *et al.* (2020). AMF diversity and richness was computed using Shannon diversity and richness indices. Maximum likelihood (ML) was used to estimate the model parameters and Akaike Information Criterion (AIC) was used for model selection. Models with the least AIC values were chosen as the best models. Where analysis of variance (ANOVA) showed significant effects, Tukey's Honest Significant Difference (HSD) test was used to separate the means at $p < 0.05$. Relationship between AMF genera and soil chemical properties and P fractions was determined using Pearson's correlation.

CHAPTER FOUR: RESULTS

4.1 Effects of land-use type on soil chemical properties

Soil chemical properties analyzed were significantly ($p < 0.001$) affected by land use type (Table 1). Apart from K, all soil chemical properties were significantly ($p < 0.001$) higher in natural forest than the other land-use types. For instance, pH was higher in soils obtained in natural forest > cypress forest > grazed pastures (4.2) > potato fields which were strongly acidic at pH of 3.8. Similarly, natural forest had significantly ($p < 0.001$) higher total C, N, Ca and Mg compared to other land uses. The CEC trend was natural forest > cypress forest > grazed pastures > potato fields as shown in Table 1.

Table 4.1: Chemical properties of soils collected from different land use types

Soil properties	Land-use type (LUT)				*p*-value (LUT)
	Natural forest	Cypress forest	Grazed pastures	Potato fields	
$pH_{(water)}$	4.9 (0.2)^{a}	4.3 (0.1)^{b}	4.2 (0.1)^{b}	3.8 (0.1)^{c}	<0.001
Total C (g kg^{-1})	69.2 (5.3)^{a}	47.2 (3.2)^{b}	38.0 (2.8)^{b}	35.3 (2.3)^{b}	<0.001
Total N (g kg^{-1})	7.8 (0.6)^{a}	3.8 (0.2)^{b}	4.9 (0.3)^{b}	4.0 (0.2)^{b}	<0.001
CEC (cmol (+) kg^{-1})	25.3 (1.3)^{a}	14.6 (1.4)^{b}	11.7 (0.9)^{bc}	9.9 (0.4)^{c}	<0.001
K (g kg^{-1})	0.4 (0.1)^{ab}	0.3 (0)^{ab}	0.5 (0)^{a}	0.2 (0)^{b}	<0.001
Ca (g kg^{-1})	4.0 (0.3)^{a}	2.3 (0.2)^{b}	1.6 (0.1)^{c}	1.4 (0.1)^{c}	<0.001
Mg (g kg^{-1})	0.5 (0)^{a}	0.2 (0)^{b}	0.2 (0)^{b}	0.2 (0)^{b}	<0.001

Abbreviations; C = carbon, N = nitrogen, CEC. = cation exchange capacity, K=potassium, Ca=calcium, Mg=magnesium. Within rows, means followed by different letters in superscript are significantly different at $p < 0.05$, and mean standard deviations are in parenthesis. Means were separated by Tukey's Honest Significant Difference (HSD) test.

4.2 Chemical characterization of plant litter

Chemical properties of litter were greatly affected by land-use type in which they were collected (Table 2). Litter from natural forest had significantly higher total N, P, Ca and Mg than in cypress plantation. However, total K and OM were similar between the land use types. On the other hand, lignin content was high in litter collected from natural forest (447.4 g kg^{-1}) compared those from cypress plantation (356.5 g kg^{-1}).

Table 4.2: Plant litter characteristics under land use types

Litter characteristics	Land-use type (LUT)		*p*-value (LUT)
	Natural forest	Cypress plantation	
Total N (g kg^{-1})	37.7 (5.7)[a]	12.7 (1.2)[b]	**0.0027**
Total P (g kg^{-1})	4.1 (0.4)[a]	1.8 (0.1)[b]	**0.0014**
OM (g kg^{-1})	810.6 (139.2)[a]	928.3 (21.8)[a]	0.1120
K (g kg^{-1})	12.9 (3.5)[a]	12.0 (0.9)[a]	0.5868
Ca (g kg^{-1})	45.9 (11.6)[a]	11.4 (0.4)[b]	**0.0056**
Mg (g kg^{-1})	16.8 (5.3)[a]	2.9 (0.2)[b]	**0.0076**
Lignin (g kg^{-1})	447.4 (17.9)[a]	356.5 (6.1)[b]	**0.0020**

Abbreviations; N = nitrogen, P = Phosphorus, C = carbon, K=potassium, Ca=calcium, Mg=magnesium, OM=organic matter. Within rows, means followed by different letters in superscript are significantly different at $p < 0.05$, and mean standard deviations are in parenthesis. Means were separated by Tukey's Honest Significant Difference (HSD) test.

4.3 Effect of land-use type on soil P fractions

Soil P fractions were significantly affected by land-use type with varying magnitudes (Table 3). Resin-P was significantly higher in soils collected from potato growing fields (34.9 mg P kg^{-1}) compared to cypress plantation (3.9 mg P kg^{-1}). Similar trends were observed with $NaHCO_3$-P_i, $NaHCO_3$-P_o and NaOH-P_i. On the other hand, residual P and sonicate NaOH-P_o fractions were higher in natural forest (574.7 mg P and 75.3 mg P kg^{-1}, respectively) compared to the other land use types. When the fractions were grouped based on availability, all the three groups were significantly affected by land-use type. Readily and moderately labile P were highest in potato growing fields (125.1 mg P and 186.1 mg P kg^{-1}, respectively) and lowest in cypress forest (36.4 mg P and 82.7 mg P kg^{-1}, respectively). However, non-labile P was highest in natural forest (690.1 mg P kg^{-1}) and lowest in cypress forest (324.5 mg P kg^{-1}).

Table 4.3: Effects of land use type on soil P fractions

P-fractions (mg kg^{-1})	Land-use type (LUT)				*p*-value (LUT)
	Natural forest	Cypress forest	Grazed pastures	Potato fields	
Resin P_i	13.7 (2.4)^{ab}	3.9 (1.2)^{b}	22.8 (3.6)^{ab}	34.9 (4.7)^{a}	**0.032**
Bicarbonate P_i	10.7 (2.2)^{ab}	2.9 (0.5)^{b}	23.1 (3.5)^{ab}	35.2 (4.7)^{a}	**0.025**
Bicarbonate P_o	26.7 (2.9)^{b}	29.6 (3.0)^{b}	48.8 (2.3)^{a}	55.0 (3.2)^{a}	**0.009**
NaOH-P_i	53.5 (5.5)^{b}	59.3 (3.1)^{b}	100.1 (7.8)^{b}	138.8 (13.4)^{a}	**0.006**
NaOH-P_o	41.9 (5.2)^{a}	23.3 (3.6)^{a}	34.1 (5.4)^{a}	47.2 (6.4)^{a}	0.189
Sonicate NaOH-P_i	15.7 (2.3)^{a}	21.9 (2.5)^{a}	20.3 (2.7)^{a}	24.0 (2.2)^{a}	0.317
Sonicate NaOH-P_o	75.3 (6.3)^{a}	51.2 (4.2)^{b}	56.5 (2.9)^{b}	48.1 (2.2)^{b}	**<0.001**
HCl-P_i	24.5 (7.8)^{a}	10.2 (1.1)^{a}	39.3 (8.0)^{a}	23.8 (3.1)^{a}	0.061
Residual P	574.7 (53.2)^{a}	241.2 (16.5)^{b}	377.4 (26.1)^{b}	300.6 (20.0)^{b}	**<0.001**
Readily labile P	51.1 (5.5)^{bc}	36.4 (3.4)^{c}	94.6 (7.8)^{ab}	125.1 (11.5)^{a}	**0.012**
Moderately labile P	95.3 (9.9)^{b}	82.7 (4.1)^{b}	134.2 (9.6)^{b}	186.1 (15.7)^{a}	**0.005**
Non-labile P	690.1 (54.5)^{a}	324.5 (15.7)^{c}	493.6 (32.8)^{b}	396.4 (21.2)^{bc}	**<0.001**

Abbreviations: P_i = inorganic phosphorus, P_o = organic phosphorus, NaOH = sodium hydroxide, HCL=hydrochloric acid, P=phosphorus. Within rows, means followed by different letters in superscript are significantly different at $p < 0.05$, and mean standard deviations are in parenthesis. Means were separated by Tukey's Honest Significant Difference (HSD) test.

4.4 Response of AMF spore abundance and root colonization to land-use type

Of the ten AMF genera identified, only *Glomus* and *Acaulospora* were significantly affected by land-use type, with the highest spore abundance in potato growing fields (81.1 spores 100 g^{-1} of soil) compared to grazed pastures (46.5 spores 100 g^{-1} of soil), cypress forest (20.0 spores 100 g^{-1} of soil) and natural forest (27.6 spores 100 g^{-1} of soil) (Table 4). All the other AMF genera were not significantly affected by land-use type. Similarly, there was no significance difference in Shannon diversity and AMF richness indices, arbuscule, vesicle, hyphae, entry point and total root colonization across the land-use types. Nonetheless, AMF diversity and richness showed a decreasing trend as potato fields > grazed pastures > natural forest > cypress plantation. Arbuscule, vesicle, hyphae and entry point showed similar trend as that of diversity and richness.

Table 4.4: Abundance of arbuscular mycorrhizal fungi (AMF) and root colonization as influenced by land-use type

AMF genera	Land-use type (LUT)				p-value (LUT)
	Natural forest	Cypress forest	Grazed pastures	Potato fields	
Acaulospora	**17.9 (5.8)^{a}**	**3.6 (1.3)^{b}**	**21.7 (4.4)^{a}**	**19.4 (5.1)^{a}**	**0.005**
Glomus	**5.1 (3.0)^{b}**	**15.7 (6.3)^{b}**	**17.0 (6.9)^{b}**	**55.3 (14.3)^{a}**	**0.005**
Septoglomus	0.2 (0.2)^{a}	0.2 (0.2)^{a}	1.1 (0.5)^{a}	0.4 (0.3)^{a}	0.551
Paraglomus	0 (0)^{a}	0 (0)^{a}	2.2 (2.2)^{a}	0.8 (0.8)^{a}	0.999
Gigaspora	0.1 (0.1)^{a}	0 (0)^{a}	0.3 (0.2)^{a}	0.4 (0.2)^{a}	0.495
Scutellospora	0.8 (0.8)^{a}	0.6 (0.6)^{a}	1.7 (1.1)^{a}	2.7 (1.2)^{a}	0.692
Funneliformis	2.7 (2.0)^{a}	0 (0)^{a}	2.4 (0.9)^{a}	1.6 (0.5)^{a}	0.759
Enterophospora	0.4 (0.4)^{a}	0 (0)^{a}	0.1 (0.1)^{a}	0.1 (0.1)^{a}	0.101
Archeospora	0.3 (0.3)^{a}	0 (0)^{a}	0 (0)^{a}	0.3 (0.2)^{a}	1.000
Ambispora	0 (0)^{a}	0 (0)^{a}	0 (0)^{a}	0.3 (0.2)^{a}	1.000
Total spore count	**27.6 (5.8)^{b}**	**20.0 (6.8)^{b}**	**46.5 (9.2)^{ab}**	**81.1 (16.2)^{a}**	**0.005**
Shannon diversity index (H)	0.37 (0.1)^{a}	0.34 (0.1)^{a}	0.52 (0.1)^{a}	0.56 (0.1)^{a}	0.742
Taxonomic richness (S)	2.00 (0.4)^{a}	1.78 (0.3)^{a}	2.29 (0.2)^{a}	2.62 (0.2)^{a}	0.348
Arbuscule	1.1 (0.8)^{a}	ND†	1.6 (0.6)^{a}	5.0 (1.5)^{a}	1.000
Vesicle	1.9 (1.0)^{a}	ND†	2.2 (0.6)^{a}	3.2 (0.8)^{a}	0.711
Hyphae	27.0 (4.3)^{a}	ND†	22.8 (2.3)^{a}	27.1 (3.1)^{a}	0.636
Entry point	3.3 (1.5)^{a}	ND†	3.3 (1.1)^{a}	6.9 (2.2)^{a}	0.438
Total root colonization	33.3 (5.8)^{a}	ND†	29.9 (9.2)^{a}	42.2 (16.2)^{a}	0.959

† ND=Not determined. Within rows, means followed by different letters in superscript are significantly different at $p < 0.05$, and mean standard deviations are in brackets. Means were separated by Tukey's Honest Significant Difference (HSD) test.

4.5 Correlation between soil chemical properties and P fractions and AMF genera

Few AMF genera showed significant correlation with soil chemical properties and P fractions (Table 5). Under natural forest, *Glomus* and *Funneliformis* were positively associated with soil exchangeable K while *Acaulospora* correlated negatively with sonicate NaOH-P_o. However, in cypress plantation, AMF genera did not show significant correlation with either soil chemical properties tested or soil P fractions. In grazed pastures, *Paraglomus* had a positive correlation with soil pH, soil exchangeable K and Ca and CEC. *Paraglomus* also showed strong positive correlation with resin P_i, NaOH-P_i, $NaHCO_3$-P_i, sonicate NaOH-P_i, HCL-P_i and residual P and a negative correlation with sonicate NaOH-P_o. On the other hand, *Funneliformis* was positively correlated with soil total N and sonicate NaOH-P_o. Similarly, *Acaulospora* had a negative correlation with resin Pi but *Glomus* was positively correlated with residual P. Under potato fields, *Scutellospora* was positively associated with soil total N while *Funneliformis* was positively related to soil exchangeable K and HCL-P_i. *Acaulospora* showed a negative relationship with $NaHCO_3$-P_o but *Paraglomus* had a positive correlation with the same P fraction. *Enterophospora* and *Archaeospora* were positively associated with residual P and $NaHCO_3$-P_i respectively.

Table 4.5: Correlation between AMF genera and soil chemical properties. Significant correlation coefficients are bolded and marked with asterisks.

Land use type	AMF genera	Soil chemical properties							P fractions								
		pH	C	N	K	Ca	Mg	CEC	Resin P	$NaHCO_3$ P_i	$NaHCO_3$ P_o	NaOH P_i	NaOH P_o	Sonicate NaOH P_i	Sonicate NaOH P_o	HCl P_i	Residual P
Natural forest	*Acaulospora*	-0.34	0.11	-0.31	-0.59	-0.09	-0.55	-0.34	-0.14	-0.06	-0.47	-0.16	-0.31	-0.39	**-0.67***	-0.34	0.32
	Glomus	-0.43	-0.50	-0.31	**0.72***	-0.58	-0.12	-0.45	-0.44	-0.58	0.16	-0.28	-0.47	-0.27	-0.16	-0.31	-0.61
	Septoglomus	-0.08	-0.46	-0.26	-0.23	-0.28	-0.47	-0.42	-0.14	-0.35	0.09	0.12	-0.03	-0.21	-0.34	-0.24	-0.17
	Paraglomus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gigaspora	-0.31	0.14	-0.08	-0.08	-0.01	-0.17	-0.07	-0.11	-0.33	-0.16	-0.54	-0.21	-0.29	-0.45	-0.24	0.19
	Scutellospora	0.54	0.02	0.39	0.14	0.29	0.13	0.30	0.38	0.24	0.26	0.15	0.09	-0.01	0.26	0.30	-0.03
	Funneliformis	-0.20	-0.50	-0.30	**0.81****	-0.64	0.38	-0.38	-0.39	-0.52	0.20	-0.21	-0.40	-0.15	-0.06	-0.32	-0.17
	Enterophospora	-0.31	0.14	-0.08	-0.08	-0.01	-0.17	-0.07	-0.11	-0.33	-0.16	-0.54	-0.21	-0.29	-0.45	-0.24	0.19
	Archeospora	-0.08	-0.46	-0.26	-0.23	-0.28	-0.47	-0.42	-0.14	-0.35	0.09	0.12	-0.03	-0.21	-0.34	-0.24	-0.17
	Ambispora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cypress plantation	*Acaulospora*	-0.04	-0.09	0.08	-0.31	0.11	0.22	0.13	-0.09	0.17	-0.24	-0.15	-0.33	-0.27	-0.48	0.12	0.08
	Glomus	-0.15	-0.33	-0.19	0.13	0.04	-0.12	0.06	-0.08	0.21	-0.33	0.14	-0.34	0.50	-0.44	0.60	0.12
	Septoglomus	0.60	0.25	0.51	0.32	0.44	-0.25	0.43	-0.24	0.08	-0.18	0.21	-0.28	-0.16	-0.60	-0.32	-0.53
	Paraglomus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gigaspora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Scutellospora	-0.19	-0.46	-0.13	0.04	-0.17	-0.25	-0.16	-0.09	0.27	-0.31	0.24	-0.23	0.38	-0.42	0.52	0.12
	Funneliformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Enterophospora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Archeospora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Ambispora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Grazed pasture	*Acaulospora*	-0.09	-0.02	0.09	0.05	-0.09	0.01	-0.07	**-0.34***	-0.16	-0.04	-0.12	0.26	-0.13	0.18	-0.17	0.02
	Glomus	0.05	0.16	0.20	0.21	0.14	0.08	0.15	0.01	-0.06	-0.11	0.00	-0.06	-0.02	0.08	0.01	**0.36***
	Septoglomus	-0.11	0.03	-0.12	-0.19	-0.03	-0.23	-0.08	0.14	0.10	0.18	0.11	-0.14	-0.05	-0.17	-0.04	-0.16
	Paraglomus	**0.31***	0.02	0.04	**0.31***	**0.31***	0.07	**0.30***	**0.38****	**0.59*****	0.06	**0.53*****	-0.14	**0.40****	**-0.39****	**0.73*****	**0.42****
	Gigaspora	0.19	0.11	0.29	-0.07	0.09	0.07	0.06	-0.05	-0.05	-0.13	-0.06	0.03	-0.03	0.07	-0.05	0.03
	Scutellospora	-0.18	-0.04	-0.18	-0.13	-0.11	-0.10	-0.13	-0.12	-0.08	0.03	-0.05	-0.08	-0.09	0.02	-0.10	-0.13
	Funneliformis	0.03	0.23	**0.32***	0.00	0.10	0.02	0.08	0.10	-0.03	0.07	0.12	-0.02	0.18	**0.30***	0.01	0.02
	Enterophospora	0.03	-0.17	-0.15	0.11	-0.04	-0.07	-0.01	-0.10	-0.10	-0.17	-0.14	-0.08	-0.12	-0.08	-0.09	-0.16
	Archeospora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Ambispora	-0.13	0.19	0.24	0.03	-0.08	-0.07	-0.07	-0.07	-0.07	0.08	0.04	-0.01	-0.03	-0.08	-0.07	0.03
Potato field	*Acaulospora*	-0.15	-0.05	0.12	-0.07	-0.15	0.14	-0.13	-0.20	-0.23	**-0.33***	-0.28	-0.25	-0.28	0.09	-0.28	0.08
	Glomus	-0.27	-0.11	-0.29	-0.21	-0.22	-0.19	-0.27	-0.01	-0.01	-0.04	-0.10	-0.07	-0.21	-0.19	-0.14	-0.21
	Septoglomus	0.02	-0.05	-0.08	-0.15	0.11	-0.13	0.03	-0.09	-0.08	0.00	-0.05	-0.13	-0.04	0.07	-0.06	0.29
	Paraglomus	0.04	0.25	-0.05	0.22	0.06	0.16	0.12	0.19	0.18	**0.35***	0.26	-0.02	0.22	-0.01	0.25	-0.10
	Gigaspora	0.05	-0.06	-0.15	0.15	0.00	0.06	0.03	-0.04	-0.06	0.11	-0.03	0.04	-0.02	-0.08	-0.01	0.13
	Scutellospora	0.22	0.22	**0.39****	0.27	0.12	0.14	0.18	0.12	0.17	-0.13	0.08	-0.18	0.15	0.09	0.27	0.15

Funneliformis	0.29	0.05	0.08	**0.37***	0.18	-0.07	0.21	0.04	0.23	0.18	0.20	-0.18	0.18	0.17	**0.36***	0.13
Enterophospora	0.07	-0.03	0.03	-0.06	0.12	-0.06	0.07	0.18	0.16	0.23	0.22	0.16	0.28	-0.09	0.18	**0.46****
Archeospora	-0.15	-0.07	-0.04	0.05	-0.04	-0.07	-0.04	0.24	**0.30***	0.02	0.25	0.01	0.18	-0.15	0.19	0.16
Ambispora	0.21	-0.02	0.05	-0.02	0.27	0.04	0.22	-0.05	-0.08	0.01	-0.05	0.06	0.03	0.21	0.01	0.18

CHAPTER FIVE: DISCUSSION

5.1 Effect of forest conversion on soil chemical properties

Forest conversion to other land use types had strong significant effect on soil chemical properties, with most elements being relatively lower in potato fields compared to those in natural forest. Removal of vegetation, which characterize forest conversion, significantly modify soil physicochemical properties partly due to reductions in the amount of litter inputs (Ayres *et al.*, 2009; Pérez-Bejarano *et al.*, 2010). Conventional management practices like mechanical soil disturbance, fertilization, monocropping and removal of crop residues after harvesting contribute significantly to changes observed in soil properties (Banerjee *et al.*, 2019). Soils under all land use types were moderately acidic and soils in the study area have been described as acidic which may be associated with acidic parent material, high rainfall amounts that causes leaching of cations and mineral fertilizer application (Mugo *et al.*, 2020). The lowest soil pH in potato fields may be attributed to continued use of inorganic fertilizers, lower litter inputs and possibly reduced soil organic matter in the soil. Continued application of inorganic fertilizers, especially DAP which is commonly used by potato farmers has been shown to further lower soil pH (Janessens *et al.*, 2013; Muthoni and Nyamongo, 2009). The lower soil pH conversely limit availability of some nutrients such as N, P, K, and this may also explain lower nutrient content in potato fields. Tillage in potato fields may also account for lower nutrient content because it exposes soil to higher temperatures, and soil organic matter to microbial attack hence accelerating decomposition and mineralization (Awiti *et al.*, 2008; Groppo *et al.*, 2015; Wei *et al.*, 2014). On the other hand, soils under cypress plantation were also relatively acidic and this may be arising from the chemical composition of cypress litter. For example, coniferous litter contain low concentrations of basic cations and produce considerable amounts of organic acids hence they cause soil acidification (Iwashima *et al.*, 2012; Zajícová and Chuman, 2019). This study's results are also in agreement with other studies reporting low content of soil nutrients under plantation forests (Chen *et al.*, 2000; Yang *et al.*, 2009). Soils under natural forest exhibited significantly higher nutrient content possibly resulting from diverse plant composition and thus sustained addition of organic inputs. Soil organic matter help maintain the capacity of soil to retain nutrients due to improved aggregation (Mugo *et al.*, 2020). Furthermore, the permanent vegetation cover in forests also allow closed nutrient cycling hence there would be minimal nutrient loss from the system which commonly happens

through crop harvests and accelerated soil erosion. Litter from broadleaved vegetation, which characterized natural forest in the study area, have higher content of N, P, K and Ca than those of conifers (Iwashima *et al.*, 2012). Therefore, forest conversion to agricultural fields would lead to loss of soil nutrients. Similar observations in the decline of soil nutrient content following deforestation have also been reported (Awoonor *et al.*, 2022; Demessie *et al.*, 2013; Jafarian and Kavian, 2013; Yang *et al.*, 2009). Nonetheless, a few studies have reported contrasting results. For example, Muchane *et al.* (2012) found higher soil nutrient concentrations (N, P and K) in agricultural ecosystems than natural ecosystems. The authors attributed these results to increased use of fertilizers. However, such changes are not sustainable in the long term, because of the constant nutrient mining and export from agroecosystems with inadequate nutrient replenishment. In addition, the gradual decline in SOM means that these nutrients are less protected and thus are more susceptible to loss through soil erosion, volatilization or leaching. Therefore, cultivated agricultural lands would continue to be deficient in nutrients even though they are supplemented with mineral fertilizers as is clearly shown by the current study.

5.2 Influence of land use type on distribution of soil P fractions

Labile P fractions were relatively low in natural forest and increased in cultivated potato fields. It is suggested that much of labile P in cultivated soils is in inorganic forms and in forest soils as organic P (Qiong *et al.*, 2008), which is consistent with the results of the study. The high content of readily and moderately labile P in potato fields may be attributed to the application of inorganic fertilizers which elevates labile P pools including $NaHCO_3$ and NaOH-P which are considered sinks for applied P (Henriquez, 2002). Lower soil pH could also have influenced P partitioning especially in NaOH fraction which is associated with Al and Fe oxides which are more active in acidic soil conditions leading to higher concentration of P in this fraction (Bayuelo-Jiménez *et al.*, 2020; Richardson *et al.*, 2009). Soil microbial activity also influence P mobilization and is mediated by increased nutrient availability (e.g., N) which was negatively affected by potato cultivation (Kunito *et al.*, 2018; Yang *et al.*, 2015). Other factors such as litter input significantly influence P distribution and an increase in litter deposition would lead to an increase in labile P (Maranguit *et al.*, 2017; Zhu *et al.*, 2021). Nonetheless, NaOH-P_o did not change even with different litter input among the land use types showing that litter input was of insignificant influence, and thus this is supported the findings of Gatiboni *et al.* (2017) which show insignificant

correlation between SOC and NaOH-P_o. Phiri *et al.* (2001) also found high proportion of labile P in fallow (enriched with Calliandra and Tithonia) and maize-bean crop rotation systems in comparison to a natural fallow. Notably, sonicate NaOH-P_o was considerably higher than other labile P fractions in natural forest which may be due to the absence of tillage which disintegrate soil aggregates hence exposing protected nutrients to mineralization. Animal grazing in pastures have been shown to exert significant influence on labile P through manure addition to the soil (Chirino-Valle *et al.*, 2016; Morlue *et al.*, 2021). For example, about 60-95% of P used by plants and taken up by animals through grazing is returned to soil in form of litter and animal excreta (Condron *et al.*, 2005). In addition, secretion of P mobilizing organic acids by grasses and accumulation of SOM via root residues and litter recycles P into labile pool (Almeida *et al.*, 2018), and thus these factors may explain the high content of labile P in grazed pastures. Non-labile P was higher in natural forest nearly twice that found in other land use types and this could be attributed in part to greater accumulation of SOM which enhances nutrient retention including P. The absence of soil mechanical disturbance means that natural forest soils are less exposed to external forces such as surface runoff and heating that would accelerate P mineralization and loss. However, cypress plantation showed an overall lower P content in labile and non-labile fractions which could be attributed to tree characteristics such as fast growth rate requiring higher nutrient uptake, lower litter quality and quantity and poor understory vegetation. It has been shown that pine, eucalyptus and cypress trees decrease organic P content and in some cases, utilize even non-labile P (Chen *et al.*, 2003; 2008; Gatiboni *et al.*, 2017). This has been associated with enhanced biological activities such as P uptake, enzymatic activities and mycorrhizal associations as well as changes in soil pH. Therefore, exotic tree plantations may seem effective in utilization of all P fractions, but it may not be a desirable land use system in restoring or maintaining P fertility. This study evidently shows that forest conversion leads to reduced non-labile P pool hence decreasing P stocks for long term sustainability of ecosystems. Furthermore, maintaining crop management practices such as fertilizer application may not alone be sufficient to maintain soil fertility for longer period of time since such practices may not fully offset nutrient losses associated with land use change.

5.3 Effects of land use type on the abundance and diversity of AMF

Spores mostly dominate croplands as a result of frequent soil disturbance and intermittent root growth while mycelia persist in forests due to minimal or absence of disturbance and presence of permanent root growth. These attributes partly explain the differences in spore abundance between agricultural fields and forested lands hence may imply that AMF existed mostly in mycelia in forest soils and in spores in potato fields explaining the higher spore abundance. Moreover, tree association with ectomycorrhizal fungi and lack of undergrowth vegetation in forest plantation may also be attributed to the low spore abundance and diversity in cypress plantation. AMF are also sensitive to soil management, for example, fertilizer application increases soil available P greatly affecting AMF spore production. Wang *et al.* (2015) reported that AMF species respond differently to soil nutrient availability. For instance, the authors found some species to prefer soils with high available P, while others thrive well in low available P and still others tolerate both extremes. However, Belay *et al.* (2015) reported a negative relationship between soil available P and spore density. Farming systems characterized by low input are reported to maintain high AMF diversity compared to high input (Muchane *et al.*, 2012). Since most farmers apply sub-optimal fertilizers and use other agrochemicals in their farms, this may have also significantly contributed to high sporulation in potato fields. Even though increasing land use intensity may lead to a reduction in AMF species richness, it may also lead to selective stimulation of species which are slow to colonize roots but produce spores more rapidly (Wang *et al.*, 2015). Grazed pastures likewise exhibited high spore abundance which may be attributed to trampling and grazing by animals which affect grass growth and increase soil disturbance, which in turn limit carbon investment below ground for establishment of mycorrhizal association and spore production. It is also likely that members of Poaceae family support high spore production partly due to greater root biomass by grasses as reported by Jefwa *et al.* (2009). Shannon-Wiener and taxonomic richness indices showed potato fields and grazed pastures to be more diverse and rich in AMF spores which is consistent with other studies (Moora *et al.*, 2014; Wang *et al.*, 2015). However, the results of this study were inconsistent with other studies that have reported significant effects of land use change on AMF diversity (de Leon *et al.*, 2018). The fact that potato fields had higher number of AMF genera shows that agricultural lands stimulate AMF development and thus may be utilized to better crop productivity and resilience of agroecosystems, owing to the immense benefits of AMF to the plant and soil. The abundance of *Glomus* and *Acaulospora spp* has been

found in most soils in the tropics (e.g., Campos *et al.*, 2018; Muchane *et al.*, 2012) although some studies have reported the abundance of *Scutellospora*, *Funneliformis* and *Claroideoglomus spp* (Belay *et al.*, 2015). Some of these species produce spores in large numbers but small-sized which distribute more easily, can germinate from mycorrhizal roots or mycelial fragments and adapt well to diverse environmental conditions (Chandrasekeran and Mahalingam, 2014). Within AMF community, there are species which are associated with certain environments, while others are generalists being found in all environments and this is mostly shaped by soil characteristics and plant type (Sharma *et al.*, 2013). For example, *Gigaspora* are mostly found in undisturbed soils but to a lesser extent in disturbed soils as depicted by the findings of this study and other studies such as (Jefwa *et al.*, 2009). Others like *Paraglomus* are strongly associated with disturbed ecosystems and managed grasslands (Van der Heyde *et al.*, 2017), which corresponds with this study which found this species to be present only in grazed pastures and potato fields. Similarly, *Archaeospora* was only found in natural forest and potato fields. *Ambispora* has been strongly associated with fertilization (Wang *et al.*, 2011) and this could explain its occurrence only in potato fields. Soil pH, organic matter content, P and N influence AMF community implying that a change in these soil properties would significantly alter AMF population and diversity (Wang *et al.*, 2015). *Glomus*, for instance, divert P and K into their spores and hyphae when they experience carbon starvation (Hammer *et al.*, 2011), pointing out to a possible limitation in spore development and hyphal growth in soils with low nutrient availability. Root colonization in plants did not differ across land use types and was generally low showing that soils supplied plants with sufficient nutrients reducing plants' dependence on AMF for increased nutrient uptake. Therefore, AMF-plant association seems to be controlled by plant's nutrient need and the capacity of soils to meet this need and at the same time the kind of benefits AMF provide to the host plant (Banerjee *et al.*, 2019; Johri *et al.*, 2015).

CHAPTER SIX: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Forest conversion to other land uses such as forest plantation, grazed pastures or cultivated croplands had significant influence on soil properties and arbuscular mycorrhizal fungi. Soil chemical properties were higher in natural forest than in cypress forest plantation, grazed pastures and potato fields showing that converting natural forests for other uses significantly alter soil chemical properties thus may influence nutrient availability for crop production. Litter collected from natural forest had higher chemical properties than those collected from cypress forest except lignin content which was lower.

Readily and moderately labile P fractions were relatively higher in potato fields and grazed pastures than forest sites which may be due to farming and soil management practices which are shown to increase the content of labile P in soil. Non-labile P was higher in natural forest, nearly twice as that found in potato fields, cypress forest plantation and grazed pastures which may be due to increased SOM content and reduced P loss through erosion or leaching.

Total spore count was higher in both potato fields and grazed pastures compared to natural forest and cypress forest plantation. *Glomus* and *Acaulospora* were significantly affected by land use type and were most abundant among AMF genera and in soils collected from potato fields. Individual AMF genera showed weak to strong or no correlation with soil chemical properties and P fractions. Therefore, the results of this study show that replacing natural forests with forest plantations and agricultural production significantly alter soil chemical and biological properties ultimately affecting soil fertility and ecosystem functioning.

6.2 Recommendations

1. There is need to adopt farming practices such as crop rotation or intercropping particularly with leguminous plant species in growing potato to ensure that soil fertility and conservation is maintained.

2. Multipurpose trees and shrubs should be integrated through agroforestry practice into agricultural production to maximize on the ecosystem services that trees and shrubs provide. Fodder tree species could be grown in grazed pastures which not only contribute to improvement of soil properties but also provide nutritive fodder for livestock, fuelwood, construction materials among other benefits.

3. Besides agroforestry, other farming practices that ensure conservation of soil such as conservation agriculture should be tested, validated and promoted.

REFERENCES

Aguiar, A. D. C. F., Cândido, C. S., Carvalho, C. S., Monroe, P. H. M., and de Moura, E. G. (2013). Organic matter fraction and pools of phosphorus as indicators of the impact of land use in the Amazonian periphery. Ecological Indicators, 30, 158-164.

Alele, P. O., Sheil, D., Surget-Groba, Y., Lingling, S., and Cannon, C. H. (2014). How does conversion of natural tropical rainforest ecosystems affect soil bacterial and fungal communities in the Nile river watershed of Uganda?. PLoS One, 9, e104818.

Almeida, D. S., Penn, C. J., and Rosolem, C. A. (2018). Assessment of phosphorus availability in soil cultivated with ruzigrass. Geoderma, 312, 64-73.

Anderson, J.M. and Ingram, J.S.I. (1993). Tropical Soil Biology and Fertility: A Handbook of Methods, CAB International, Wallingford, UK. pp. 68-71.

Awiti, A. O., Walsh, M. G., and Kinyamario, J. (2008). Dynamics of topsoil carbon and nitrogen along a tropical forest–cropland chronosequence: Evidence from stable isotope analysis and spectroscopy. Agriculture, ecosystems & environment, 127, 265-272.

Awoonor, J. K., Adiyah, F., and Dogbey, B. F. (2022). Land-Use Change on Soil C and N Stocks in the Humid Savannah Agro-Ecological Zone of Ghana. Journal of Environmental Protection, 13, 32-68.

Ayres, E., Steltzer, H., Berg, S., Wallenstein, M. D., Simmons, B. L., and Wall, D. H. (2009). Tree species traits influence soil physical, chemical, and biological properties in high elevation forests. Plos One, 4, e5964.

Bainard, L. D., Klironomos, J. N. and Gordon, A. M. (2011). Arbuscular mycorrhizal fungi in tree-based intercropping systems: A review of their abundance and diversity. Pedobiologia, 54, 57–61.

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A. Y., Gattinger, A. and Van Der Heijden, M. G. (2019). Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. The ISME journal, 13, 1722-1736.

Bayuelo-Jiménez, J. S., Muraoka, T., de la Cruz-Torres, E., Quintero-Ponce, E., Paredes-Gutiérrez, L. C., and Zaman, M. (2020). Phosphorus fractions and dynamics as affected by land-use changes in the Central Mexican highlands. Soil Use and Management, 36, 240-249.

Begum, N., Qin, C., Ahanger, M. A., Raza, S., Khan, M. I., Ashraf, M., Ahmed, N. and Zhang, L. (2019). Role of Arbuscular Mycorrhizal Fungi in Plant Growth Regulation : Implications in Abiotic Stress Tolerance. 10, 1–15.

Belay, Z., Vestberg, M., and Assefa, F. (2015). Diversty and abundance of arbuscular mycorrhizal fungi across different land use types in a humid low land area of Ethiopia. Tropical and Subtropical Agroecosystems, 18, 47-69.

Benhin, J. K. (2006). Agriculture and deforestation in the tropics: a critical theoretical and empirical review. AMBIO: A Journal of the Human Environment, 35, 9-16.

Betencourt, E., Duputel, M., Colomb, B., Desclaux, D., and Hinsinger, P. (2012). Intercropping promotes the ability of durum wheat and chickpea to increase rhizosphere phosphorus availability in a low P soil. Soil Biology and Biochemistry, 46, 181–190.

Campos, P., Borie, F., Cornejo, P., López-Ráez, J. A., López-García, A., and Seguel, A. (2018). Phosphorus acquisition efficiency related to root traits: Is mycorrhizal symbiosis a key factor to wheat and barley cropping? Frontiers in Plant Science, 9, 1–21.

Carbonnel, S., and Gutjahr, C. (2014). Control of arbuscular mycorrhiza development by nutrient signals. Frontiers in Plant Science, 5, 462.

Carter, M. (Ed.), and Gregorich, E. (Ed.). (2007). Soil Sampling and Methods of Analysis (2nd ed.). Boca Raton: CRC Press. URL https://doi.org/10.1201/9781420005271

Chandrasekeran, A., and Mahalingam, U.P. (2014). Diversity of Arbuscular Mycorrhizae Fungi from Orchard Ecosystem. Journal of Plant Pathology and Microbiology, 5, 1-6.

Chen, M., Arato, M., Borghi, L., Nouri, E., and Reinhardt, D. (2018). Beneficial services of arbuscular mycorrhizal fungi–from ecology to application. Frontiers in Plant Science, 9, 1270.

Chen, C. R., Condron, L. M., Davis, M. R., and Sherlock, R. R. (2000). Effects of afforestation on phosphorus dynamics and biological properties in a New Zealand grassland soil. Plant and Soil, 220, 151-163.

Chen, C. R., Condron, L. M., Davis, M. R., and Sherlock, R. R. (2003). Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. Forest Ecology and Management, 177, 539-557.

Chen, C. R., Condron, L. M., and Xu, Z. H. (2008). Impacts of grassland afforestation with coniferous trees on soil phosphorus dynamics and associated microbial processes: a review. Forest Ecology and Management, 255, 396-409.

Chimdi, A., Esala, M., and Ylivainio, K. (2014). Sequential fractionation patterns of soil phosphorus collected from different land use systems of Dire Inchine District, West Shawa Zone, Ethiopia. American-Eurasian Journal of Scientific Research, 9, 51-57.

Chirino-Valle, I., Davis, M. R., and Condron, L. M. (2016). Impact of different tree species on soil phosphorus immediately following grassland afforestation. Journal of soil science and plant nutrition, 16, 477-489.

Chu, Q., Zhang, L., Zhou, J., Yuan, L., Chen, F., Zhang, F., Feng, G., and Rengel, Z. (2020). Soil plant-available phosphorus levels and maize genotypes determine the phosphorus acquisition efficiency and contribution of mycorrhizal pathway. Plant and Soil, 449, 357–371.

Condron, L. M., Turner, B. L., and Cade-Menun, B. J. (2005). Chemistry and dynamics of soil organic phosphorus. In: Thomas Sims, J., Sharpley, N. A., and Westermann, T. D. (Eds.). Phosphorus. Agriculture and the environment, 46, 87-121.

Daniels, B. A., and Skipper, H. D. (1982). Methods for the recovery and quantitative estimation of propagules from soil. In: Schneck NC. (Eds.) Methods and principles of mycorrhizal Research (pp. 29-85). American Phytopathological Society, St Paul, Minnesota.

Davari, M., Gholami, L., Nabiollahi, K., Homaee, M., and Jafari, H. J. (2020). Deforestation and cultivation of sparse forest impacts on soil quality (case study: West Iran, Baneh). Soil and Tillage Research, 198, 104504.

de Graaff, M. A., Hornslein, N., Throop, H. L., Kardol, P., and van Diepen, L. T. (2019). Effects of agricultural intensification on soil biodiversity and implications for ecosystem functioning: a meta-analysis. Advances in Agronomy 155, 1-44.

de Leon, D. G., Davison, J., Moora, M., Öpik, M., Feng, H., Hiiesalu, I., and Zobel, M. (2018). Anthropogenic disturbance equalizes diversity levels in arbuscular mycorrhizal fungal communities. Global Change Biology, 24, 2649-2659.

De Schrijver, A., Vesterdal, L., Hansen, K., De Frenne, P., Augusto, L., Achat, D. L., and Verheyen, K. (2012). Four decades of post-agricultural forest development have caused major redistributions of soil phosphorus fractions. Oecologia, 169, 221-234.

Delavaux, C. S., Smith-Ramesh, L. M., and Kuebbing, S. E. (2017). Beyond nutrients: a meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. Ecology, 98, 2111-2119.

Demessie, A., Singh, B. R., and Lal, R. (2013). Soil carbon and nitrogen stocks under chronosequence of farm and traditional agroforestry land uses in Gambo District, Southern Ethiopia. Nutrient Cycling in Agroecosystems, 95, 365-375.

Desjardins, T., Barros, E., Sarrazin, M., Girardin, C., and Mariotti, A. (2004). Effects of forest conversion to pasture on soil carbon content and dynamics in Brazilian Amazonia. Agriculture, Ecosystems & Environment, 103, 365-373.

Dobo, B., Asefa, F., and Asfaw, Z. (2018). Effect of tree-enset-coffee based agro-forestry practices on arbuscular mycorrhizal fungi (AMF) species diversity and spore density. Agroforestry systems, 92, 525-540.

Don, A., Schumacher, J., and Freibauer, A. (2011). Impact of tropical land-use change on soil organic carbon stocks–a meta-analysis. Global Change Biology, 17, 1658-1670.

Eclesia, R. P., Jobbagy, E. G., Jackson, R. B., Biganzoli, F., and Piñeiro, G. (2012). Shifts in soil organic carbon for plantation and pasture establishment in native forests and grasslands of South America. Global Change Biology, 18, 3237-3251.

Evrendilek, F., Celik, I., and Kilic, S. (2004). Changes in soil organic carbon and other physical soil properties along adjacent Mediterranean forest, grassland, and cropland ecosystems in Turkey. Journal of arid environments, 59, 743-752.

Faggioli, V. S., Cabello, M. N., Grilli, G., Vasar, M., Covacevich, F., and Öpik, M. (2019). Root colonizing and soil borne communities of arbuscular mycorrhizal fungi differ among soybean fields with contrasting historical land use. Agriculture, Ecosystems and Environment, 269, 174–182.

Franco, A. L., Sobral, B. W., Silva, A. L., and Wall, D. H. (2019). Amazonian deforestation and soil biodiversity. Conservation Biology, 33, 590-600.

Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. Annual Review of Ecology, Evolution and Systematics, 50, 237-259.

Friberg, S. (2001). Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa. CBM: s Skriftserie, 3, 53-80.

Garcia de Leon, D., Davison, J., Moora, M., Öpik, M., Feng, H., Hiiesalu, I., and Zobel, M. (2018). Anthropogenic disturbance equalizes diversity levels in arbuscular mycorrhizal fungal communities. Global Change Biology, 24, 2649-2659.

Garcia-Montiel, D. C., Neill, C., Melillo, J., Thomas, S., Steudler, P. A., and Cerri, C. C. (2000). Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon. Soil Science Society of America Journal, 64, 1792-1804.

Gatiboni, L. C., Vargas, C. O., Albuquerque, J. A., Almeida, J. A., Stahl, J., Chaves, D. M., and Rauber, L. P. (2017). Phosphorus fractions in soil after successive crops of *Pinus taeda* L. without fertilization. Ciência Rural, 47, 1-8.

Giovannetti, M., and Mosse, B. (1980). An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New phytologist, 84, 489-500.

Glaze-Corcoran, S., Hashemi, M., Sadeghpour, A., Jahanzad, E., Keshavarz Afshar, R., Liu, X., and Herbert, S. J. (2020). Understanding intercropping to improve agricultural resiliency and environmental sustainability. Advances in Agronomy, 162, 199-256.

Grant, C., Bittman, S., Montreal, M., Plenchette, C., and Morel, C. (2005). Soil and fertilizer phosphorus: Effects on plant P supply and mycorrhizal development. Canadian Journal of Plant Science, 85, 3–14.

Groppo, J. D., Lins, S. R. M., Camargo, P. B. D., Assad, E. D., Pinto, H. S., Martins, S. C., and Martinelli, L. A. (2015). Changes in soil carbon, nitrogen, and phosphorus due to land-use changes in Brazil. Biogeosciences, 12, 4765-4780.

Hammer, E. C., Pallon, J., Wallander, H., and Olsson, P. A. (2011). Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. Federation of European Microbiological Societies microbiology ecology, 76, 236-244.

Hedley, M. J., Stewart, J. W. B., and Chauhan, B. (1982). Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. Soil Science Society of America Journal, 46, 970-976.

Helfenstein, J., Pistocchi, C., Oberson, A., Tamburini, F., Goll, D. S., and Frossard, E. (2020). Estimates of mean residence times of phosphorus in commonly considered inorganic soil phosphorus pools. Biogeosciences, 17, 441-454.

Henriquez, C. (2002). Assessing soil phosphorus status under different agronomic land use. Retrospective Theses and Dissertations Paper, lowa State University.

Hinds, A., and Lowe, L. E. (1980). Ammonium-N determination. Soil nitrogen. Berthelot reaction. Soil Science and Plant Analysis, 11, 469–475.

Hinsinger, P., Betencourt, E., Bernard, L., Brauman, A., Plassard, C., Shen, J., Tang, X., and Zhang, F. (2011). P for two, sharing a scarce resource: Soil phosphorus acquisition in the rhizosphere of intercropped species. Plant Physiology, 156, 1078–1086.

Igiehon, N. O., and Babalola, O. O. (2017). Biofertilizers and sustainable agriculture: exploring arbuscular mycorrhizal fungi. Applied microbiology and biotechnology, 101, 4871-4881.

INVAM (International Culture Collection of Arbuscular and Vesicular-Arbuscular Endomycorrhizal Fungi, see homepage: www.invam.wvu.edu).

Iwashima, N., Masunaga, T., Fujimaki, R., Toyota, A., Tayasu, I., Hiura, T., and Kaneko, N. (2012). Effect of vegetation switch on soil chemical properties. Soil Science and Plant Nutrition, 58, 783-792.

Jaetzold, R., and Schmidt, H. (1983). Farm management handbook of Kenya, Vol. II/B. Ministry of Agriculture. Kenya and German Agency for Technical Cooperation (GTZ), Nairobi, Kenya.

Jaetzold, R., Schemidt, H., Hornetz, B., and Shisanya, C. (2006). Farm Management Handbook of Kenya, Vol. II/A. Ministry of Agriculture. Kenya and German Agency for Technical Cooperation (GTZ), Nairobi, Kenya.

Jafarian, Z., and Kavian, A. (2013). Effects of land-use change on soil organic carbon and nitrogen. Communications in soil science and plant analysis, 44, 339-346.

Janessens, S. R. M., Wiersema, S. G., Goos, H., and Wiersma, W. (2013). The value chain for seed and ware potatoes in Kenya. Opportunities for development. (Memorandum / LEI Wageningen UR; No. 13-080). LEI Wageningen UR. https://edepot.wur.nl/279729

Jansa, J., Bukovská, P., and Gryndler, M. (2013). Mycorrhizal hyphae as ecological niche for highly specialized hypersymbionts–or just soil free-riders? Frontiers in Plant Science, 4, 134.

Jefwa, J., Mungatu, J., Okoth, P., Muya, E., Roimen, H., and Njuguini, S. (2009). Influence of land use types on occurrence of arbuscular mycorrhizal fungi in the high altitude regions of Mt. Kenya. Tropical and Subtropical Agroecosystems, 11, 277-290.

Jefwa, J. M., Okoth, S., Wachira, P., Karanja, N., Kahindi, J., Njuguini, S., Ichami, S., Mung'atu, J., Okoth, P., and Huising, J. (2012). Impact of land use types and farming practices on

occurrence of arbuscular mycorrhizal fungi (AMF) Taita-Taveta district in Kenya. Agriculture, Ecosystems and Environment, 157, 32–39.

Johri, A. K., Oelmüller, R., Dua, M., Yadav, V., Kumar, M., Tuteja, N., and Stroud, R. M. (2015). Fungal association and utilization of phosphate by plants: success, limitations, and future prospects. Frontiers in microbiology, 6, 984.

Kaguongo, W., Gildemacher, P., Demo, P., Wagoire, W., Kinyae, P., Andrade, J., and Thiele, G. (2008). Farmer practices and adoption of improved potato varieties in Kenya and Uganda. International Potato Center.

Kamau, S., Awiti A., Shah, S., and Liebetrau, L. (2019). A food systems approach to understanding food and nutrition insecurity in Kenya: A case study of the Nyandarua County. Technical Report, East Africa Institute of the Aga Khan University. DOI: 10.13140/RG.2.2.19481.44645

Kamau, S., Barrios, E., Karanja, N. K., Ayuke, F. O., and Lehmann, J. (2017). Spatial variation of soil macrofauna and nutrients in tropical agricultural systems influenced by historical charcoal production in South Nandi, Kenya. Applied Soil Ecology, 119, 286-293.

Kamau, S., Barrios, E., Karanja, N. K., Ayuke, F. O., and Lehmann, J. (2020). Dominant tree species and earthworms affect soil aggregation and carbon content along a soil degradation gradient in an agricultural landscape. Geoderma, 359. https://doi.org/10.1016/j.geoderma.2019.113983

Kehri, H. K., Akhtar, O., Zoomi, I., and Pandey, D. (2018). Arbuscular mycorrhizal fungi: taxonomy and its systematics. International Journal of Life Sciences Research, 6, 58-71.

KFS. (2010). Aberdare Forest Reserve Management Plan. Kenya Forest Service, Nairobi, Kenya.

KNBS. (2019). 2019 Kenya Population and Housing Census Volume I: Population by County and Sub-County. Kenya National Bureau of Statistics, Nairobi, Kenya.

Kibunja, C. N., Ndungu-Magiroi, K. W., Wamae, D. K., Mwangi, T. J., Nafuma, L., Koech, M. N., and Kitonyo, E. M. (2017). Optimizing fertilizer use within the context of integrated soil fertility management in Kenya. Fertilizer use optimization in sub-Saharan Africa, 82-99.

Kim, S. J., Eo, J. K., Lee, E. H., Park, H., and Eom, A. H. (2017). Effects of arbuscular mycorrhizal fungi and soil conditions on crop plant growth. Mycobiology, 45, 20-24.

Konieczny, A., and Kowalska, I. (2017). Arbuscular mycorrhiza-partner in communication. Acta Scientiarum Polonorum-Hortorum Cultus, 16, 73-78.

Kunlanit, B., Khwanchum, L., and Vityakon, P. (2020). Land use changes affecting soil organic matter accumulation in topsoil and subsoil in Northeast Thailand. Applied and Environmental Soil Science, 2020, 1-15.

Kunito, T., Hiruta, N., Miyagishi, Y., Sumi, H., and Moro, H. (2018). Changes in phosphorus fractions caused by increased microbial activity in forest soil in a short-term incubation study. Chemical Speciation and Bioavailability, 30, 9-13.

Lee, E. H., Eo, J. K., Ka, K. H., and Eom, A. H. (2013). Diversity of arbuscular mycorrhizal fungi and their roles in ecosystems. Mycobiology, 41, 121-125.

Lemenih, M., Karltun, E., and Olsson, M. (2005). Assessing soil chemical and physical property responses to deforestation and subsequent cultivation in smallholders farming system in Ethiopia. Agriculture, Ecosystems & Environment, 105, 373-386.

Li, C., Li, H., Hoffland, E., Zhang, F., Zhang, J., and Kuyper, T. W. (2022). Common Mycorrhizal Networks Asymmetrically Contribute to Increased N and P Acquisition by Millet/Chickpea Mixture. Plant and soil, 2022, 1-15.

Mafaziya, F., and Madawala, S. (2015). Abundance, richness and root colonization of arbuscular mycorrhizal fungi in natural and semi-natural land use types at upper Hantana. Ceylon Journal of Science (Biological Sciences), 44, 25-34.

Maharjan, M., Maranguit, D., and Kuzyakov, Y. (2018). Phosphorus fractions in subtropical soils depending on land use. European Journal of Soil Biology, 87, 17-24.

Mahmood, M., Tian, Y., Ma, Q., Ahmed, W., Mehmood, S., Hui, X., and Wang, Z. (2020). Changes in Phosphorus Fractions and Its Availability Status in Relation to Long Term P Fertilization in Loess Plateau of China. Agronomy, 10, 1818.

Mandere, N., Anderberg, S., Armah, F. A., and Abaya, S. W. (2011). Assessing the contribution of alternative agriculture to poverty reduction and employment creation: A case study of sugar beet cultivation in Kenya. African Journal of Agricultural Research, 6, 440–450.

Maranguit, D., Guillaume, T., and Kuzyakov, Y. (2017). Land-use change affects phosphorus fractions in highly weathered tropical soils. Catena, 149, 385-393.

McGrath, D. A., Smith, C. K., Gholz, H. L., and de Assis Oliveira, F. (2001). Effects of land-use change on soil nutrient dynamics in Amazonia. Ecosystems, 4, 625-645.

Moora, M., Davison, J., Öpik, M., Metsis, M., Saks, Ü., Jairus, T., Vasar, M., and Zobel, M. (2014). Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. FEMS Microbiology Ecology, 90, 609–621.

Morlue B., Kamau S., Ayuke F.O., Kironchi G., 2021. Land use change, but not soil macrofauna, affects soil aggregates and aggregate-associated C content in central highlands of Kenya. Journal of Soils and Sediments 21, 1360–1370.

Muchane, M. N., Muchane, M., Mugoya, C., and Clet, W. (2012). Effect of land use system on Arbuscular Mycorrhiza fungi in Maasai Mara ecosystem, Kenya. African Journal of Microbiology Research, 6, 3904-3916.

Mugo, J. N., Karanja, N. N., Gachene, C. K., Dittert, K., Nyawade, S. O., and Schulte-Geldermann, E. (2020). Assessment of soil fertility and potato crop nutrient status in central and eastern highlands of Kenya. Scientific Reports, 10, 1-11.

Muindi, E. M. (2019). Understanding Soil Phosphorus. International Journal of Plant & Soil Science, 31, 1-18.

Murphy, J., and Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. Analytica chimica acta, 27, 31-36.

Murty, D., Kirschbaum, M. U., Mcmurtrie, R. E., and Mcgilvray, H. (2002). Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. Global change biology, 8, 105-123.

Muthoni, J. (2016). Soil fertility situation in potato producing Kenyan highlands-Case of KALRO-Tigoni. International Journal of horticulture, 6, 1-11.

Muthoni, J., Nyamongo, D. N., and Mbiyu, M. (2017). Climatic change, its likely impact on potato (*Solanum tuberosum* L.) production in Kenya and plausible coping measures. International Journal of Horticulture, 7, 115-123.

Muthoni, J., and Nyamongo, D.O. (2009). A review of constraints to ware Irish potatoes production in Kenya. Journal of Horticulture and Forestry, 1, 98-102.

Muthoni, J., Shimelis, H., and Melis, R. (2013). Potato production in Kenya: Farming systems and production constraints. Journal of Agricultural Science, 5, 182-197.

Nash, D. M., Haygarth, P. M., Turner, B. L., Condron, L. M., McDowell, R. W., Richardson, A. E., and Heaven, M. W. (2014). Using organic phosphorus to sustain pasture productivity: A perspective. Geoderma, 221, 11-19.

Negassa, W., and Leinweber, P. (2009). How does the Hedley sequential phosphorus fractionation reflect impacts of land use and management on soil phosphorus: A review. Journal of Plant Nutrition and Soil Science, 172, 305-325.

Nelson, D. W., and Sommers, L. E. (1996). Total carbon, organic carbon, and organic matter. Methods of soil analysis: Part 3 Chemical methods, 5, 961-1010.

Nishigaki, T., Sugihara, S., Kobayashi, K., Hashimoto, Y., Kilasara, M., Tanaka, H., and Funakawa, S. (2018). Fractionation of phosphorus in soils with different geological and soil physicochemical properties in southern Tanzania. Soil Science and Plant Nutrition, 64, 291-299.

Nunes, R. D. S., de Sousa, D. M. G., Goedert, W. J., de Oliveira, L. E. Z., Pavinato, P. S., and Pinheiro, T. D. (2020). Distribution of Soil Phosphorus Fractions as a Function of Long-Term Soil Tillage and Phosphate Fertilization Management. Frontiers in Earth Science, 8, 350.

Nyawade, S. O. (2015). Effect of potato (*Solanum tuberosum* L.) cropping systems on soil and nutrient losses through runoff in a humic nitisol. Doctoral dissertation, University of Nairobi.

Nyawade, S. O., Karanja, N. N., Gachene, C. K., Schulte-Geldermann, E., and Parker, M. (2018). Effect of potato hilling on soil temperature, soil moisture distribution and sediment yield on a sloping terrain. Soil and Tillage Research, 184, 24-36.

Owuor, S. O., Butterbach-Bahl, K., Guzha, A. C., Jacobs, S., Merbold, L., Rufino, M. C., and Breuer, L. (2018). Conversion of natural forest results in a significant degradation of soil hydraulic properties in the highlands of Kenya. Soil and tillage Research, 176, 36-44.

Pepe, A., Giovannetti, M., and Sbrana, C. (2020). Appressoria and phosphorus fluxes in mycorrhizal plants: connections between soil-and plant-based hyphae. Mycorrhiza, 30, 589-600.

Pérez-Bejarano, A., Mataix-Solera, J., Zornoza, R., Guerrero, C., Arcenegui, V., Mataix-Beneyto, J., and Cano-Amat, S. (2010). Influence of plant species on physical, chemical and biological soil properties in a Mediterranean forest soil. European Journal of Forest Research, 129, 15-24.

Philips, J. M., and Hayman, D. S. (1970). Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal for rapid assessment of infection. Transactions British Mycological Society, 55, 156-161.

Phiri, S., Barrios, E., Rao, I. M., and Singh, B. R. (2001). Changes in soil organic matter and phosphorus fractions under planted fallows and a crop rotation system on a Colombian volcanic-ash soil. Plant and Soil, 231, 211-223.

Pinho, R. C., Miller, R. P., and Aflaia, S. S. (2012). Agroforestry and improvement of soil fertility: a view from Amazonia. Applied and Environmental Soil Science, 2012, 1-11.

Powell, J. R., and Rillig, M. C. (2018). Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. New Phytologist, 220, 1059-1075.

Prasad, R., and Chakraborty, D. (2019). Phosphorus Basics: Understanding Phosphorus Forms and Their Cycling in the Soil. Alabama Cooperative Extension System. URL https://www.aces.edu/.

Pulido, S. J. B., Silva, I. C., and Robles, E. O. L. (2021). Effect of different land use on chemical properties of an Andosol in Michoacan, Mexico. Tropical and Subtropical Agroecosystems, 24, 121.

Qin, X. M., Zheng, Y., Tang, L., and Long, G. Q. (2017). Crop rhizospheric microbial community structure and functional diversity as affected by maize and potato intercropping. Journal of Plant Nutrition, 40, 2402-2412.

Qiong, Z. H. A. O., De-Hui, Z. E. N. G., Zhi-Ping, F. A. N., and Lee, D. K. (2008). Effect of land cover change on soil phosphorus fractions in Southeastern Horqin Sandy Land, Northern China. Pedosphere, 18, 741-748.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rachilo, J. R. (1978). Soil conditions in the Kinangop area: A preliminary investigation (Report No. 34). Ministry of Agriculture, Nairobi, Kenya.

Ranjan, K., Paula, F. S., Mueller, R. C., Jesus, E. D. C., Cenciani, K., Bohannan, B. J., and Rodrigues, J. L. (2015). Forest-to-pasture conversion increases the diversity of the phylum Verrucomicrobia in Amazon rainforest soils. Frontiers in microbiology, 6, 779.

Ratti, N., Kumar, S., Verma, H. N., and Gautam, S. P. (2001). Improvement in bioavailability of tricalcium phosphate to *Cymbopogon martinii* var. motia by rhizobacteria, AMF and Azospirillum inoculation. Microbiological research, 156, 145-149.

Richardson, A. E., Hocking, P. J., Simpson, R. J., and George, T. S. (2009). Plant mechanisms to optimise access to soil phosphorus. Crop and Pasture Science, 60, 124-143.

Rochange, S. (2010). Strigolactones and their role in arbuscular mycorrhizal symbiosis. In: Koltai H., Kapulnik Y. (Eds.). Arbuscular Mycorrhizas: Physiology and Function, (2nd ed., pp.73-90). Springer, Dordrecht. URL https://doi.org/10.1007/978-90-481-9489-6_4

Rosling, A., Midgley, M. G., Cheeke, T., Urbina, H., Fransson, P., and Phillips, R. P. (2016). Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto-and arbuscular mycorrhizal trees. New Phytologist, 209, 1184-1195.

Ryan, J., George, E., and Rashid, A. (2001). Soil and plant analysis laboratory manual (2nd ed., pp. 46-48). International Center for Agricultural Research in the Dry Areas (ICARDA) and the National Agricultural Research Centre (NARC). URL https://books.google.com/

Ryan, J., Ibrikci, H., Delgado, A., Torrent, J., Sommer, R., and Rashid, A. (2012). Significance of phosphorus for agriculture and the environment in the West Asia and North Africa region. Advances in Agronomy, 114, 91-153.

Saharan, K., Schütz, L., Kahmen, A., Wiemken, A., Boller, T., and Mathimaran, N. (2018). Finger millet growth and nutrient uptake is improved in intercropping with pigeon pea through "biofertilization" and "bioirrigation" mediated by arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria. Frontiers in Environmental Science, 6, 46.

Saltali, K., Kılıç, K., and Koçyigit, R. (2007). Changes in sequentially extracted phosphorus fractions in adjacent arable and grassland ecosystems. Arid Land Research and Management, 21, 81-89.

Sankaralingam, S., Kathiresan, D., Harinathan, B., Palpperumal, S., Shankar, T., Ramya, B., and Prabhu, D. (2016). Effect of arbuscular mycorrhizae fungi on growth and development of Carica papaya. Scientific Journal of Seoul Sciences, 4, 1–7.

Sanyal S.K., and De Datta S.K. (1991). Chemistry of Phosphorus Transformations in Soil. In: Stewart B.A. (Ed.) Advances in Soil Science. Springer, New York, NY. Advances in Soil Science, 16, 1-120.

Sato, S. (2003). Phosphorus sorption and desorption in a Brazilian Ultisol: Effects of pH and organic anions on phosphorus bioavailability. Doctoral Dissertation, University of Florida.

Schulte-Geldermann, E. 2013. Tackling low potato yields in Eastern Africa: an overview of constraints and potential strategies. In: Woldegiorgis, G., Schulz, S., and Berihun, B. (Eds.). Seed potato tuber production and dissemination, experiences, challenges and prospects: Proceedings. National Workshop on Seed Potato Tuber Production and Dissemination. Bahir

Dar (Ethiopia). 12-14 Mar 2012. (Ethiopia). Ethiopian Institute of Agricultural Research (EIAR), Amhara Regional Agricultural Research Institute (ARARI) and International Potato Center ISBN 978-99944-53-87-x. pp. 72-80.

Schwendenmann, L., and Pendall, E. (2006). Effects of forest conversion into grassland on soil aggregate structure and carbon storage in Panama: evidence from soil carbon fractionation and stable isotopes. Plant and Soil, 288, 217-232.

Scott, D. A., and Messina, M. G. (2010). Soil properties in 35 y old pine and hardwood plantations after conversion from mixed pine-hardwood forest. The American Midland Naturalist, 163, 197-211.

Sharma, C., Gupta, R. K., Pathak, R. K., and Choudhary, K. K. (2013). Seasonal Colonization of Arbuscular Mycorrhiza Fungi in the Roots of *Camellia sinensis* (Tea) in Different Tea Gardens of India. ISRN Biodiversity, 2013, 1–6.

Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., and Zhang, F. (2011). Phosphorus dynamics: from soil to plant. Plant physiology, 156, 997-1005.

Shi, Y., Ziadi, N., Messiga, A. J., Lalande, R., and Hu, Z. (2013). Changes in soil phosphorus fractions for a long-term corn-soybean rotation with tillage and phosphorus fertilization. Soil Science Society of America Journal, 77, 1402-1412.

Soka, G. E., and Ritchie, M. E. (2018). Arbuscular mycorrhizal spore composition and diversity associated with different land uses in a tropical savanna landscape, Tanzania. Applied Soil Ecology, 125, 222-232.

Solomon, D., Lehmann, J., Mamo, T., Fritzsche, F., and Zech, W. (2002). Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highlands. Geoderma, 105, 21-48.

Soltangheisi, A., de Moraes, M. T., Cherubin, M. R., Alvarez, D. O., de Souza, L. F., Bieluczyk, W., and de Camargo, P. B. (2019). Forest conversion to pasture affects soil phosphorus dynamics and nutritional status in Brazilian Amazon. Soil and Tillage Research, 194, 104330.

Srinivasan, R., Yandigeri, M. S., Kashyap, S., and Alagawadi, A. R. (2012). Effect of salt on survival and P-solubilization potential of phosphate solubilizing microorganisms from salt affected soils. Saudi Journal of Biological Sciences, 19, 427-434.

Stomph, T., Dordas, C., Baranger, A., de Rijk, J., Dong, B., Evers, J., and van der Werf, W. (2020). Designing intercrops for high yield, yield stability and efficient use of resources: are there principles? Advances in Agronomy, 160, 1-50.

Stover, H. J., Thorn, R. G., Bowles, J. M., Bernards, M. A., and Jacobs, C. R. (2012). Arbuscular mycorrhizal fungi and vascular plant species abundance and community structure in tallgrass prairies with varying agricultural disturbance histories. Applied Soil Ecology, 60, 61-70.

Su, Y. Y., and Guo, L. D. (2007). Arbuscular mycorrhizal fungi in non-grazed, restored and over-grazed grassland in the Inner Mongolia steppe. Mycorrhiza, 17, 689-693.

Syibli, M. A., Muhibuddin, A., and Djauhari, S. (2013). Arbuscular mycorrhiza fungi as an indicator of soil fertility. AGRIVITA, Journal of Agricultural Science, 35, 44-53.

Tanganelli, K. M. (2011). Sequential fractionation and water soluble phosphorus methods to investigate soil phosphorus in a long-term manure application. Doctoral dissertation, Oklahoma State University.

Taoheed, A. M., Ateka, E. M., and Losenge, T. (2018). Arbuscular mycorrhiza fungi promotes growth of tomato seedlings in the absence of phosphate in nutrient solution. Asian Journal of Natural and Applied Sciences, 7, 1-9.

Thirkell, T. J., Charters, M. D., Elliott, A. J., Sait, S. M, and Field, K. J. (2017). Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. Journal of Ecology, 105, 921-929.

Thomas Sims, J., and Pierzynski, G. M. (2005). Chemistry of phosphorus in soils. Chemical processes in soils, 8, 151-192.

Tikhonovich, I. A., and Provorov, N. A. (2007). Beneficial plant-microbe interactions. In: Dyakov, T. Y., Dzhavakhiya, G. V., and Korpela, T., (Eds.). Studies in plant science. In Comprehensive and Molecular Phytopathology (pp. 365–420). Elsiever.

Tolimir, M., Kresović, B., Životić, L., Dragović, S., Dragović, R., Sredojević, Z., and Gajić, B. (2020). The conversion of forestland into agricultural land without appropriate measures to conserve SOM leads to the degradation of physical and rheological soil properties. Scientific Reports, 10, 1-12.

Treseder, K. K. (2013). The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content. Plant and Soil, 371, 1–13.

van der Heyde, M., Ohsowski, B., Abbott, L. K., and Hart, M. (2017). Arbuscular mycorrhizal fungus responses to disturbance are context-dependent. Mycorrhiza, 27, 431-440.

Van Soest, P.J., and Wine, R.H. (1968). Determination of lignin and cellulose in acid-detergent fibre with permanganate. Association of Official Agricultural Chemists Journal 51, 780-785.

Veldkamp, E., Schmidt, M., Powers, J.S., and Corre, M.D. (2020). Deforestation and reforestation impacts on soils in the tropics. Nature Reviews Earth and Environment, 1, 590-605.

Verchot, L.V. (2010). Impacts of forest conversion to agriculture on microbial communities and microbial function. In Soil biology and agriculture in the tropics. Springer, Berlin, Heidelberg, pp. 45-63.

Wang, C., Gu, Z., Cui, H., Zhu, H., Fu, S., and Yao, Q. (2015). Differences in arbuscular mycorrhizal fungal community composition in soils of three land use types in subtropical hilly area of Southern China. PLoS One, 10, e0130983.

Wang, F. Y., Hu, J. L., Lin, X. G., Qin, S. W., and Wang, J. H. (2011). Arbuscular mycorrhizal fungal community structure and diversity in response to long-term fertilization: a field case from China. World Journal of Microbiology and Biotechnology, 27, 67-74.

Wang, J., Wang, G.G., Zhang, B., Yuan, Z., Fu, Z., Yuan, Y., and Zhang, J. (2019). Arbuscular mycorrhizal fungi associated with tree species in a planted forest of Eastern China. Forests, 10, 424.

Wang, Y., Chen, L., Xiang, W., Ouyang, S., Zhang, T., Zhang, X., and Kuzyakov, Y. (2021). Forest conversion to plantations: A meta-analysis of consequences for soil and microbial properties and functions. Global Change Biology, 27, 5643-5656.

Wei, X., Huang, L., Xiang, Y., Shao, M., Zhang, X., and Gale, W. (2014). The dynamics of soil OC and N after conversion of forest to cropland. Agricultural and forest meteorology, 194, 188-196.

Weldmichael, T. G., Michéli, E., and Simon, B. (2021). The response of soil physicochemical properties and soil microbial respiration to different land use types: A case of areas in Central-North Hungary region. Agrochemistry and Soil science, 2021, 1-16.

Were, K. O., Singh, B. R., and Dick, Ø. B. (2015). Effects of land cover changes on soil organic carbon and total nitrogen stocks in the Eastern Mau Forest Reserve, Kenya. In: Lal, R., Singh, B., Mwaseba, D., Kraybill, D., Hansen, D., and Eik, L. (Eds.). Sustainable

Intensification to Advance Food Security and enhance climate resilience in Africa (pp. 113-133). Springer, Cham.

Wittwer, R.A., Dorn, B., Jossi, W., and Van Der Heijden, M.G. (2017). Cover crops support ecological intensification of arable cropping systems. Scientific Reports, 7, 1-12.

Yang, Y., Guo, J., Chen, G., Yin, Y., Gao, R., and Lin, C. (2009). Effects of forest conversion on soil labile organic carbon fractions and aggregate stability in subtropical China. Plant and soil, 323, 153-162.

Yang, Q., Ravnskov, S., and Neumann, A.M. (2020). Nutrient uptake and growth of potato: Arbuscular mycorrhiza symbiosis interacts with quality and quantity of amended biochars. Journal of Plant Nutrition and Soil Science, 183, 220–232.

Yang, K., Zhu, J., Gu, J., Yu, L., and Wang, Z. (2015). Changes in soil phosphorus fractions after 9 years of continuous nitrogen addition in a Larix gmelinii plantation. Annals of Forest Science, 72, 435-442.

Zajícová, K., and Chuman, T. (2019). Effect of land use on soil chemical properties after 190 years of forest to agricultural land conversion. Soil and water research, 14, 121-131.

Zhang, Y., Bhattacharyya, R., Dalal, R. C., Wang, P., Menzies, N. W., and Kopittke, P. M. (2020). Impact of land use change and soil type on total phosphorus and its fractions in soil aggregates. Land Degradation and Development, 31, 828-841.

Zhu, X., Fang, X., Wang, L., Xiang, W., Alharbi, H. A., Lei, P., and Kuzyakov, Y. (2021). Regulation of soil phosphorus availability and composition during forest succession in subtropics. Forest Ecology and Management, 502, 119706.