PHOSPHORUS FRACTIONS AND ARBUSCULAR MYCORRHIZAL FUNGI AS INFLUENCED BY FOREST CONVERSION IN CENTRAL HIGHLANDS OF KENYA †

[FRACCIONES DE FÓSFORO Y HONGOS MICORRÍZICOS ARBUSCULARES INFLUENCIADOS POR LA CONVERSIÓN FORESTAL EN LAS TIERRAS ALTAS CENTRALES DE KENIA]

Gladys Cheruto[1,2*], Nancy N. Karanja[1] and Solomon Kamau[3]

[1]Department of Land Resource Management and Agricultural Technology (LARMAT), College of Agriculture and Veterinary Sciences, University of Nairobi, P. O. Box 29053-00625, Nairobi, Kenya. Email:cherutoglad00@gmail.com
[2] Kenya Agricultural and Livestock Research Organization, P.O. Box 57811-00200, Nairobi, Kenya.
[3] School of Agriculture and Natural Resources, Moi University, P. O. Box 3900-30100, Eldoret, Kenya.
** Corresponding author*

SUMMARY

Background: Forest conversion to other land use types lead to changes in soil physico-chemical properties and a reduction in soil fertility. Although forest conversion is extensively recognized to alter soil properties, the influence on distribution of soil phosphorus (P) fractions and abundance and diversity of soil biota is not well explored. **Objective:** To assess the effects of converting undisturbed natural forest to plantation forest (cypress), grazed pastures and potato fields on soil phosphorus (P) fractions and abundance and diversity of arbuscular mycorrhizal fungi (AMF) in Nyandarua County, Kenya. **Methodology:** Transects laid out in triplicate were established in each land use type. In potato fields and grazed pastures, transects measured 50 m with three sampling points established 15 m apart along each transect, each point measuring 1 m^2 divided into 25 grids with each grid being 400 cm^2. Transect length was increased to 150 m in forest sites due to relatively larger size of the area studied and sampling points were placed at 50 m apart, each point measuring 25 m^2 and divided into 1^2 m grids. Soil and plant samples were randomly collected from sampling points and were used to determine chemical properties, soil P fractions and AMF spore examination. Data were analyzed by analysis of variance (ANOVA). **Results:** Soil chemical properties were significantly (p<0.001) higher in natural forest compared to potato fields, grazed pasture and cypress forest. On the contrary, readily labile and moderately labile P was higher in fields cultivated with potato (125.3 mg and 258.2 mg P kg^{-1}, respectively) than in natural forest (51.1 mg and 95.3 mg P kg^{-1}) and cypress forest (36.4 mg and 82.7 mg P kg^{-1}, respectively). However, non-labile P was higher in natural forest (599.1 mg P kg^{-1}) and lower in cypress forest (251.3 mg kg^{-1}). Of the ten AMF genera identified, only *Glomus* and *Acaulospora* were significantly (p<0.01) affected by land use change, where they were more abundant in fields cultivated with potato than the other three land use types. Land use type did not significantly influence diversity and richness in AMF. However, AMF composition varied across the land use types. **Implication:** Land use change may negatively affect soil chemical properties, enhance redistribution of soil P, and change AMF community composition, and this could have long-term implications on soil fertility. **Conclusion:** Land use change from natural ecosystems to croplands, grazed pastures and tree plantations alter soil chemical properties, AMF composition and spore abundance, and redistribute soil P fractions by increasing labile P and reducing non-labile P fractions showing that the type of land use chosen significantly influence soil physical and chemical properties and soil biodiversity.

Key words: Forest conversion; land use type; spore abundance; soil properties; genera.

RESUMEN

Antecedentes: La conversión de bosques a otros tipos de uso de la tierra provoca cambios en las propiedades físico-químicas del suelo y una reducción en la fertilidad del suelo. Aunque se reconoce ampliamente que la conversión de bosques altera las propiedades del suelo, la influencia en la distribución de las fracciones de fósforo (P) del suelo y la abundancia y diversidad de la biota del suelo no está bien explorada. **Objetivo:** Evaluar los efectos de convertir bosques

† *Submitted November 1, 2022 – Accepted June 27, 2023. http://doi.org/10.56369/tsaes.4599*

ISSN: 1870-0462.
ORCID = Gladys Cheruto: http://orcid.org/0000-0001-9127-6624

naturales no perturbados en bosques de plantación (ciprés), pastos de pastoreo y campos de papa en las fracciones de fósforo (P) del suelo y la abundancia y diversidad de hongos micorrízicos arbusculares (AMF) en el condado de Nyandarua, Kenia. **Metodología:** Se establecieron transectos trazados por triplicado en cada tipo de uso de suelo. En campos de papa y pastos pastoreados, los transectos midieron 50 m con tres puntos de muestreo establecidos a 15 m de distancia a lo largo de cada transecto, cada punto medía 1 m² dividido en 25 cuadrículas con cada cuadrícula de 400 cm². La longitud del transecto se incrementó a 150 m en sitios forestales debido al tamaño relativamente mayor del área estudiada y los puntos de muestreo se colocaron a 50 m de distancia, cada punto medía 25 m² y se dividía en cuadrículas de 1 m^2. Las muestras de suelo y plantas se recolectaron aleatoriamente de los puntos de muestreo y se usaron para determinar las propiedades químicas, las fracciones de P del suelo y el examen de esporas de AMF. Los datos se analizaron mediante análisis de varianza (ANOVA). **Resultados:** Las propiedades químicas del suelo fueron significativamente ($p<0.001$) más altas en el bosque natural en comparación con los campos de papa, los pastos de pastoreo y el bosque de cipreses. Por el contrario, el P fácilmente lábil y moderadamente lábil fue mayor en campos cultivados con papa (125.3 mg y 258.2 mg P kg^{-1}, respectivamente) que en bosque natural (51.1 mg y 95.3 mg P kg^{-1}) y bosque de ciprés (36.4 mg P kg^{-1}). g y 82.7 mg P kg^{-1}, respectivamente). Sin embargo, el P no lábil fue mayor en bosque natural (599.1 mg P kg^{-1}) y menor en bosque de ciprés (251.3 mg kg^{-1}). De los diez géneros de HMA identificados, solo Glomus y Acaulospora se vieron afectados significativamente ($p<0.01$) por el cambio de uso del suelo, donde fueron más abundantes en los campos cultivados con papa que en los otros tres tipos de uso del suelo. El tipo de uso del suelo no influyó significativamente en la diversidad y riqueza de los HMA. Sin embargo, la composición de AMF varió entre los tipos de uso de la tierra. **Implicación:** El cambio de uso de la tierra puede afectar negativamente las propiedades químicas del suelo, mejorar la redistribución del P del suelo y cambiar la composición de la comunidad de AMF, y esto podría tener implicaciones a largo plazo en la fertilidad del suelo. **Conclusión:** El cambio de uso de la tierra de ecosistemas naturales a tierras de cultivo, pastizales y plantaciones de árboles altera las propiedades químicas del suelo, la composición de los AMF y la abundancia de esporas, y redistribuye las fracciones de P del suelo al aumentar el P lábil y reducir las fracciones de P no lábil, lo que demuestra que el tipo de uso de la tierra elegidos influyen significativamente en las propiedades físicas y químicas del suelo y en la biodiversidad del suelo.
Palabras clave: Conversión forestal; tipo de uso del suelo; abundancia de esporas; propiedades del suelo; géneros.

INTRODUCTION

Maintenance of soil fertility is crucial for ecosystem functioning and crop productivity yet human activities such as forest clearance alter soil properties thus compromise soil fertility (McGrath *et al.*, 2001; Veldkamp *et al.*, 2020). Small-scale subsistence farming has been named among the primary drivers in forest conversion especially in Sub-Saharan Africa owing to the growing human population and reduced crop productivity due to declining soil fertility (Benhin, 2006; Pinho *et al.*, 2012). Cultivated area has risen by 500% globally in the last five decades, with significant proportion of this being in Africa (Banerjee *et al.*, 2019). However, the tendency to exploit more forest lands to increase the overall agricultural production could have negative effects on soil fertility and biodiversity due to alteration of soil properties and reduction in soil organic matter content (de Graaff *et al.*, 2019; Tolimir *et al.*, 2020). Reduction in soil organic matter content, for instance, causes a collapse in soil structure and a weakening of soils' capacity to retain nutrients (Qiong *et al.*, 2008; Gatiboni *et al.*, 2017).

Soil P is the second most limiting nutrient after N, and it is highly unstable and easily fixed especially in acidic tropical soils. Phosphorus availability and lability is mediated by chemical processes, soil microbial and plant's roots activities (Betencourt *et al.*, 2012; Srinivasan *et al.*, 2012). The alteration of soil properties and vegetation by forest conversion influence P transformation and distribution within soil compartments (Bayuelo-Jiménez *et al.*, 2020; Zhu *et al.*, 2021). Indeed, researchers have suggested that P may change from one chemical form to another within a shorter period (<50 years) following land use change than thousands of years under natural conditions (Garcia-Montiel *et al.*, 2000; De Schrijver *et al.*, 2012; Chimdi *et al.*, 2014). This accelerated process could be attributed to changes in soil chemical properties such as pH and organic matter content which determine P dynamics in soil (Richardson *et al.*, 2009; Bayuelo-Jiménez *et al.*, 2020). For instance, low soil pH would lead to P binding with Al and Fe forming P compounds that are less labile (Richardson *et al.*, 2009). Soil management practices such as fertilizer application may lead to a short-term increase in labile P but more of this P end up being fixed or lost through soil erosion and harvested crop (Henriquez, 2002; Nunes *et al.*, 2020).

Soil biota play a critical role in nutrient cycling and maintenance of ecosystem functioning. Arbuscular mycorrhizal fungi (AMF) which are associated with over 80% of terrestrial plants provide several ecosystem services including enhanced nutrient uptake, protection against diseases and pathogens, increased tolerance to other environmental stresses, mediate nutrient cycling, and improves soil physical properties (Syibli *et al.*, 2013; Chandrasekeran and Mahalingam, 2014; Campos *et al.*, 2018; Chu *et al.*, 2020). However, forest conversion influence AMF, with a decline or increase in composition and abundance (van der Heyde *et al.*, 2017; Belay *et al.*, 2020). Soil disturbance brought about by tillage may stimulate increased spore production in AMF species like *Glomus* but cause a reduction in *Gigasporaceae* species, with fertilizer use also exhibiting similar effects in AMF species (Jefwa *et al.*, 2009; Dobo *et al.*, 2018). Although soil biota may exhibit some level of resilience to land use change as reported by Alele *et al.* (2014), it is not certain to what extent this resilience will persist and if such resilience is exhibited by AMF. Thus, this study aimed to evaluate the effect of converting natural forest to other land use types on distribution of P fractions and AMF abundance and diversity under four land use types: natural forest, forest plantation, grazed pasture and potato field. We hypothesized that converting natural forest to cultivated croplands, grazed pastures or tree plantations would lead to (1) modify distribution of soil P fractions and (2) a shift in composition, abundance and diversity of AMF.

MATERIALS AND METHODS

Description of study site

The study was carried out in South Kinangop in Nyandarua County in Kenya, which lies at 0.95° S and 36.76° E at an altitude of 2552 m above sea level. The study area has a cool and temperate climate, and has an annual mean rainfall of 1200 mm and annual mean temperature range of 10° C to 15° C. Rainfall is distributed in two seasons; the first season locally called 'long rains' occur from March to May, and the second season called 'short rains' from October to December (Jaetzold *et al.*, 2006; Haile *et al.*, 2023). Soil sampling was done in February 2021, and monthly mean rainfall and monthly mean temperature was 190 mm and 16° C, respectively, between December 2020 and March 2021 (Haile *et al.*, 2023). Soils are predominantly Planosols (FAO/UNESCO Soil classification system) which are characterized by poor drainage and a low to moderate soil fertility (Jaetzold *et al.*, 2006). The study area was initially a bushland before it was cleared to settle farmers in 1963 (Rachilo, 1978). The increased human population growth in the last four decades (from 233,302 persons in 1979 to 638,289 persons in 2019) has caused fragmentation of farms from an average of 20 ha to less than 0.5 ha (Jaetzold and Schmidt, 1983; KNBS, 2019; Kamau *et al.*, 2019). Majority of the farmers practice mixed farming, with cultivation of crops such as potatoes and vegetables including carrots, kales and cabbages and keeping of local dairy cows and sheep.

Four land use types common within the study area were purposely selected for this study: 1) A natural forest within Aberdare Forest reserve on the Southern Kinangop block was chosen as a reference site and a benchmark area of 9.9 ha was selected. Aberdare forest reserve is situated between longitude 36° 30′ E to 36° 55′ E and latitude 0° 05′ S to 0° 45′ S, and is surrounded by four counties; Kiambu, Nyeri, Murang'a and Nyandarua. The forest reserve is also surrounded by local communities who rely heavily on agriculture (KFS, 2010). The natural forest had *Dombeya goetzenii* K. Schum as the dominant tree species; 2) Plantation forest constituted a pure *Cupressus lusitanica* Mill. (cypress) and a benchmark area of 4.9 ha was established for the study; 3) Grazed pastures were dominated by Kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov) and the Kenyan Holstein-Friesian (*Bos taurus taurus*) dairy cows and Corriedale (*Ovis aries*) sheep were animals grazed on these pastures; and 4) Cultivated fields were mainly planted with potato for three consecutive growing seasons and Diammonium Phosphate (DAP) and Calcium Ammonium Nitrate (CAN) were used to fertilize the crop.

Soil and litter sample collection

Soils were collected in each land use type following transects, laid out in triplicate in a zigzag manner as illustrated in Figure 1. In potato fields and grazed pastures, transects measured 50 m and three sampling points, each point measuring 1 m², were established 15 m from one sampling point to the other. Each sampling point was divided into 25 grids, where each grid measured 400 cm². However, the length of transects in natural forest and cypress forest was increased since the area studied was relatively larger in size compared to the farms. Therefore, each transect measured 150 m and had sampling points marked at 50 m apart. Each sampling point measured 25 m² and was divided into equivalent number of grids where each grid was 1 m². Soil samples were randomly taken from five grids in each sampling point to a depth of 30 cm using a soil auger. The soils were mixed thoroughly, and a composite soil sample of 2 kg was taken for laboratory analysis. From each field, nine (9) soil samples were collected (3 transects × 3 sampling points per transect). Plant litter on the ground in natural and cypress forests were randomly hand-picked from each sampling point and composited. Soil samples were divided into two portions for chemical analysis and for AMF spore extraction. Soil samples for chemical analysis were ground and passed through 2 mm sieve.

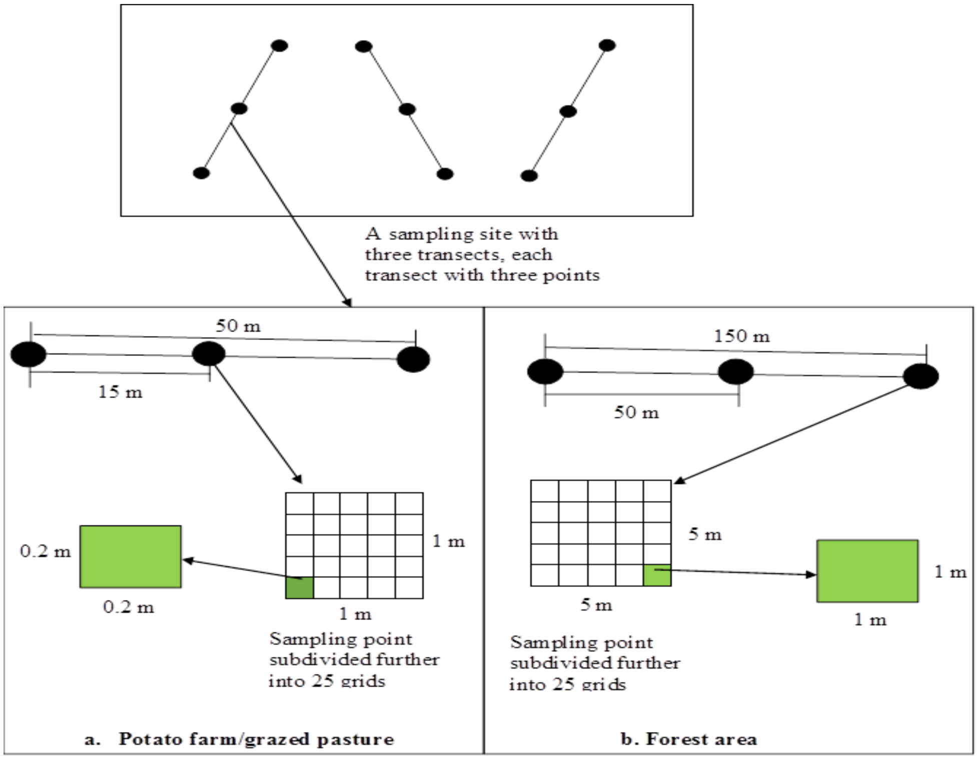

Figure 1. Sampling framework

Determination of soil and plant litter chemical properties

Soils were analyzed for pH, total organic C, N, Ca, K, Mg and CEC. Soil pH was measured in deionized water-soil suspension (1:2.5 soil: water) using a pH meter (Anderson and Ingram, 1993). Total organic C was determined by Walkley-Black method (Nelson and Sommers, 1996). Total N was determined by Kjedhal method (Hinds and Lowe, 1980). Exchangeable Ca, K and Mg were extracted using ammonium acetate method and determined by atomic absorption spectrophotometer as described by Anderson and Ingram (1993). Plant litter was analyzed for total N, P, Ca, Mg, K, organic matter and lignin content. Total N, P, Ca, Mg and K were extracted using mixed reagent (selenium powder, lithium sulphate, hydrogen peroxide and concentrated sulphuric acid), after which determination of total N was done according to Kjedhal method (Hinds and Lowe, 1980), total P according to Murphy and Riley (1962) method and Ca, Mg and K using atomic absorbance spectrophotometer. Organic matter (OM) content was determined by complete combustion method (Carter and Gregorich, 2007).

Determination of soil P fractions using Hedley sequential fractionation method

Hedley sequential fractionation method (Hedley *et al.*, 1982) uses a sequence of chemical solutions that increase in dissolution strength which first removes labile inorganic and organic P, and then non-labile P. Soil P fractions were quantified and presented as resin-P_i, $NaHCO_3$-P_i, $NaHCO_3$-P_o, NaOH-P_i, NaOH-P_o, sonicate NaOH-P_i, sonicate NaOH-P_o, HCl-P_i and residual P. The fractions were further grouped into readily labile P (resin-P_i + $NaHCO_3$ P_i and P_o), moderately labile P (NaOH P_i and P_o) and non-labile P (sonicate NaOH P_i and P_o + HCl-P_i + residual P). One gram of air-dried soil was repeatedly extracted starting with dilute alkali and acid and eventually with concentrated acid in the following sequential order: Resin-P was extracted by first saturating resin strips (1.5 cm × 5 cm) with 1 M $NaHCO_3$ for 1 hour and rinsed with distilled water. The saturated resin strips were put in 50 ml centrifuge tubes containing soil and to which 30 ml of distilled water was added. The contents were shaken for 16 hours, and resin strips were removed using tweezers and washed off using distilled water into the centrifuge tubes. To remove P adsorbed on the exchange sites of resin strips, resin strips were transferred into centrifuge tubes containing 20 ml of 0.5 M L^{-1} HCl and shaken for 1 hour after which resin strips were removed. The extract was used to determine the content of P (resin-P_i). The centrifuge tubes containing soil were centrifuged at 5000 rpm for 10 minutes and water decanted and discarded. $NaHCO_3$-P was determined by dispensing 30 ml of 0.5 M L^{-1} $NaHCO_3$ into the centrifuge tubes containing soil and was shaken for 16 hours. The soil suspension was centrifuged at 5000 rpm for 10 minutes and

$NaHCO_3$ extract was carefully decanted into new sets of centrifuge tubes to be used for P determination. NaOH-P was determined by dispensing 30 ml of 0.1 M L^{-1} NaOH into the centrifuge tubes containing soil and shaken for 16 hours. The soil suspension was centrifuged at 5000 rpm for 10 minutes and the extract kept for P determination. Sonicate 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 and kept for P determination. HCl-P 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, and HCl extract was collected in new sets of centrifuge tubes and kept for P determination. The soil in centrifuge tubes was quantitatively transferred into 75 ml digestion tubes with distilled water and put in the oven at 70° C to evaporate excess water. The soil was added 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 and used for P determination. Inorganic P (P_i) in extracts of resin, $NaHCO_3$, NaOH, sonicate NaOH, HCl and residual P was determined directly by taking an aliquot of 6 ml and P concentration measured according to Murphy and Riley method (Murphy and Riley, 1962). To determine organic P (P_o) in $NaHCO_3$, NaOH and sonicate NaOH extracts, a separate aliquot (6 ml) was taken from their extracts and digested with 6 ml of acidified ammonium persulfate at 15 psi, 120° C for 1 hour to convert all the dissolved organic P into inorganic P, and the content of P determined in the digest was quantified as total P (tP). Organic P was then computed as the difference between tP and P_i. The pH for the final extracts was first adjusted using either an acid or alkali and P was determined according to Murphy and Riley method (Murphy and Riley, 1962) and absorbance taken at 880 nm using UV Spectrophotometer. Phosphorus concentration was calculated based on soil dry weight (mg P kg^{-1}).

Spore extraction and identification

Spores were extracted using wet sieving and sucrose (50 %) density centrifugation method. A 100 g of air-dried soil was washed through 710 µm sieve into 45 µm sieve, repeatedly. The soil remaining on 45 µm sieve was gently washed into 50 ml centrifuge tubes and centrifuged at 1500 revolutions per minute (rpm) for 5 minutes. The supernatant was carefully poured out and 50 % of sucrose solution was added onto the tubes containing the soil and filled up to the 50 mark and centrifuged again at 1500 rpm for 1 minute. The supernatant was collected on 50 ml plastic beaker. The supernatant was transferred to a petri dish with grid lines in order to count, collect and separate spores under a dissecting microscope. Spores were separated based on morphological characteristics such as spore color using Edinburgh Botanic Gardens color chart, size, shape, presence or absence of hyphae attachment and surface appearance. The spores were mounted on glass slides using polyvinyl lacto glycerol (PVLG), in which the spores were maintained whole, and Meltzer's reagent, in which the spores were slightly crushed for finer details. To identify spore morphotypes, a compound microscope was used to examine spores for more details such as spore wall, number of spore walls, wall ornamentation, type of hyphae, germination characteristics and reaction to Meltzer reagent. The morphological spore characteristics were recorded and matched with species characteristics described by International Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM) database available online (https://invam.ku.edu/) and Schenck and Perez (1990). The spore morphotypes were identified to family and genus levels. The AMF spore specimens were preserved and deposited at the Mycology laboratory at the Department of Botany of the National Museums of Kenya.

Statistical analysis

Data on soil chemical properties, P fractions and plant litter properties were first converted into standard measurement units. Spore abundance was calculated from direct count of spores per 100 g of air-dried soil. Vegan package in R statistical software was used to determined species richness and Shannon-Weiner diversity indices. The effect of land use type on soil chemical properties and P fractions were determined using generalized linear models (GLMs) using lme4 package. Data on spore count, species richness and diversity were analyzed by generalized linear mixed models (GLMMs), and since the data contained significant number of zero values, negative binomial regression was chosen as an extension of Poisson distribution as described by Kamau *et al.* (2020), and thus the models were fitted using *glmer.nb* function in R statistical software. Sampling site was fitted in the models as a random factor while land use type as a fixed factor. Estimation of model parameters was done using maximum likelihood (ML), and Akaike Information Criterion (AIC) was used to select models, where models with least values of AIC were chosen to be the best models. Where analysis of variance (ANOVA) showed significant effect of land use type, means were separated by Tukey's Honest Significant Difference (HSD) test at α=0.05. All data analysis was done in R statistical software version 4.0.4 (R Core Team, 2021).

RESULTS

Soil chemical properties

Land use type had significant (p<0.001) effect on soil chemical properties measured (Table 1). Generally, natural forest had higher contents of total organic C, N, exchangeable Ca and Mg than other land use types. However, soil K was higher in grazed pastures. Soil pH was significantly higher in natural forest (4.9) compared to that in potato fields (3.8), but it was not significantly different between cypress forest and grazed pastures. Natural forest also had higher CEC (25.3 cmol kg^{-1}) than cypress forest (14.6 cmol kg^{-1}), potato fields (9.9 cmol kg^{-1}) and grazed pastures (11.7 cmol kg^{-1}). Other soil chemical properties showed similar differences across grazed pastures, potato fields and cypress forest.

Chemical characteristics 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 (p<0.01) higher total N, P, Ca and Mg than in cypress plantation. However, total K and OM were similar between the two forests. 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}).

Distribution of soil P fractions

Soil P fractions were significantly affected by land-use type with varying magnitudes (Table 3). For example, resin-P was significantly (p<0.05) higher in soils collected from potato growing fields (34.9 mg P kg^{-1}) compared to cypress forest (3.9 mg P kg^{-1}). Similar differences were observed for $NaHCO_3$-P_i, $NaHCO_3$-P_o and NaOH-P_i. On the other hand, residual P and sonicate NaOH-P_o fractions were higher (p<0.001) in

Table 1. Soil chemical properties as affected by land use types in the study site.

Soil properties	Land-use type				*p*-value
	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.

Table 2. Chemical characteristics of litter collected from the floor of the two forests.

Litter characteristics	Land-use type		*p*-value
	Natural forest	Cypress forest	
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.

Table 3. Distribution of soil P fractions as affected by land use types in the study site.

P-fractions (mg kg^{-1})	Land-use type				*p*-value
	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**
$NaHCO_3$- P_i	10.7 (2.2)^{ab}	2.9 (0.5)^{b}	23.1 (3.5)^{ab}	35.2 (4.7)^{a}	**0.025**
$NaHCO_3$- 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.

natural forest (574.7 P mg 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 P mg and 186.1 mg P kg^{-1}, respectively) and lowest in cypress forest (36.4 P mg and 82.7 P mg kg^{-1}, respectively). However, non-labile P was highest (p<0.001) in natural forest (690.1 P mg kg^{-1}) and lowest in cypress forest (324.5 P mg kg^{-1}).

Spore abundance, AMF richness and diversity

Of the ten AMF genera identified, only *Glomus* and *Acaulospora* were significantly (p<0.01) affected by land-use type. The highest spore abundance was found 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, AMF taxonomic richness and diversity was not significantly different across the four land use types.

Correlation between AMF abundance, soil chemical properties and P fractions

The Canonical Correspondence Analysis (CCA) plot between soil chemical properties and AMF abundance and diversity showed strong but negative relationship between soil pH and two AMF genera; *Glomus* and *Acaulospora* as well as the total spore count (Figure 2). In this case, the two AMF genera and the total spore count were found to be abundant in acidic soils, a characteristic which was predominant in potato fields. There was also a negative but a weaker relationship between genera *Ambispora*, *Funneliformis*, *Septoglomus*, and *Scutellospora* with NaOH-P_o. There were no unique patterns that could be drawn for the other AMF genera. In addition, the variation explained by the two axes (axis 1 and 2) was very low, with axis 1 explaining about 20% of the variation and axis 2 about 12%, for a combined value of just above 30%.

DISCUSSION

Soil chemical properties

Forest conversion to other land use types had strong significant effect on soil chemical properties. Soil organic C, N, K, Ca and Mg were relatively lower in potato fields than in natural forest suggesting that converting natural forest for agricultural crop production result to degradation of the soil. Removal of vegetation, which characterize forest conversion lead to changes in litter quantity and quality hence negatively influencing soil physical, chemical and biological properties (Pérez-Bejarano *et al.*, 2010). Litter input and quality affect the build-up of soil organic matter and key functions such as nutrient cycling, nutrient retention capacity of soil and soil aggregation. Thus, lack of permanent vegetation cover in cultivated agricultural fields due to removal of

Table 4. Effect of land use type on spore abundance, AMF richness and diversity in the study site.

AMF genera	**Land use type**				***p*-value**
	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

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.

residues from the farms for other competitive use like animal feed result to reduction in litter input to soil, and consequently reduced soil chemical properties as found in potato fields. Furthermore, conventional crop management practices such as continued application of inorganic fertilizers, especially DAP, which is commonly used by potato farmers has been shown to further lower soil pH (Muthoni and Nyamongo, 2009; Banerjee *et al.*, 2019). Frequent tilling of soil also exposes soil to higher temperatures and soil organic matter to microbial attack hence accelerates decomposition and mineralization processes, thus a reduction in soil nutrient content (Awiti *et al.*, 2008; Groppo *et al.*, 2015). In addition, cultivation of potato has been associated with declining soil fertility due to sub-optimal fertilizer application and lack of fallow periods between growing seasons leading to nutrient mining (Muthoni and Nyamongo, 2009; Muthoni, 2016). The cumulative effect of these agronomic practices in potato fields could therefore explain the lower soil chemical properties found in this study, and that these practices in potato cropping systems may be slowly degrading soil fertility. Soils under cypress forest were also relatively acidic and had the lowest soil chemical properties which may be attributed, but not limited, to the chemical composition of cypress litter. The dominant tree species exert significant influence on soil chemical properties of the upper soil layer through litter quality which determines soil nutrient availability and decomposition rate (Iwashima *et al.*, 2012). For example, coniferous litter contain low concentrations of basic cations and produce considerable amounts of organic acids hence causing soil acidification (Iwashima *et al.*, 2012; Zajícová and Chuman, 2019), implying that soils under coniferous trees could exhibit low nutrient content due to poor nutrient replenishment through litter input. Cypress litter had lower chemical (N, P, Ca and Mg) properties than litter from natural forest hence may also be contributing to the lower soil chemical properties found in cypress forest plantation. Chen *et al.* (2000) also reported a reduction in soil C, N and P under pine forest plantation. Similar observations in the decline of soil N and organic C content following deforestation for crop cultivation and grazed pastures have also been reported (Jafarian and Kavian, 2013; Kamau *et al.*, 2017; Awoonor *et al.*, 2022). Soils under natural forest exhibited significantly higher nutrient content than soils under grazed pastures, cypress forest plantation and potato fields possibly from sustained build-up of soil organic matter, which play a key role in maintaining soil's capacity to retain nutrients. The permanent vegetation cover in natural forests also allow closed nutrient cycling leading to minimal nutrient loss from the system which commonly does not happen in agroecosystems due to crop harvests and accelerated soil erosion. Trees are well known to pump nutrients from the subsoil layers and redistribute them on the surface soil via throughfall and litterfall (Qiong et al., 2008). In addition, the nutrient-rich litter, i.e., higher total N, P, Ca and Mg, from the common tree species (*Dombeya goetzenii* K.) in natural forest could

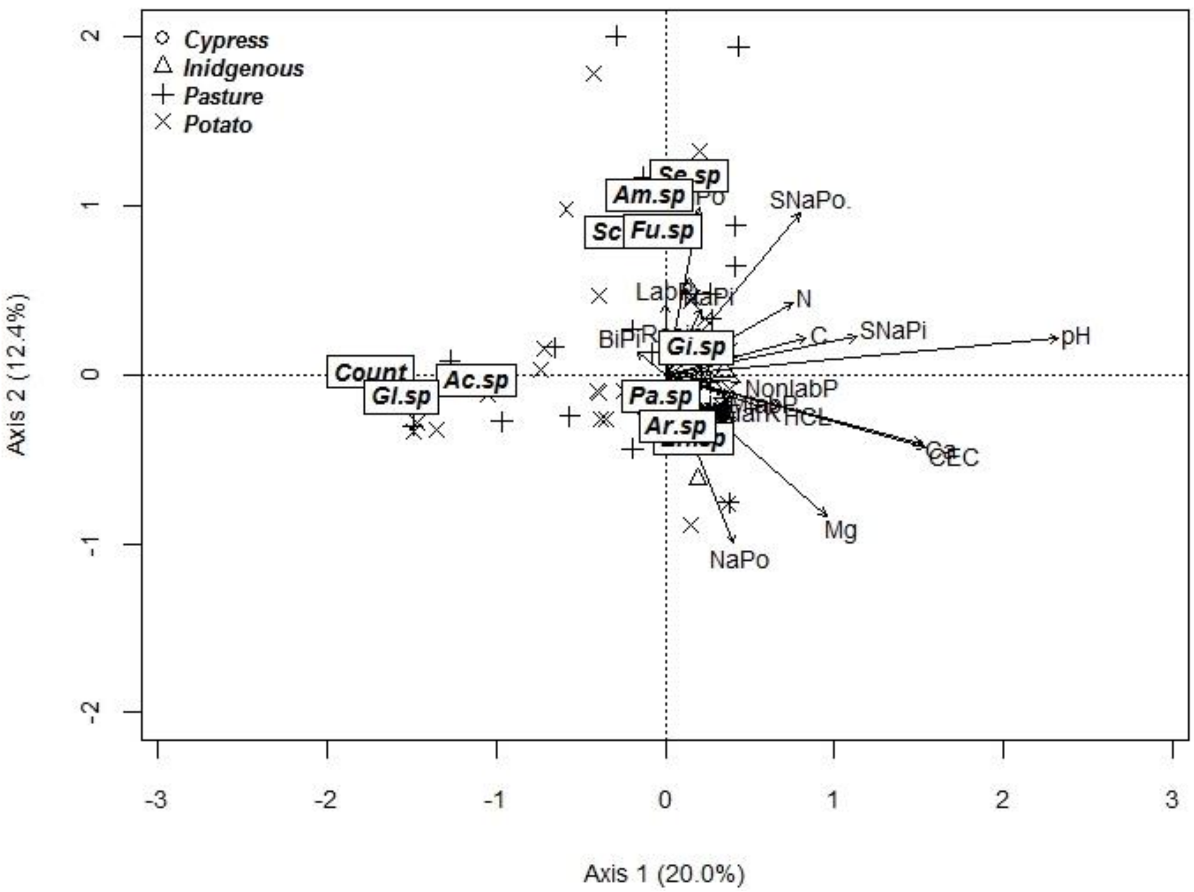

Figure 2. Canonical Correspondence Analysis (CCA) of AMF genera and soil chemical properties and soil P fractions in South Kinangop Sub-county, Nyandarua County. Abbreviations for soil chemical properties: C-organic carbon, N-nitrogen, CEC-cation exchange capacity, Mg-magnesium, Ca-calcium and K-potassium. Abbreviations for soil P fractions: BiPi-$NaHCO_3$ inorganic phosphorus (P_i), BiPo-$NaHCO_3$ organic phosphorus (P_o), NaPi-NaOH inorganic phosphorus (P_i), NaPo-NaOH organic phosphorus (P_o), SNaPi-sonicate NaOH inorganic phosphorus (P_i), SNaPo-sonicate NaOH organic phosphorus (P_o), HCL-HCl inorganic phosphorus (P_i), Res-residual phosphorus, LabP-labile phosphorus, ModLabP-moderately labile phosphorus and Nonlab-non labile phosphorus. Abbreviations for AMF genera: *Ac.sp-Acaulospora*, *Gl.sp-Glomus*, *Sp.sp-Septoglomus*, *Pa.sp-Paraglomus*, *Gi.sp-Gigaspora*, *Sc.sp-Scutellospora*, *Fu.sp-Funneliformis*, *En.sp-Enterophospora*, *Ar.sp-Archeospora*, *Am.sp-Ambispora* and Count-Total spore count.

have partly contributed to enrichment of soils. Iwashima *et al.* (2012) observed that soils under broadleaved vegetation dominated by Japanese oak (*Quercus crispula* Blume) had higher pH, inorganic N, Ca and Mg than those under conifers, *Picea jezoensis* (Siebold and Zucc.) and *Abies sachalinensis* (F. Schmidt) Mast, and they attributed this to litter characteristics between the Japanese oak and conifers where the former had higher N, Ca, Mg and K than the latter. Contrary to the findings of this study, Muchane *et al.* (2012) found higher soil nutrient concentrations (N, P and K) in agricultural ecosystems than in natural ecosystems which they attributed 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 soil organic matter means that these nutrients are less protected and retained 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.

Changes in soil P fractions

Labile P fractions (resin, $NaHCO_3$ and NaOH) were relatively low in natural forest and increased in cultivated potato fields. Agronomic practices in cultivated croplands significantly influence P transformation and distribution in soil. For instance, McLaren et al. (2015), when assessing fertilized and unfertilized pastures, found that fertilizer application led to an increase in P in $NaHCO_3$ and NaOH fractions, and observed that applied P may accumulate in less labile fractions (e.g., NaOH) than in more labile fractions ($NaHCO_3$). The results of this study are consistent with those of McLaren et al. (2015) since $NaHCO_3$-P and NaOH-P were higher in cultivated potato fields receiving fertilizer. Henriquez (2002) also reported an increased P in labile ($NaHCO_3$-P and NaOH-P) fractions after fertilizer application, and concluded that these fractions may be important sinks for applied P. The results of this study and those reported (e.g., Henriquez, 2002; McLaren et al., 2015) show that the use of inorganic fertilizers greatly influence labile P pool more than non-labile P pool. The use of phosphate fertilizers like DAP for long durations further lower soil pH, indirectly influencing sorption-desorption processes governing P availability. Low soil pH increases P sorption by soil minerals such as Al and Fe oxides hence the lower soil pH in potato fields could have also influenced P partitioning, especially in NaOH fraction which is associated with Al and Fe oxides leading to higher moderately labile P (Richardson *et al.*, 2009; Bayuelo-Jiménez *et al.*, 2020). Grazed pastures as well exhibited higher content of labile and moderately labile P which may be partly due to animal grazing which has been shown to exert significant influence on labile P (Chirino-Valle *et al.*, 2016). It has been reported that 60-95% of P used by plants and taken up by animals through grazing is returned to the 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 from non-labile pool into labile pool (Almeida *et al.*, 2018). For example, Almeida et al. (2018) found that growing Ruzi grass after soya bean crop led to an increase in labile P (resin, $NaHCO_3$ and NaOH P) which they attributed to higher SOM deposition and secretion of low molecular weight organic acids by Ruzi grass. On the other hand, non-labile P (sonicate NaOH P_i & P_o, HCl-P and residual-P) in natural forest was nearly twice that found in other land uses and this could be attributed in part to greater accumulation of SOM. The absence of soil disturbance through tillage means that natural forest soils are less exposed to external forces such as surface runoff, heating and disintegration of soil aggregates that would accelerate SOM P mineralization and loss. The higher content of sonicate NaOH-P_o in natural forest, for instance, reveals that soils under natural forest have stable aggregates since P bound in this fraction is considered to be physically protected by soil aggregation. It has also been found that majority of P in natural forest soils tend to accumulate in non-labile forms (Garcia-Montiel et al., 2000), indicating that natural forests may be good in conserving soil P. However, cypress forest 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. In assessing the role of soil P fractions to tree nutrition in a short-term experiment, Niederberger et al. (2017) found poplar trees to decrease readily and moderately labile P fractions, thus showing the importance of these fractions in tree nutrition. It has also been shown that pine, eucalyptus and cypress trees decrease organic P content and, utilize even non-labile P due to enhanced enzymatic activities, mycorrhizal associations as well as changes in soil pH, which enhances P mineralization (Chen *et al.*, 2008; Gatiboni *et al.*, 2017). Phosphorus is mainly recycled into the soil through litterfall in forests (Qiong et al., 2008) hence litter input and quality greatly influence P concentration in forest soils. Cypress litter had low nutrient (N, P, Ca and Mg) content compared to litter from natural forest which may have partly led to lower P concentration in cypress forest soils. Therefore, continuous cultivation of cypress trees may decreasing P stocks in the long-term, and thus may not be a desirable land use system wherein the ultimate goal is to restore and maintain high fertility of P.

Response of AMF to change in land use type

Spores mostly dominated cultivated potato fields than natural forest which could be attributed to frequent soil disturbance from agronomic practices such as tillage, application of mineral fertilizers and pesticides and monocropping. These agronomic practices have been shown to influence AMF spore and hyphal abundance and consequently alter AMF community composition (Muchane *et al.*, 2012; Campos *et al.*, 2018; Dobo et al., 2018). Tilling the land, for instance, may cause a positive or negative effect on AMF depending on how AMF species resident in that particular ecosystem respond to stress. Tilling soil essentially destroy spores and hyphae reducing spore abundance and AMF's potential for new colonization in soils (Soka et al., 2015). However, some AMF species which are considered 'generalists' (i.e. found in most soils) may respond to stress associated with land use change by increased sporulation. Thus it is possible that the common AMF species, e g., *Glomus*, *Acaulospora*, in soils of the study area were being stimulated by stress to sporulate. *Acaulospora* and *Glomus* species are reported to be common in most soils in the tropics (Campos *et al.*, 2018; Dobo et al., 2018). The application of sub-optimal fertilizers by farmers in growing potato may have also contributed to high spore abundance in potato fields since the soluble P added through mineral fertilizers to the soil may not be sufficient enough to suppress AMF spore production and colonization. This is in line with other studies that have found low input farming systems to maintain high AMF abundance and diversity (Muchane *et al.*, 2012; Belay *et al.*, 2015). This is because the use of optimum P-based fertilizers in crop cultivation increase P availability for plant uptake reducing the need to establish association with AMF, hence suppressing root colonization and spore production (Sharma *et al.*, 2013). While some AMF species may be suppressed in soils receiving fertilization, others like *Ambispora* are reported to be stimulated in such soils (Wang et al., 2011), which was what was found in this study where the genus was found only in potato fields receiving mineral fertilizers. Grazed pastures likewise exhibited high spore abundance, richness and diversity which could be attributed to soil disturbance through animal trampling which cause AMF to produce spores in response to stress. Defoliation through grazing may limit C allocation to the roots of the host plant reducing AMF root colonization, and instead triggers AMF to produce spores (Soka and Ritchie, 2018). The abundance of spores in pastures has also been associated with greater root density in grasses which improve availability of resources for AMF colonization, and produce high mycelial biomass for abundant spore production (Picone, 2000). Forests recorded low AMF spore abundance and richness and diversity, with cypress forest plantation having the lowest values. Soil acidity, and reduced undergrowth in forests especially in coniferous forest plantations limit substrate availability to AMF hence suppress their growth and abundance (Moora et al., 2014). The low abundance of spores in forests has also been attributed to feeding by soil arthropods which are more abundant in forests than other land use types (Picone, 2000). Soil physical and chemical properties also influence AMF community structure leading to changes in spore abundance (Dobo et al., 2018). More importantly, soil pH, organic matter content, P and N influence AMF, implying that any alteration in these soil properties may significantly alter AMF community structure. For example, *Glomus hoi, Septoglomus constrictum, Funneliformis coronatum* are stimulated in soils by high available P while *Scutellospora projecturata, Rhizophagus clarus, R. irregularis, R. intraradice* thrive well in low available P, whereas *Funneliformis geosporum, F. mosseae, F. fragilistratum, F. verruculosum* tolerate both extremes (Wang *et al.*, 2015). It is also reported that *Glomus* accumulate 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 content of P and K. Based on canonical correspondence analysis (CCA), there was generally a weak relationship between AMF parameters and soil chemical properties and P fractions showing that soil properties and P availability were not the primary factors influencing AMF composition and abundance. Converting natural forests may not only influence AMF abundance and diversity but can also lead to changes in ecosystem functions provided by AMF such as improved soil texture and structure, mobilization of soil nutrients and water relations as well as important interactions with other soil microorganisms thus affecting the overall ecosystem functioning and sustainability.

CONCLUSION

Forest conversion to other land use types led to lower soil chemical properties showing that soil nutrient availability may not be maintained after forest conversion. This may be associated with gradual loss of soil organic matter, which is key in nutrient cycling, partly caused by reduced litter input and soil management practices that accelerate decomposition and mineralization of soil organic matter. The results of this study also demonstrate that forest conversion alter P distribution and lead to greater accumulation of labile P than non-labile P. The elevated labile P may present a short-term P availability for plant use but may not be sustainable in the long run due to losses through soil erosion and crop harvests. In addition, land uses particularly those of conifer tree plantations may deplete all P fractions as the stand ages hence may not be a desirable land use system in restoration and maintenance of soil P.

A shift in land use from natural forest to agricultural use led to higher spore abundance and AMF species richness and diversity. In particular, potato fields had the highest spore abundance and number of AMF genera which may imply that farming practices induce stress on AMF causing them to sporulate, and may also be stimulating AMF species which are present but dormant in the soils of the study area. Therefore, a change in land use from natural forest lead to soil degradation, and the extent to which soil is degraded may be determined by the type of land use and present management practices.

Acknowledgement
We would like to thank Susan Mwai, assistant scientist at the National Museums of Kenya for her assistance in AMF identification. We also thank Peter Wakaba, senior laboratory technologist at Soil chemistry laboratory, Food Crops Research Centre-Muguga South of the Kenya Agricultural and Livestock Research Organization (KALRO) for his immense guidance and assistance in soil chemical analyses. We are also indebted to Kenya Forest Service (KFS), Mustafa Haile, James Githua and farmers of Gathaara ward for supporting us during soil sampling.

Funding. This work was supported by Kenya Climate Smart Agricultural Project (Grant Number: KCSAPCGS/CRGS-AD 2019/CSC/01-5/POTATO).

Conflict of interest. The authors declare that there are no known conflicts of interest associated with this article.

Compliance with ethical standards do not apply. Not applicable. There were no animal or human subjects used in this study by any of the authors.

Data availability. Data is available with Gladys Cheruto (cherutoglad00@gmail.com).

Author contribution statement (CRediT). Gladys Cheruto- conceptualization, investigation, data curation, methodology, project execution, visualization, funding acquisition and writing the original draft. **Nancy N. Karanja and Solomon Kamau**-supervision, validation, review and editing.

REFERENCES

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*(8), p.e104818. https://doi.org/10.1371/journal.pone.0104818

Almeida, D.S., Penn, C.J. and Rosolem, C.A., 2018. Assessment of phosphorus availability in soil cultivated with ruzigrass. *Geoderma*, *312*, pp.64-73. https://doi.org/10.1016/j.geoderma.2017.10.003

Anderson, J.M. and Ingram, J.S.I. eds., 1993. Tropical Soil Biology and Fertility: A Handbook of Methods. *CAB International, Wallingford, UK*, *12*, 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 and Environment*, *127*(3-4), pp.265-272. https://doi.org/10.1016/j.agee.2008.04.012

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*, pp.32-68. https://doi.org/10.4236/jep.2022.131003

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R. 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*(7), pp.1722-1736. https://doi.org/10.1038/s41396-019-0383-2

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* (2), pp.240-249. https://doi.org/10.1111/sum.12550

Belay, Z., Negash, M., Kaseva, J., Vestberg, M. and Kahiluoto, H., 2020. Native forests but not agroforestry systems preserve arbuscular mycorrhizal fungal species richness in southern Ethiopia. *Mycorrhiza*, *30*(6), pp.749-759. https://doi.org/10.1007/s00572-020-00984-6

Belay, Z., Vestberg, M. and Assefa, F., 2015. Diversity and abundance of arbuscular mycorrhizal fungi across different land use types in a humid low land area of Ethiopia. *Tropical and Subtropical Agroecosystems*, *18*(1), pp.47-69. https://www.revista.ccba.uady.mx/ojs/index.php/TSA/article/view/1992

Benhin, J. K., 2006. Agriculture and deforestation in the tropics: a critical theoretical and empirical review. *AMBIO: A Journal of the Human Environment*, *35*(1), pp.9-16. https://doi.org/10.1579/0044-7447-35.1.9

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*, pp.181–190. https://doi.org/10.1016/j.soilbio.2011.11.015

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*, pp.1–21. https://doi.org/10.3389/fpls.2018.00752

Carter, M., Gregorich, E. eds., 2007. Soil Sampling and Methods of Analysis. Boca Raton: CRC Press.

Chandrasekeran, A. and Mahalingam, U.P., 2014. Diversity of Arbuscular Mycorrhizae Fungi from Orchard Ecosystem. *Journal of Plant Pathology and Microbiology*, *5*(2), pp.1-6.

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*(1), pp.151-163. https://doi.org/10.1023/A:1004712401721

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*(3-4), pp.396-409. https://doi.org/10.1016/j.foreco.2007.10.040

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*(3), pp.51-57. DOI: 10.5829/idosi.aejsr.2014.9.3.1138

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*(2), pp.477-489. http://dx.doi.org/10.4067/S0718-95162016005000040

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*(1), pp.357-371. https://doi.org/10.1007/s11104-020-04494-4

Condron, L.M., Turner, B.L. and Cade-Menun, B.J., 2005. Chemistry and dynamics of soil organic phosphorus. *Phosphorus: Agriculture and the Environment*, *46*, pp.87-121. https://doi.org/10.2134/agronmonogr46.c4

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*, pp.1-44. https://doi.org/10.1016/bs.agron.2019.01.001

De Schrijver, A., Vesterdal, L., Hansen, K., De Frenne, P., Augusto, L., Achat, D.L., Staelens, J., Baeten, L., De Keersmaeker, L., De Neve, S. and Verheyen, K., 2012. Four decades of post-agricultural forest development have caused major redistributions of soil phosphorus fractions. *Oecologia*, *169*(1), pp.221-234. https://doi.org/10.1007/s00442-011-2185-8

Dobo, B., Asefa, F. and Asfaw, Z., 2018. Diversity and abundance of arbuscular mycorrhizal fungi under different plant and soil properties in Sidama, southern Ethiopia. *Agroforestry Systems*, *92*(1), pp.91-101. https://doi.org/10.1007/s10457-016-0017-x

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*(5), pp.1792-1804. https://doi.org/10.2136/sssaj2000.6451792x

Gatiboni, L.C., Vargas, C.O., Albuquerque, J.A., Almeida, J.A., Stahl, J., Chaves, D.M., Brunetto, G., Dall'Orsoletta, D.J. and Rauber, L.P., 2017. Phosphorus fractions in soil after successive crops of *Pinus taeda* L. without fertilization. *Ciência Rural*, *47*, pp.1-8. https://doi.org/10.1590/0103-8478cr20160595

Groppo, J.D., Lins, S.R.M., Camargo, P.B.D., Assad, E.D., Pinto, H.S., Martins, S.C., Salgado, P.R., Evangelista, 3., Vasconcellos, E., Sano, E.E. and Pavão, E., 2015. Changes in soil carbon, nitrogen, and phosphorus due to land-use changes in Brazil. *Biogeosciences*, *12*(15), pp.4765-4780. https://doi.org/10.5194/bg-12-4765-2015

Haile, M.A., Karanja, N.N., Nyawade, S.O., Gitari, H.I., Cheruto, G., Nyawira, L., Raza, M.A. and Kamau, S., 2023. Lupin and Lima Beans Diminish Potatoes' N and P Uptake, Uptake Efficiency and Use Efficiency. *Potato Research*, pp.1-17. https://doi.org/10.1007/s11540-023-09625-9

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*(2), pp.236-244. https://doi.org/10.1111/j.1574-6941.2011.01043.x

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*(5), pp.970-976. https://doi.org/10.2136/sssaj1982.03615995004600050017x

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*, pp.469-475.

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*(6), pp.783-792. https://doi.org/10.1080/00380768.2012.738183

Jaetzold, R. and Schmidt, H., 1983. Farm Management Handbook of Kenya: Natural Conditions and Farm Management Information–Central Kenya, Vol II/B. *Nairobi: Ministry of Agriculture, Kenya, in cooperation with the Germany Agricultural Team (GAT) of the Germany Agency for Technical Cooperation (GTZ)*.

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*(1-4), pp.339-346.https://doi.org/10.1080/00103624.2013.741949

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*(2), pp.277-290.

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*, p.113983. https://doi.org/10.1016/j.geoderma.2019.113983

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. http://doi.org/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*, pp.286-293. https://doi.org/10.1016/j.apsoil.2017.07.007

KFS., 2010. Aberdare Forest Reserve Management Plan 2010-2019. *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*.

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*(7), pp.625-645. https://doi.org/10.1007/s10021-001-0033-0

McLaren, T.I., Simpson, R.J., McLaughlin, M.J., Smernik, R.J., McBeath, T.M., Guppy, C.N. and Richardson, A.E., 2015. An assessment of various measures of soil phosphorus and the net accumulation of phosphorus in fertilized soils under pasture. *Journal of Plant Nutrition and Soil Science*, *178*(4), pp.543-554. https://doi.org/10.1002/jpln.201400657

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*(3), pp.609–621. https://doi.org/10.1111/1574-6941.12420

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*(17), pp.3904-3916. http://doi.org/10.5897/AJMR12.155

Murphy, J. and Riley, J. P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, *27*, pp.31-36. https://doi.org/10.1016/S0003-2670(00)88444-5

Muthoni, J., 2016. Soil fertility situation in potato producing Kenyan highlands Case of KALRO-Tigoni. *International Journal of Horticulture*, *6*(25). http://doi.org/10.5376/ijh.2016.06.0025

Muthoni, J. and Nyamongo, D.O., 2009. A review of constraints to ware Irish potatoes production in Kenya. *Journal of Horticulture and Forestry*, 1(7), pp.98-102.

Niederberger, J., Kohler, M. and Bauhus, J., 2017. The relevance of different soil phosphorus fractions for short-term tree nutrition: results from a mesocosm bioassay. *Forestry: An International Journal of Forest Research*, *90*(2), pp.258-267. https://doi.org/10.1093/forestry/cpw050

Nelson, D. W. and Sommers, L. E., 1996. Total carbon, organic carbon, and organic matter. *Methods of soil analysis: Part 3 Chemical Methods*, 5, pp.961-1010. https://doi.org/10.2134/agronmonogr9.2.2ed.c29

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*, p.350. https://doi.org/10.3389/feart.2020.00350

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*(1), pp.15-24. https://doi.org/10.1007/s10342-008-0246-2

Picone, C., 2000. Diversity and abundance of arbuscular–mycorrhizal fungus spores in tropical forest and pasture 1. *Biotropica*, *32*(4a), pp.734-750. https://doi.org/10.1111/j.1744-7429.2000.tb00522.x

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*, pp.1-11. https://doi.org/10.1155/2012/616383

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*(6), pp.741-748. https://doi.org/10.1016/S1002-0160(08)60069-7

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 N0. 34)*. Ministry of Agriculture, Nairobi, Kenya.

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*(2), pp.124-143. https://doi.org/10.1071/CP07125

Schenck, N.C. and Perez, Y., 1990. Manual for the Identification of VA Mycorrhizal Fungi. Synergistic Publications, Gainesville

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. *International Scholarly Research Notices Biodiversity*, *2013*, pp.1-6. http://dx.doi.org/10.1155/2013/593087

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*, pp.222-232. https://doi.org/10.1016/j.apsoil.2018.01.013

Soka, G. E., Ritchie, M. E. and Mayemba, E. P., 2015. Influence of current land use and edaphic factors on arbuscular mycorrhizal (AM) hyphal abundance and soil organic matter in and near Serengeti National Park. *Journal of Ecology and the Natural Environment*, *7*(5), pp.158-169. http://doi.org/10.5897/JENE2015.0506

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*, pp.427-434. https://doi.org/10.1016/j.sjbs.2012.05.004

Syibli, M.A., Muhibuddin, A. and Djauhari, S., 2013. Arbuscular mycorrhiza fungi as an indicator of soil fertility. *AGRIVITA, Journal of*

Agricultural Science, 35, pp.44-53. http://doi.org/10.17503/agrivita.v35i1.228

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, 13668, pp.1-12. https://doi.org/10.1038/s41598-020-70464-6

van der Heyde, M., Ohsowski, B., Abbott, L. K. and Hart, M., 2017. Arbuscular mycorrhizal fungus responses to disturbance are context-dependent. *Mycorrhiza*, *27*, pp.431-440. https://link.springer.com/article/10.1007/s00572-016-0759-3

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*, pp.590-605. https://doi.org/10.1038/s43017-020-0091-5

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*, p.e0130983. https://doi.org/10.1371/journal.pone.0130983

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*, pp.67-74. https://doi.org/10.1007/s11274-010-0427-2

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*, pp.121-131. http://doi.org/10.17221/5/2018-SWR

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*, p.119706. https://doi.org/10.1016/j.foreco.2021.119706