Uncovering the complex relationship between plant diversity, soil properties, and mycorrhizal inoculum potential in threatened miombo woodlands

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Abstract

Aboveground biodiversity and physicochemical properties influence soil microbial communities. Arbuscular mycorrhizal fungi (AMF) are key members of these microbial communities and play a key role in regulating ecosystem processes. However, the mutual interdependence of plants and AMF in threatened forests is poorly understood. In this study, we investigated the relationship between plant ecological indicators and soil mycorrhizal inoculum potential (MIP) in the Miombo forest fallow of Haut-Katanga, DRC, and identified plant species that positively influence soil MIP. We conducted a floristic inventory on 32 plots and collected soil cores for physicochemical and AMF characterization. An AMF bioassay using *Crotalaria juncea* seedlings was performed to determine the soil MIP. We also tested the AMF colonization status of randomly collected living roots of mature woody and dominant herbaceous species to identify explanatory variables for MIP. Our results showed that MIP was higher in silty clay soils (63.13%) than in clay soils (30%) ($F = 57.07$; $p < 0.0001$). Furthermore, MIP increased accordingly with the relative abundance of a group of woody and herbaceous species (e.g. *Albizia adianthifolia*, *Baphia bequaertii* and *Setaria pumila*) and decreased with others (e.g. *Combretum collinum*, *Harungana madagascariensis* and *Hyparrhenia diplandra*). Linear regressions showed that MIP increased significantly with the specific richness of woody species identified as indicators and with the amount of annual herbs. Woody legumes with high root colonization by AMF appeared to be refuge plants, and primary AMF dispersal vectors, increasing soil MIP. This study provides baseline data that can be used to formulate ecological restoration strategies, including soil and vegetation protection.

Introduction

Arbuscular mycorrhizal fungi (AMF) are highly prevalent in terrestrial ecosystems, colonizing approximately 72% of host plant species (Brundrett and Tedersoo 2018). Mycotrophic shrubs, trees, and herbaceous species are important for maintaining the soil mycorrhizal inoculum potential (MIP) in degraded forest patches and improving the establishment and growth of planted seedlings (Duponnois et al. 2013). The ability of soil fungal propagules to form mycorrhizal associations is a fundamental feature of soil health and fertility, especially in the context of threatened forest restoration. Indeed, AMF fungi can improve seedling fitness by linking them to the existing mycelial network and providing them with nutrients (van der Heijden 2004).

In tropical degraded open forests, such as the Miombo woodlands, Högberg and Piearce (1986) observed that woody species are predominantly colonized by AMF. These woody species ensure the spread (Lies et al. 2017) and survival (Fortin et al. 2015) of AMF, thereby regulating the soil MIP (Hafidi et al. 2013; Benkhoua et al. 2017). However, studies on the mycorrhizal status (AMF vs. ectomycorrhizae) (Hogberg and Piearce 1986) and diversity (Jefwa et al. 2012; Rodríguez-Echeverría et al. 2017) in forest fallows are exploratory and cannot be used to improve natural regeneration or reforestation efforts, as has been done in African Mediterranean regions (Duponnois et al. 2013).

Anthropogenic pressures, combined with harsh climatic conditions affect the survival of woody species (Chidumayo 2001), and lead to over-exploitation of timber, resulting in the degradation and deforestation of tropical seasonal forests such as the Miombo woodlands. The Miombo woodlands are a vital band of tropical seasonal forest stretching from Angola, southern Democratic Republic of Congo (DRC), Malawi, parts of Zambia and Zimbabwe, to Mozambique and Tanzania (Timberlake et al. 2010). They are important habitats for a wide range of wildlife, including iconic animals such as elephants, antelopes and primates. They also provide important ecosystem services such as carbon sequestration, soil conservation and water regulation. Miombo forests are also an important source of timber, fuelwood and non-timber forest products for local communities. They support the livelihoods of approximately 100 million people, mainly through agriculture and energy production (Syampungani et al. 2016; Kiruki et al. 2017).

Soils in the Miombo woodlands are typically acidic (Mapanda et al. 2013; Bauman et al. 2016), low in available phosphorus and organic matter, and high in aluminium and iron (Bauman et al. 2016). Given these edaphic constraints, the development and productivity of woody seedlings would be facilitated in part by soil microorganisms such as AMF.

Woody species such as *Albizia* spp, *Baphia bequaertii*, *Pterocarpus* spp (Hogberg and Piearce 1986), *Combretum collinum, Pterocarpus tinctorius* (Kaumbu, personal observation) in the Miombo forest fallows are mainly colonized by AMF. *Albizzia* spp, *B. bequaertii*, *Pterocarpus* spp, are also found in deforested savannas, together with *Diplorhynchus condilocarpon* (Syampungani et al. 2016) and are associated with herbaceous species such as *Hyparhenia variabilis* and *Pteridium aquilinum* (Stromgaard 1986).

The aim of this study was to investigate the relationship between plant ecological indicators and soil MIP in the Miombo forest fallow, and to identify plant species that positively influence soil MIP. Specifically, we focused on woody and herbaceous species present in the savannah areas resulting from deforestation activities in two forest fallow areas, Mikembo and Kipopo. To achieve this, we conducted two observational studies to achieve this objective. The first study involved a floristic inventory to document the plant species present in the area, while the second study investigated the interdependence between above- and below-ground communities. This included characterization of MIP, soil physicochemical properties, and AMF colonization of field roots. To the best of our knowledge, this is the first study to attempt to identify these relationships in the Miombo forest fallow. The baseline data obtained from this study will be useful in formulating strategies for ecological restoration of threatened forests, including soil conservation.

Materials and methods

Description of the study area

The study was conducted in two forest fallow sites, Mikembo and Kipopo, located in Haut-Katanga province in southeastern DR Congo (**Figure S1**). The Mikembo site, located 34.5 km northeast of

Lubumbashi, is part of a forest reserve established to conserve exotic fauna and indigenous flora. It is located on the Kasenga road at coordinates 11°28'5.22" S, 27°39'35.7" E, at an altitude of 1192 m above sea level. The Kipopo site is located on a concession of the Institut National pour l'Étude et la Recherche Agronomique (INERA), located 18 km north-west of Lubumbashi at 11°34'23.58" S, 27°24'108" E, at an altitude of 1286 m above sea level. The study area falls under the Köppen-Geiger Cwa climate classification (Peel et al. 2007). The climate is characterized by a 185-day dry season (April to October) and an average annual rainfall of 1200 mm, peaking in December. The average annual temperature is 20°C, with the warmest months being October and November. The average annual humidity is 68%, with a monthly average of 47% during the dry season in September, and 86% during the rainy season in February (Mpundu 2010).

Ferralsols dominate at both sites, with a high proportion of haplic Ferralsols and a low occurrence of plinthic and rhodic Ferralsols (Ngongo et al. 2009). These soils are acidic in nature with high concentrations of aluminium and iron (Bauman et al. 2016). They are also nutrient deficient with low concentrations of nitrogen and phosphorus (Mpundu 2010; Bauman et al. 2016).

Field investigation

The floristic inventory was conducted at the two sites, Kipopo and Mikembo, using a comprehensive design of 16 plots (4 transects and 4 inventory plots) at each site. To estimate tree density and herbaceous species abundance, we established inventory plots at 50 m intervals along each transect. Woody species were inventoried using a 10 m × 10 m square quadrat, while herbaceous species were inventoried using a 1 m × 1 m square quadrat, placed at five points in the main plot. The number of stems of each identified woody species was counted to determine the percentage relative density (RD %, number of individuals of a species divided by the number of all individuals of all species). The relative abundance-dominance cover (AD %) of herbaceous layers was determined using the quadrat method. Spatial geographic coordinates (longitude and latitude) and elevation were recorded at each site using a GPS device. Species were identified in the field while unidentified specimens were collected and taken to the Botany Laboratory of the Faculty of Agricultural Sciences, University of Lubumbashi, DRC, for further examination. Specimens were identified taxonomically using the Angiosperm Phylogeny Group (APG) III system (Chase and Reveal 2009).

Mycorrhizal inoculum potential experiment

To assess the variability of soil MIP variability among different ecological vegetation groups, two experiments were conducted. The first experiment compared the spontaneous colonization of *Brachystegia spiciformis* Benth and *Pterocarpus tinctorius* Welw seedlings in three ecological groups (Chipya, Uapaca and Miombo). The results (data not shown) revealed that AMF colonization was higher in the Chipya group for *P. tinctorius* roots while *B. spiciformis* had very low (or no) ectomycorrhizal fungal colonization. Based on these results, we decided to assess the effect of floristic composition on soil MIP

in the forest fallow (Chipya). The second experiment involved an experimental bioassay, following the methodology described by Brundrett and Abbott (1995) and Bois et al. (2005). We used a series of successive soil dilutions to determine infectious AMF propagules, and used *Crotaliaria juncea* seedlings, which have a high mycorrhizal dependence, as a host trap culture.

Soil sampling procedure

Soil samples were collected along four parallel transects that were 150 m in length and spaced 50 cm apart, as illustrated in **Figure S2**. Four soil cores were collected at regular intervals of 50 m along each transect using 10 cm × 11 cm polyvinyl chloride (PVC) tubes. A total of 64 soil samples were collected per site, placed in polyethylene bags, and transported on ice to the Faculty of Agricultural Sciences, University of Lubumbashi, DR Congo. After thorough homogenization and removal of roots, soil samples were sieved through a 2 mm mesh and divided into two subsamples. One subsample was stored at 4°C for characterization of soil physical and chemical properties, while the other subsample was used for experimental bioassay in the nursery.

Determination of arbuscular mycorrhizal inoculum potential

A randomized experimental bioassay was conducted under nursery conditions to determine the MIP of soils from the Kipopo and Mikembo sites. Soil origin was considered as the treatment, and plots and samples as pseudo-replicates (**Figure S3A**). Soil dilutions were prepared by thoroughly mixing each original soil with the same autoclaved soil (140°C, 45 min). Dilutions ranging from 10^{-1} to 10^{-6} were prepared, and five replicates were used per dilution. The soil was placed in PVC tubes and ten pregerminated *C. juncea* seeds were transplanted into each tube. The bioassay was conducted under nursery conditions (**Figure S3B**) and the plants were watered daily with 25 mL of distilled tap water per tube. After two weeks of growth, the seedlings were carefully removed from the tubes to prevent root colonization from one seedling to another. The entire root system of each plant was gently rinsed with tap water to remove soil, cleared with KOH for 30 min and stained using the method of Vierheilig et al. (1998). Root colonization was observed under a compound microscope at 250× magnification. MIP values were estimated by calculating the percentage of colonized root seedlings out of a total of ten seedlings.

Soil physicochemical characterization

Soil texture was determined from the percentage of clay (< 0.002 mm), fine silt (0.002 to 0.02 mm), coarse silt (0.02 to 0.05 mm) and sand (0.05 to 2 mm) fractions by the improved hydrometric method (Bouyoucos 1962). The pH was measured electrometrically in a suspension of 10 g of soil and 20 mL distilled water. Soil chemical properties including pH, extractable cations (calcium, magnesium, potassium and sodium), cation exchange capacity (CEC) and base saturation were determined using

standard procedures (Bray and Kurtz, 1945). Total aluminium, iron and phosphorus were dissolved according to the manufacturer's instructions (CEM Corporation 2016). All elements were measured by inductively coupled plasma spectrometry (ICP Agilent 5110 SVDV). Available phosphorus (Pbray2) was extracted using the Bray and Kurtz (1945) two-reagent system (0.03 N NH_4F: 0.1 N HCl) and analyzed by flow injection analysis (FIA) using Quikchem method 12-115-01-1-A (Zellweger Analytics, Lachat Instruments Division, Milwaukee, WI, USA). Total nitrogen and organic carbon were analyzed using the Kjeldahl and Walkley-Black methods, respectively. Total nitrogen, carbon and sulphur were measured by high temperature combustion and infrared detection in an elemental analyzer (TruMac CNS, LECO Instruments ULC, Mississauga, ON, Canada). Soil organic matter was determined directly as weight loss during combustion. All the analyses were carried out in the soil laboratory of the Faculty of Forestry, Geography and Geomatics, Université Laval (Québec, Canada) using standard protocols.

Field root sampling procedure

To investigate the influence of plant species composition on soil MIP, we examined the AMF colonization of field roots as a variable for the dominant plants. Specifically, we collected field roots from five individual woody species (including four legume species: *Acacia polyacantha* subsp. campylacantha (Hochst. ex A. Rich.) Brenan, *Albizia adianthifolia* (Schumach.) W. Wight, *Baphia bequaertii* De Wild, *P. tinctorius*, and one Combretaceae: *Combretum collinum*) and three herbaceous species (*Hyparhenia diplandra*, *Imperata cylindrica* (L.) P. Beauv. and *Bidens oligoflora* (Klatt) Wild). Root sampling was conducted at the end of May 2018, at the beginning of the dry season. Fine roots were sampled from three individuals per woody species at four cardinal points around the stem. For each herbaceous species, the root system of the dominant species was sampled in three plots. A minimum of 80 fine roots, greater than 5 cm in length, were collected per individual and per plot. Notably, *B. bequaertii* and *B. oligoflo*ra were absent from the Mikembo site and were therefore excluded from the statistical analysis between sites, as well as from the interspecific variability in root AMF colonization.

Determination of field root AMF colonization

Fine roots were collected, gently washed under running water, and cleared in 10% KOH at 96°C for 24 h for woody root species (Onguene and Kuyper 2001) and 1 h for herbaceous root species (Sanon 2005). The roots were then acidified in a 1% HCl solution and stained according to Vierheilig et al. (1998) for 30 min for woody species (Onguene and Kuyper 2001) and for 15 min for herbaceous species (Sanon 2005). The roots were then cut into 1–2 cm pieces and placed on slides for microscopic observation at 40× magnification. The frequency of mycorrhizal colonization (F%) was determined according to the method of Trouvelot et al. (1986): F (%) = (number of colonized root sections/total number) × 100).

Statistical analyses

MIP data were pre-processed using the arc sin $\sqrt{(X/100)}$ transformation followed by analysis of variance. Sites and plots were considered as fixed and random factors, respectively. Post-hoc analysis of means was performed using the Tukey HSD test. Correlations between MIP and soil physicochemical properties were determined using Pearson's correlation coefficients, calculated using the function *rcorr* from in the R package *Hmisc* v.4.1-1 library (Harrell 2018). Generalized linear mixed models (GLMMs) were used to determine the relationship between soil MIP and the relative abundance of woody and herbaceous species, calculated using the *MRT* and *IndVal* functions from the R packages *MVPARTwrap* v.0.1–9.2 (Ouellette 2011) and *labdsv* 1.8.0 (Roberts 2016). Indicator plants were used to determine dissimilarities between sites. Two MLGMs were then constructed using the vegan v2.5-2 library (Oksanen et al. 2019) to determine the relationship between soil MIP and plant indicator abundance. The models were developed by grouping woody and herbaceous species, for the two sites, separated by *IndVal* analysis according to the percentage of clay. To ensure the accuracy of the models, collinearity between species was tested using variance inflation factors (VIF), and species with a VIF greater than 5 were excluded from the models. Finally, the Poisson regression was applied to both models, using the function family = Poisson (link = "log").

Species richness (S), Shannon-Wiener (H'), Simpson (Ds), and Pielou (J') diversity indices and Raunkiaer's biological types were calculated as ecological indicators for the two sites (Peet and Roberts 2013). Species richness, Shannon-Wiener, Simpson and Pielou indices were assessed using the relative abundance-dominance (A-D) values for herbaceous species and the relative density (RD) values for woody species using the vegan v2.5-2 library (Oksanen et al. 2019). Presence-absence data were used to calculate the percentage of each biological type (geophytes, hemicryptophytes, phanerophytes, and therophytes). The Mann-Whitney-Wilcoxon rank test was used to calculate the inter-site dependence (Kipopo vs. Mikembo) of physicochemical parameters and ecological indicators. Simple linear regression was also used to show the relationship between soil MIP, plant ecological indicators and floristic composition and biological types, using the *lm* function implemented in the R software.

The normality of the data was assessed using using the Shapiro-Wilk test. Homogeneity of the variance, the independence of residuals and linearity were assessed using the Goldfeld-Quandt (*gqtest*), Durbin-Watson (*dwtest*) and Rainbow (*raintest*) tests, respectively, using the R package *lmtest* (Zeileis and Hothorn 2002). MIP and geophyte percentages were first log-transformed to ensure normality, homogeneity of variance, independence of residuals and linearity of the regression. Data on AMF colonization of field roots were first transformed by arc sin $\sqrt{(X/100)}$. Comparisons between sites were made using two-way analysis of variance. Means were compared using the Tukey HSD test ($p < 0.05$). All data analyses were performed with R software v3.4.4 (R Development Core Team 2018).

Results

Mycorrhizal soil infectivity

Arbuscules, vesicles and intra-root hyphae were observed in *C. juncea* (Figs. 1A to 1D). The AMF colonization of the roots was identified as Arum-type, characterized by terminal arbuscules and intercellular hyphae (Figs. 1C **and D**).

The bioassay analyses showed that the density of infective propagules varied greatly between sites, and this was influenced by soil physicochemical properties (Fig. 2B to 2E) and the relative abundance of plant indicators. Soil clay content was significantly higher at Mikembo site (40.3 ± 0.5%) than at Kipopo (26.3 ± 1.7) (Fig. 2B). Conversely, total nitrogen and available phosphorus were significantly higher at Kipopo (0.26 ± 0.01% and 29.6 ± 5.2 ppm) than at Mikembo (0.18 ± 0.03% and 5.03 ± 1.7 ppm) (Figs. 2C **and D**). MIP was significantly higher ($F_{(1, 96)} = 57.07$; $p < 0.001$; Fig. 2A) in clay-silty soils (Kipopo: 63.13%) than in clay soils (Mikembo: 30%). Overall, MIP was positively correlated with soil physicochemical properties ($r > 0.60$; $p < 0.05$), but negatively correlated with soil acidity ($r = -0.71$; $p = 0.05$), aluminium ($r = -0.76$; $p = 0.03$), clay ($r = -0.9$; $p = 0.002$), and fine silt content ($r = -0.92$; $p = 0.001$) (Fig. 2E).

The *Indval* analysis of 25 herbaceous and 54 woody species identified 11 (44%) and herbaceous and 16 (29.6%) woody species as indicators (Table S1). The soil MIP was positively associated with the abundance of seven woody species indicators (*Albizzia adianthifolia*, *Cussonia sp.*, *D. condilocarpon*, and *U. kirkiana* ($p < 0.001$); *B. berquaertii* ($p = 0.01$), *M. marcroura* ($p = 0.001$), *M. katangensis* ($p = 0.01$)) and two herbaceous species indicators (*I. cylindrica* ($p = 0.04$) and *S. pumila* ($p = 0.01$)). On the other hand, soil MIP was negatively correlated with the relative abundance of the six woody species indicators (*A. antunesiana*, *C. acutifolium*, and *C. collinum* ($p < 0.001$), *H. madagascariensis* ($p = 0.02$), and *Hymenocardia acida* ($p = 0.01$) and *Securidaca longipendoculata* ($p = 0.01$)) and three herbaceous species (*Hyparhenia diplandra*, *Panicum maximum* ($p = 0.001$) and *Pteridium acquilinum* ($p < 0.001$), Fig. 3).

Relationship between plant ecological indicators and soil MIP

Analysis of the diversity indices and Raunkiaer's biological types showed significant differences between the Kipopo and Mikembo sites (Fig. 4). The Kipopo site had significantly higher values for the Shannon-Wiener ($p = 0.01$), Simpson ($p = 0.01$), and Pielou ($p = 0.01$) indices for herbaceous species than for the Mikembo forest fallow. The same trend was observed for species richness ($p = 0.05$) and Pielou index ($p = 0.01$) for woody composition species. In addition, the abundance of therophytes was significantly higher in the Kipopo site ($p = 0.001$) than in the Mikembo forest fallow. However, the relative abundances of hemicryptophytes ($p < 0.001$) and geophytes ($p = 0.08$) were significantly higher at the Mikembo site than at the Kipopo site. Soil MIP increased significantly with woody species richness and the relative abundance of therophytes, while it decreased significantly with the relative abundance of hemicryptophytes and geophytes (Fig. 5).

Field root mycorrhizal fungal colonization

Only intra-root hyphae and vesicles were observed in field roots after root staining (Fig. 6). AMF colonization of field roots was influenced by host plant identity and habitat site or a combination of both. Significant differences were found between species ($F_{(5, 24)} = 86.4$; $p < 0.0001$), forest fallow sites ($F_{(1, 24)} = 117.8$; $p < 0.0001$), and the interaction of species by site ($F_{(5, 24)} = 27.9$; $p < 0.0001$). For example, AMF colonization of legumes such as *A. polyancatha*, *A. adianthifolia* and *P. tinctorius* was 22.08 ± 7.16, 20 ± 2.7 and 16.66 ± 5.8 in the Kipopo site and 11.66 ± 1.55; 10 ± 2.04 and 5 ± 1.02 in the Mikembo forest fallow (Fig. 7). Legumes were more infected than other plant species, such as *C. collinum* (5.41 ± 1.55 and 5 ± 1.02 in Kipopo and Mikembo forest fallow, respectively). The herbaceous species showed poor mycorrhization such as *Hyparrhenia diplandra* (5.83 ± 1.17 in Kipopo and 5 ± 1.02 in Mikembo) and *Imperata cylindrica* (5.08 ± 1.02 in Kipopo and 2 ± 0.58 in Mikembo). The legume species *A. polyancatha*, *A. adianthifolia* and *P. tinctorius*, had their highest root AMF colonization in the Kipopo forest fallow, while the mycorrhizal colonization of the same species was 2 to 3 times lower for in Mikembo. The legume species *B. bequaertii* and *B. oligoflora* (Asteraceae) were found only at Kipopo and showed root AMF colonization of 17.5 ± 1.02 and 5.83 ± 1.55% respectively. The data indicate the mycotrophic nature of legume species and their potential role in maintaining soil mycorrhizal propagules in forest fallow.

Discussion

After two weeks of growth, efficient AMF colonization of *Crotalaria juncea* roots was observed as evidenced by the presence of Arum-type arbuscules, intra-root hyphae and vesicles. Analysis of soil AMF propagules using *C. juncea* showed that MIP was significantly higher in the silty clay soils of Kipopo than in the clay soils of Mikembo. The high clay content at the latter site may have limited root development and hence the spread of AMF propagules. The relationship between soil clay content and soil nutrient availability was previously investigated by Mujinya et al. (2013) in Lubumbashi. Their study showed a positive correlation between soil clay and aluminium and iron content. Although these elements are important sources of free oxides in the soil, they can also be toxic to AMF. Seguel et al. (2013) reported an intra- and inter-specific sensitivity of AMF to aluminium, which can reduce soil MIP. This suggests that aluminium toxicity could be a potential cause of the reduced MIP observed in the Mikembo clay soils.

Indicator plants were identified to determine dissimilarities in soil MIP between the sites. The indicator species *Albizzia adianthifolia* was more abundant in the Kipopo site than in the Mikembo forest fallow, while *Combretum acutifolium* and *C. collinum* were more abundant in the Mikembo site. Species belonging to the genera *Albizzia* and *Combretum* have been reported as indicator species in agroforestry fallow (Gonçalves et al. 2017). It appears that the presence of *A. adianthifolia* and other legumes may play an important functional role in increasing soil MIP. To investigate the underlying mechanisms driving these relationships, we analyzed the root colonisation of these plant indicators in the field. We found interspecific variability in AMF colonisation of the field roots between woody and herbaceous indicator species. The results are consistent with a previous report by Onguene and Kuyper (2001), who demonstrated interspecific variability in AMF colonization within the same rainforest site in Cameroon.

Our data support the highly mycotrophic nature of woody legume species and their potential role in maintaining high levels of soil mycorrhizal propagules in forest fallows. Three woody legume species (*A. adianthifolia*, *B. bequaertii* and *P. tinctorius*) were identified as potential refuge plants and primary vectors of AMF propagules in Kipopo and Mikembo forest fallows. Positive relationships were found between soil MIP and the diversity and evenness of these plant species in both forest fallows. We also found that the root systems of woody legumes were more colonized by AMF than those of herbaceous plants. This result is in agreement with Belay et al. (2013), who reported an AMF colonization ranging from 12 to 67% in 12 native acacia legume species in different land uses in Ethiopia. In addition, most of the tropical legume species tested in the DR Congo showed a high dependence on mycorrhizal fungi (Khasa et al. 1990; 1992; Bulakali et al. 1999). Other studies focusing on soil AM and ectomycorrhizal fungi in relation to vegetation gradients (Hogberg and Piearce 1986) or AMF biodiversity (Jefwa et al. 2012; Rodríguez-Echeverría et al. 2017) have also highlighted the role of plant host composition in maintaining or shifting the development of the belowground mycorrhizal population. Our results are consistent with studies from other African countries, where mycotrophic plant species have been reported to improve soil MIP (Duponnois et al. 2011; Hafidi et al. 2013; Benkhoua et al. 2017).

The high relative abundance of therophytes at the Kipopo site and hemicryptophytes at the Mikembo site suggests their potential contribution in maintaining or disturbing soil MIP. For example, *S. pumila*, an annual therophyte, and *I. cylindrica*, a perennial rhizomatous geophyte (Schmitz 1971), showed an affinity for woody species at Kipopo, where soil MIP was high. While therophytes have a sparse taproot system and are expected to contribute less to soil MIP, *H. diplandra* and *Panicum maximum*, both perennial hemicryptophytes (Schmitz 1971) with a very dense and shallow fasciculate root system, were abundant at the Mikembo site, where soil MIP was low. Hemicryptophytes are less dependent on AMF mycorrhization and therefore contribute less to maintaining soil MIP at the Mikembo site. Other studies have shown that AMF diversity was higher in annual herbaceous species compared to perennial herbaceous species (Shannon index = 1.36 ± 0.01 and 0.79 ± 0.05; respectively) (Torrecillas et al. 2012). In Senegal, the positive role of the legume herb *Cassia obtusifolia* L. in the efficient dispersal of AMF propagules has been demonstrated in both natural and man-made forests (Duponnois et al. 2001; Sene et al. 2012a, b). Results from Zhang and Liu (2004) in deforested and natural forest areas in the subtropical region of China, and Guadarrama et al. (2008) in a secondary dry forest in Oaxaca, Mexico, also suggest that herbaceous plants may be particularly efficient in spreading AMF. It has also been reported that neighboring weeds influence the formation of arbuscular mycorrhizae on the roots of grapevines in southern Croatia (Radić et al. 2012).

In the Lubumbashi region, and particularly in the Miombo ecosystem, the dry season lasts 7 months and the dried out herbaceous cover is usually consumed by bush fires (Schmitz 1971; Malaisse 1997). In this context, woody plants are the preferred partners of AMF, which can provide them with carbohydrates during the dry season. Moreover, in natural ecosystems, Rodríguez-Echeverría et al. (2017) showed that AMF diversity is higher in habitats with high tree density (mixed dry forest and open forest, Miombo) compared to shrub and grass savannas in Mozambique. Furthermore, in their study, the herbaceous cover was dominated by hemicryptophytes, which in our linear model could explain the decrease in soil MIP

with increasing mean relative abundance of hemicryptophytes. These data and those obtained from our study suggest that woody plants, and especially woody legumes, act as refuges and vectors for the AMF community. Our results are significant because based on seedling productivity (volume index), the early successional species *P. tinctorius* has been recommended among the potential candidates for afforestation and agroforestry in the Miombo degraded ecosystem (Kaumbu et al. 2021).

In conclusion, the density of infective propagules varied greatly between sites, and this was influenced by soil physicochemical properties and the relative abundance of plant indicators. Soil MIP increased significantly with woody species richness and the relative abundance of therophytes, whereas it decreased significantly with the relative abundance of hemicryptophytes and geophytes. The woody species *A. adianthifolia*, *B. bequaertii* and *P. tinctorius* and their associated herbaceous species *I. cylindrica* and *S. pumila* were identified as potential drivers of soil MIP in Kipopo and Mikembo forest fallows. The higher AMF colonization status of the formers compared to Combretaceae, geophytes and hemicryptophytes may partly explain their association with higher soil MIP. Several soil properties also showed a positive correlation with soil MIP, while acidity, aluminium and iron content, clay and fine silt were negatively correlated. These results support the habitat hypothesis (Zobel and Öpik 2014), which suggests that the relationship between plants and AMF is co-dependent. However, further studies using metagenomic approaches on a vegetation gradient or soil gradient in the Miombo forest are needed to isolate the effects of plant cover and physicochemical parameters on the observed relationship. Our results also highlight the importance of identifying and protecting tree species with high mycorrhizal dependence to promote soil health and biogeochemical cycling, and to enhance natural or assisted regeneration processes of open forests.

Declarations

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Author contributions

JMKK and DPK conceived and designed the experiments. JMKK performed all the experiments and analyses. JMKK and GS wrote the first draft of the manuscript. FS co-supervised JMKK and rewrote the subsequent version of the manuscripts with GS. DPK was responsible for supervision and project management, as well as funding and resource acquisition. All authors provided critical input to the drafts and gave final approval for publication.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Availability of data and materials

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

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Figures

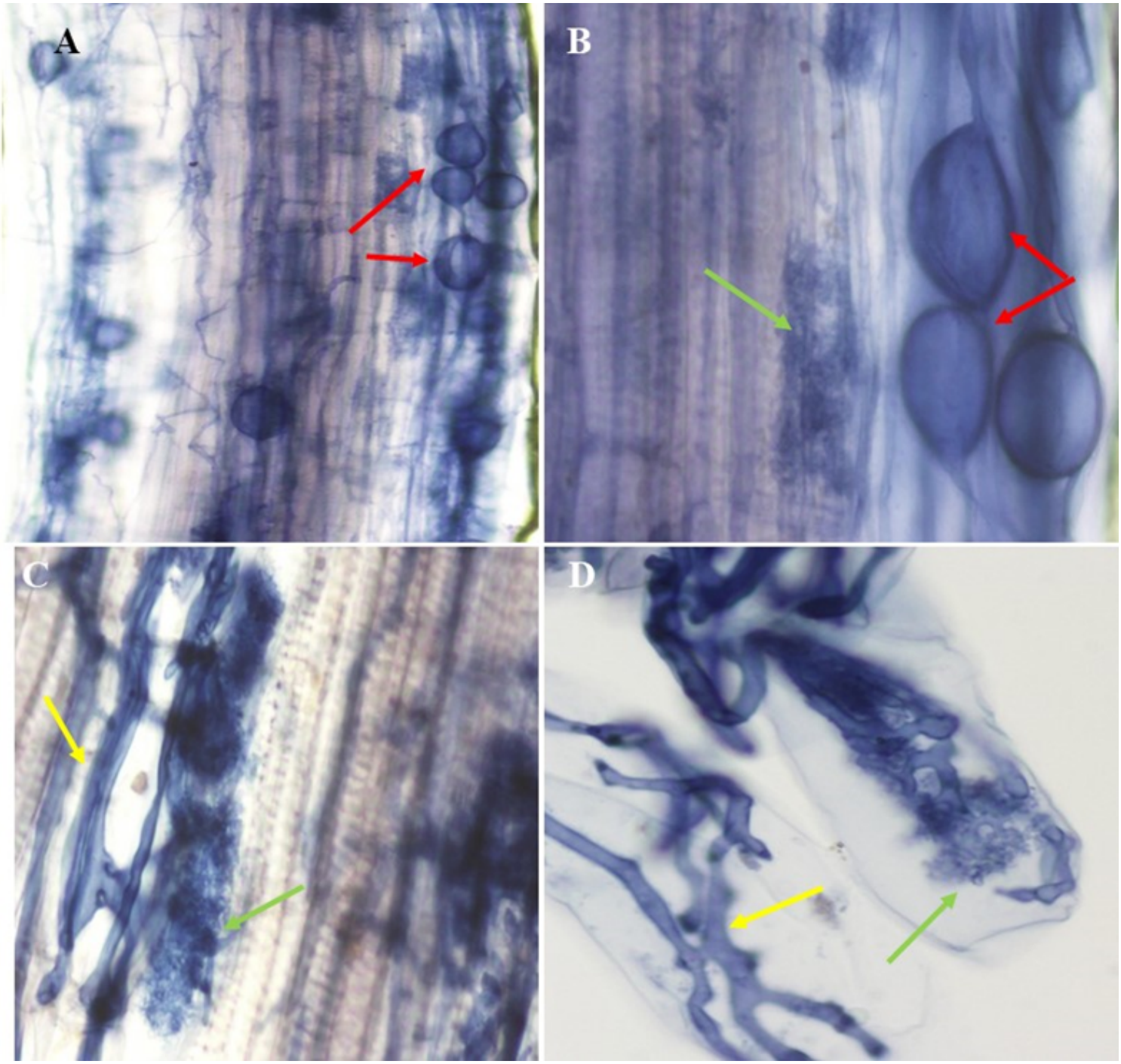

Figure 1

Anatomical structure of arbuscular mycorrhizal fungi (AMF) in the roots of *C. juncea*. A) vesicles (10X), B) arbuscules (green) and vesicles (red) (20X), C and D) arbuscules (green) and intercellular hyphae (yellow) (40X), AMF Arum type.

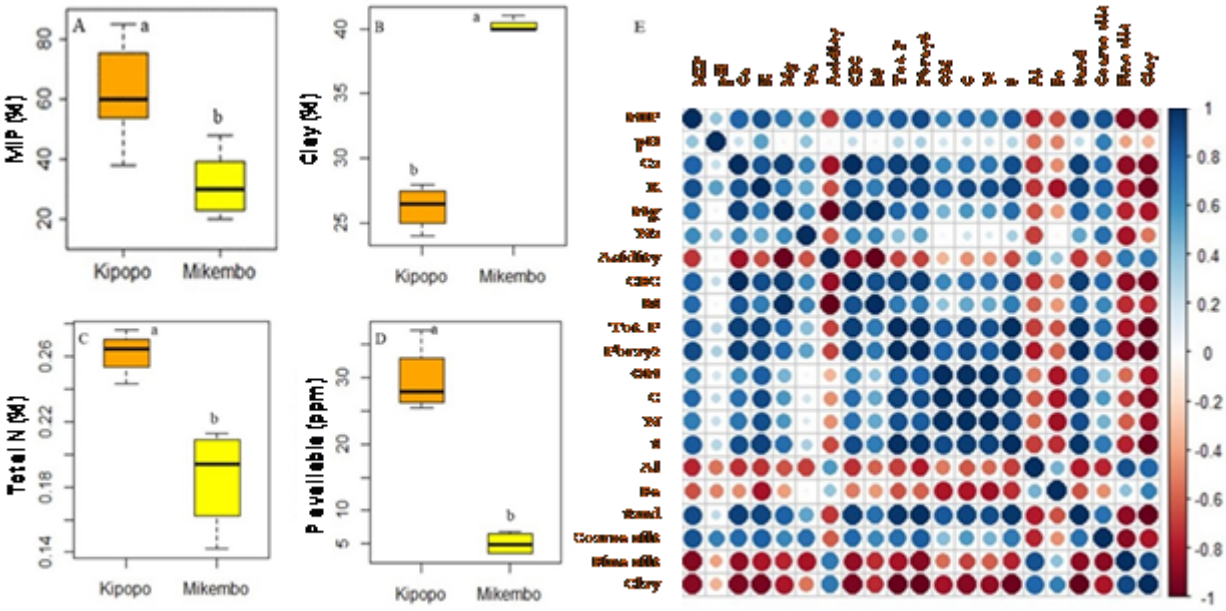

Figure 2

Variability between sites (n = 16 plots per site) of soil arbuscular mycorrhizal inoculum potential (MIP) and soil physicochemical parameters. A) soil MIP, B) clay content, C) total nitrogen, D) available phosphorus and E) Pearson correlation between soil MIP and physicochemical parameters. Al (aluminium), Ca (calcium), C (organic carbon), CEC (cation exchange capacity), Fe (iron), K (potassium), Mg (magnesium), MO (organic matter), N (total nitrogen), Na (sodium), P bray2 and P tot (available and total phosphorus), S (sulphur), and BS (base saturation ratio). Letters on the whisker bars indicate significant differences between two sites according to Tukey's HSD test for MIP ($p < 0.05$) and Wilcoxon non-parametric rank sum test (Clay, total N and available P; $p < 0.05$).

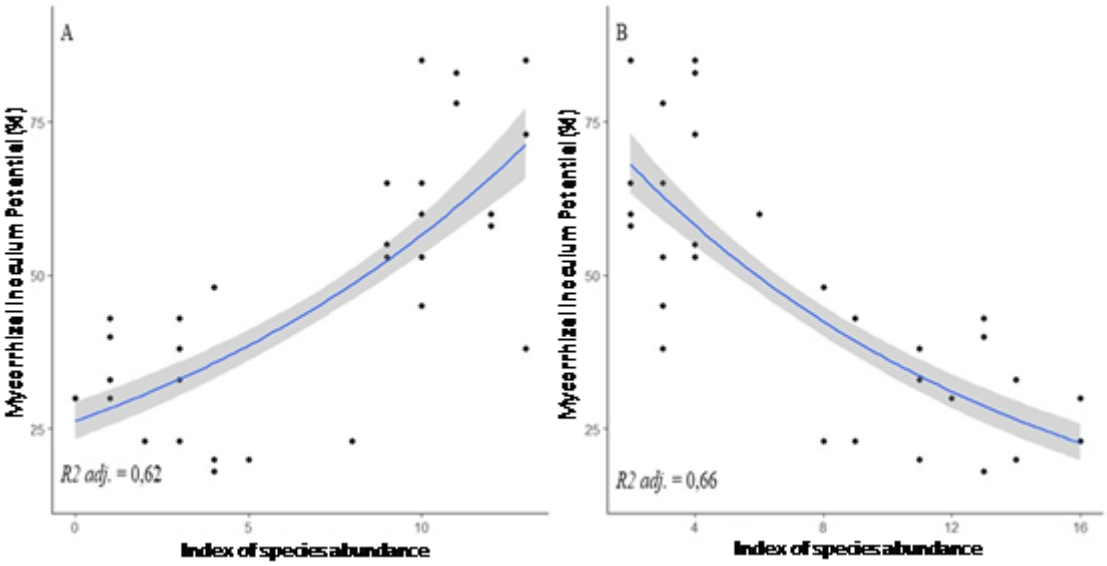

Figure 3

Generalised linear mixed models (GLMM) illustrating the relationship between soil arbuscular mycorrhizal potential (MIP) and the abundance of woody and herbaceous species. N = 16 plots per site. A. Kipopo site (MIP = 3.4 - 0.05AAD - 0.01BBE + 0.08CAN + 0.05DC + 0.002MM + 0.11MK + 0.1UK + 0.08IC + 0.25SP). B. Mikembo site (MIP = 4.5 - 0.1AAN + 0.03CA - 0.17CCO - 0.07HM - 0.01IS + 0.05SL - 0.14HS - 0.36PA - 0.15PS. For tree species: AAD: Albizia adianthifolia, AAN: A. antunesiana, BBE: Baphia bequaertii, CA: Combretum acutifolium, CCO: C. collinum, CAN: Cussonia sp., DB: Dalbergia boehmii, DC: Diplorhynchus condylocarrpon, HM: Harungana madagascariensis, IS: Hymenocardia acida, MK: Monotes katangensis, MM: Marquesia macroura, SL: Securidaca longipendoculata. For herbaceous species: HD: Hyparhenia diplandra, IC: Imperata cylindrica, PAC: Pteridium acquilinum, PS: Panicum maximum and SB: Setaria pumila.

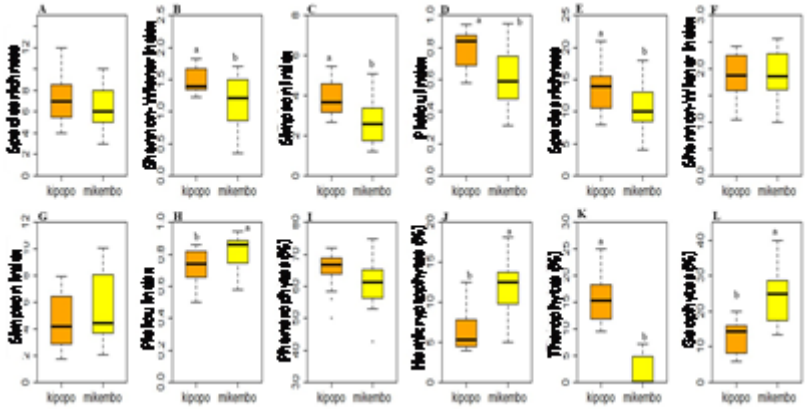

Figure 4

Ecological indicators of floristic composition in two sites (Kipopo and Mikembo) of the degraded open forest (Miombo). N = 16 plots per site. For herbaceous species: A) species richness, B) Shannon-Wiener index, C) Simpson index and D) Pielou index. For woody species: E) species richness, F) Shannon-Wiener index, G) Simpson index, and H) Pielou index. For the biological spectrum of Raunkiaer: I) phanerophytes, J) hemicryptophytes, K) therophytes and L) geophytes.

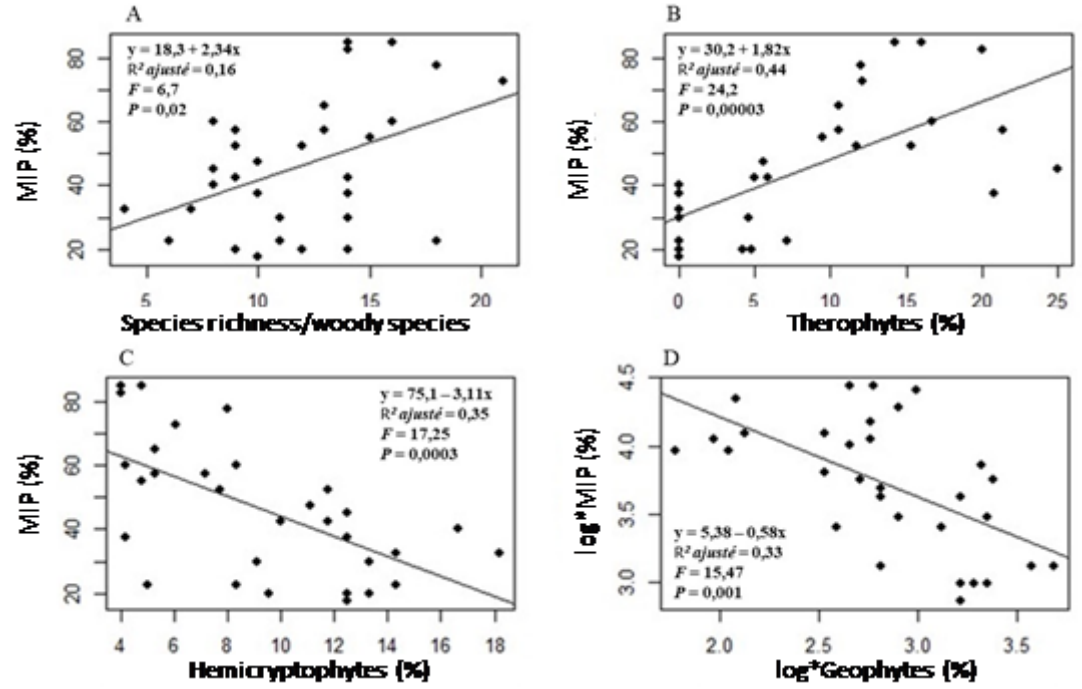

Figure 5

Linear relationship between arbuscular mycorrhizal inoculum potential and the woody species richness (A), therophytes (B), hemicryptophytes (C) and geophytes (D). N = 16 plots per site.

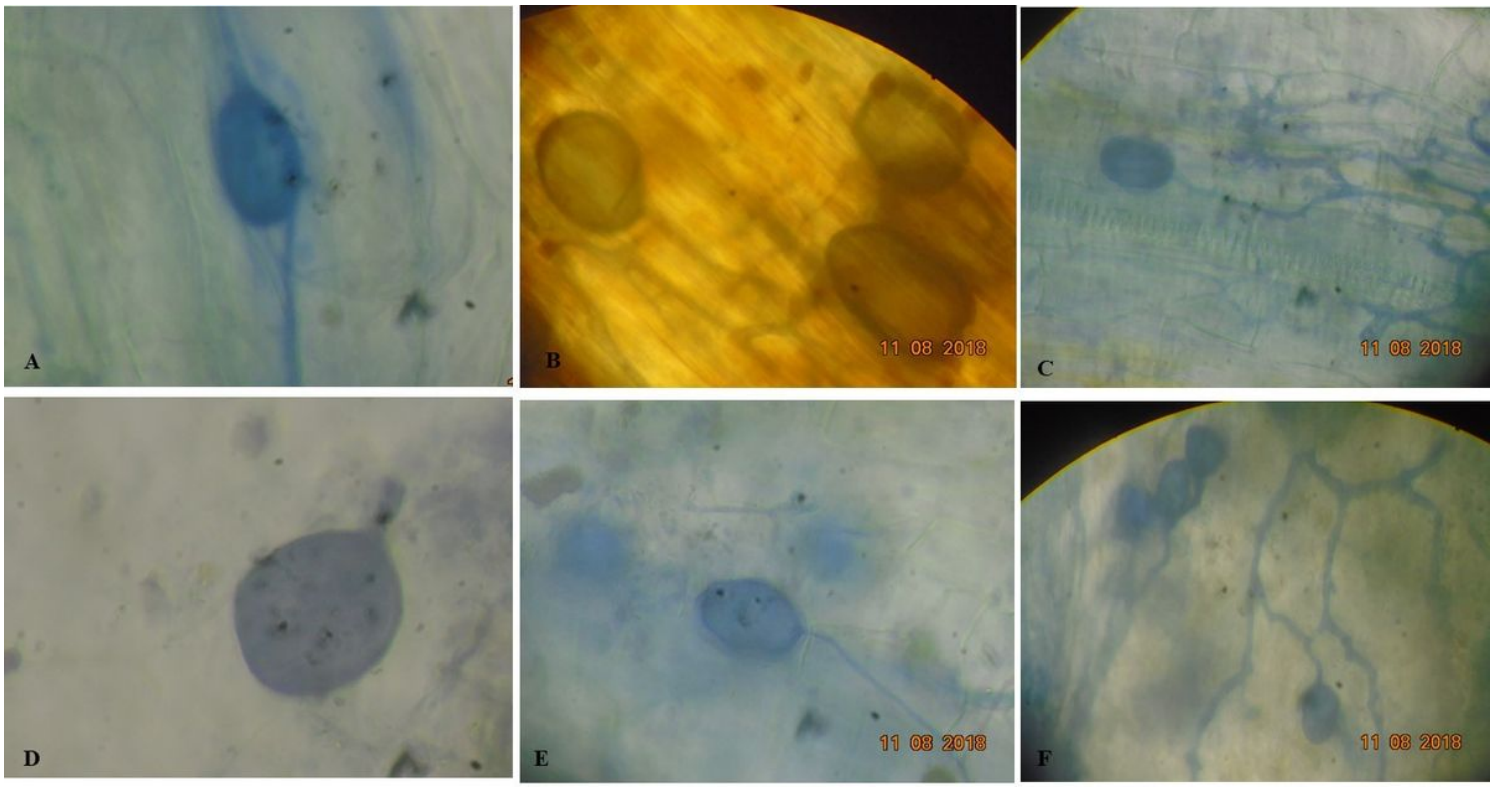

Figure 6

Arbuscular mycorrhizal fungal structures showing vesicles and hyphae in root systems of tree, shrub and herbaceous species collected from the forest fallow (Miombo). A) *A. adianthifolia*, B) *A. polyacantha*, C) *Bidens oligoflora*, D) *C. collinum*, E) *H. diplandra* and F) *P. tinctorius*.

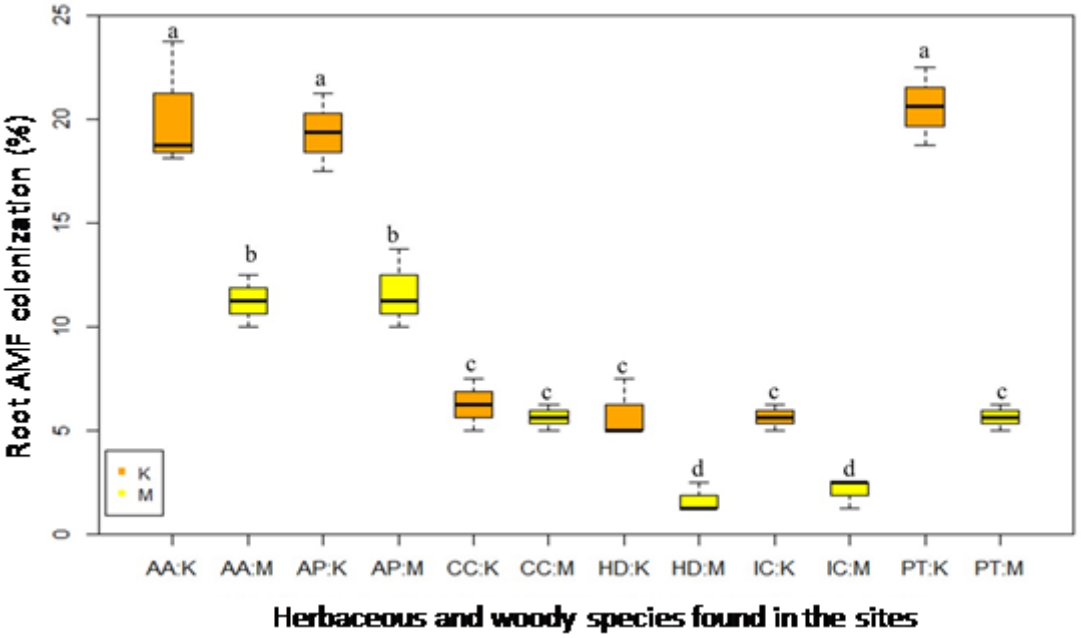

Figure 7

Arbuscular mycorrhizal root colonisation of woody species (AP: A. polyacantha subsp. campylacantha (Hochst. ex A. Rich.) Brenan and PT: P. tinctorius), shrubs (AA: A. adianthifolia and CC: C. collinum) and herbaceous species (HD: H. diplandra, IC: I. cylindrica) in forest fallow (Miombo). K and M correspond to the Kipopo and Mikembo sites respectively. N = 3 individuals per species and per site. Different letters above the box plots indicate significant differences based on Tukey's HSD test ($p < 0.05$).

Supplementary Files

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