

Full Length Research Paper

Ectomycorrhizal mushroom yield association with woody species and leaf litter in miombo woodland, central Zimbabwe

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Abstract

Ectomycorrhizal mushrooms (ECM) symbiotic with woody species develop caps in two successive flushes in the rainy season. Sporocarp yield is influenced by size of woody host and leaf litter density as carbon sources. Yields of four ECM species, and yield associations with basal areas of possible host tree species and ground leaf litter mass were investigated in two different miombo stands. We also compared sporocarp yields of two flushes during the rainy season. We found higher yields ($p < 0.05$) of *L. Kabansus* in one site but similar yields of the other ECM between sites; higher yields ($p < 0.05$) for *C. heinemannianus* and *L. Kabansus* in second flushes, and similar flush yields for *A. loosii* and *C. Miomboensis* between flushes. We found a weak positive correlation ($r = 0.174$) and ($r = 0.247$) between yields of *A. Loosii* and *C. Miomboensis* with *J. Globiflora* basal areas respectively. A negative correlation ($r = -0.338$) between yield of *L. Kabansus* and leaf litter mass was also found. We conclude that host species basal area and leaf litter mass do have a relationship with ECM yields in the miombos.

Key words: Basal area, ectomycorrhizal mushrooms, litter, miombo, mushroom flushes, sporocarp yields.

INTRODUCTION

Ectomycorrhizal mushrooms (ECM) are an important dietary component of many rural households worldwide. Mushrooms are epigeous sporocarps of macrofungi in the Basidiomycota Division. While most mushrooms are saprotrophic, numerous species with less saprotrophic ability to form ectomycorrhizal associations with plant roots (Kernaghan, 2005). Through ectomycorrhizae, ECM obtain organic nutrients from their host plants in exchange for water and essential mineral nutrients, particularly nitrogen

and phosphorus in nutrient-poor soils (Finlay, 2008; Egli et al., 2010; Näsholm et al., 2013; Bödeker et al., 2014). Such nutrient exchange improves host tolerance to stress, viz. drought, high soil salinity and low soil fertility (Hawley and Dames, 2004). The organic food gained by ECM is largely used for sporocarp formation.

In Southern Africa, many communities gather ECM from miombo woodlands for food during the rainy season (Lowore, 2006; Bloesch and Mbago, 2008; Tibuhwa, 2013; Degreef et al., 2016). These ECM have been found to associate with Caesalpinioidae woody species, notably *Julbernardia* and *Brachystegia* genera (Sharp, 2007) but the association between specific ECM yield with woody plant hosts is still unclear. Furthermore, ECM productivity

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arising from these mycorrhizal associations has not been systematically investigated for Zimbabwean miombo woodlands.

Mushroom genera *Amanita*, *Lactarius*, *Russula* and *Cantharellus* contribute to food security and income generation during the rainy season (December to March) in central Zimbabwe (Mlambo and Maphosa, 2017), Tanzania (Bloesch and Mbago, 2008; Tibuhwa, 2013) and Malawi (Lowore, 2006). These ECM genera were found to fruit only when in association with yet unconfirmed miombo woody hosts (Sharp, 2007). Commonly traded ECM species in central Africa include *Amanita loosii*, *Lactarius kabansus*, *Lactifluus velutissimus*, *Russula oleifera*, *Cantharellus miomboensis*, *C. heinemannianus*, *C. symoensii* (Lowore, 2006; Bloesch and Mbago, 2008; Mlambo and Maphosa, 2017). Determining the associations between ECM yields and basal area of host tree species will help in guiding gatherers where to pick desired ECM species.

Miombo woodlands comprise *Brachystegia spiciformis*, *B. glaucescens*, *B. boehmii*, *Julbernardia globiflora*, *Parinari curatellifolia*, *Pericopsis angolensis* and *Pterocarpus angolensis* (Bloesch and Mbago, 2008). Minor species of *Acacia*, *Faidherbia*, *Terminalia* and *Combretum* genera also constitute miomboeco systems (Sharp, 2007; Malambo and Syampungani, 2009; Dewees et al., 2010; Lupala et al., 2015). About 200 woody species are found in the miombo woodlands, making it difficult to determine ECM-woody species association (Dewees et al., 2010), hence the need to examine ECM yield relationships with basal area of possible host tree species.

Most edible ECM of Southern Africa selectively form sporocarps on specific woody plant host species (Bloesch and Mbago, 2008; Epps and Arnold, 2018), although there are reports of possible host-switching by ECM elsewhere outside Southern Africa. This exacerbates current scarcity of knowledge on ECM-host species association for the miombo habitats (Boddy et al., 2013; Sato et al., 2017). Studies have also proved that plant host taxonomic family has the strongest influence on phylogenetic composition of ECM, further complicating determination of miombo ECM hosts, where the major woody species family Caesalpiniaceae comprises over eight different woody species (Tedersoo et al., 2012). Host leaf (carbon) economics and soil factors are also recorded to have a strong influence on ECM-woody species association (Bauman et al., 2016). Hence, ECM occurrence is inextricably bound to woody host partners stand structure, its basal area being a strong possible predictor of ECM productivity (Bonet et al., 2010; Martínez-Peña et al., 2012).

Host woody species shed litter which sustains germination of ECM spores and growth of their superficial mycelia (Aučina et al., 2007; Pritsch and Garbaye, 2011). Although a small proportion (2%) of ECM carbon is supplied by leaf litter (Treseder et al., 2006) and the remainder contributed by host plants through mycorrhizae, litter remains the principal calcium source for mycorrhization (Treseder et al., 2006; Aponte et al., 2010). Addition of leaf litter to soil was found to enhance mycorrhization in pine forests (Jonsson et al., 2006;

Aučina et al., 2007), while sporocarp formation for *Tricholoma matsutake* was found to be positively correlated with leaf litter cover (Sysouphanthong et al., 2010; Vaario et al., 2013). However, fresh leaf litter was found not to promote early mycelial growth for ECM (Lindahli et al., 2007) because mycorrhizal fungi rather colonize older leaf litter for their organic carbon supply (Lindahli and Tunlid, 2015). These findings suggest that forest surface must accumulate old leaf litter for successful ECM productivity. Claridge et al. (2000) found leaf litter thickness to positively influence ECM sporocarp emergence, suggesting that similar influences may occur among miombo habitats. Leaf litter is also known to influence soil nitrification and mineral nitrogen availability that ECM transfer for host use after meeting their own requirements (Wieder et al., 2013). Litter of different tree species was found to increase soil available nutrients and promote growth for some ECM (Mukhopadhyay and Joy, 2010). Since different plant species produce litter of varying quantity, ECM requiring that litter also differ (Vivanco and Austin, 2008). While the foregoing studies have focused on leaf litter influence on ECM sporocarp occurrence, no study has investigated associations between ECM yields and leaf litter quantity in miombo ecosystems.

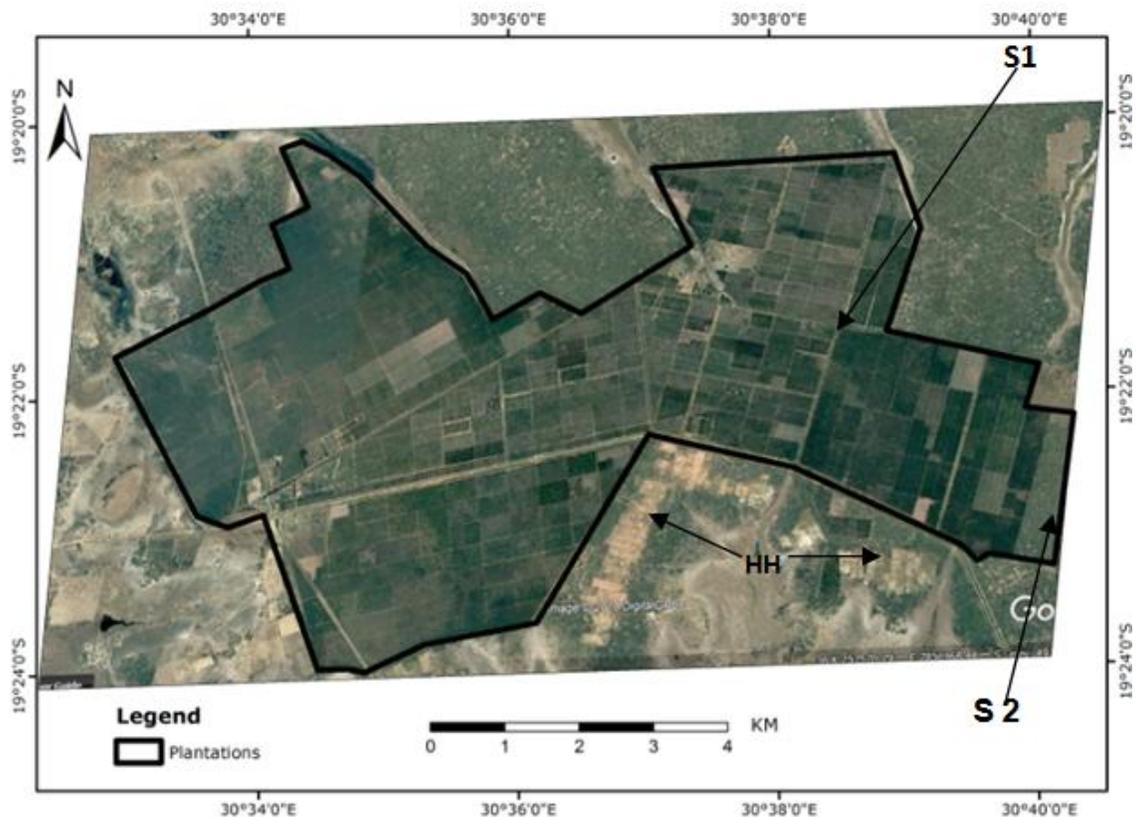
Mushrooms in sub-tropical woodlands experiencing mid-season dry spells in summer typically show growth flushes following the rainfall pattern. This bimodal pattern of ECM emergence was also found in Mediterranean forests (Ágreda et al., 2015; Primicia et al., 2016) over three seasons. Seasonal ECM yields were found to reach their peak at canopy closure of woody vegetation (Wallander et al., 2010). It would be of interest to investigate the ECM sporocarp yield variations among sites and flushes in the same season, while it would be equally important to determine sporocarp yield associations with key woodland variables. Yield differences of four ECM species, *A. loosii*, *C. miomboensis*, *C. heinemannianus* and *L. kabansus* between two sites and between early and late sporocarp emergence flushes were investigated in one season. ECM yield correlations with basal area of two dominant miombo species, *J. globiflora* and *B. spiciformis*, and ECM yield correlation with leaf litter quantity within sites were also investigated.

MATERIALS AND METHODS

Study sites and land use

This research was done at Mtao Forest in Mvuma, central Zimbabwe (Figure 1), for the rainy season between December 2017 and February 2018.

The study area was selected based on good security of undisturbed miombo woodlands in a state-owned estate. Two sites with mature miombo woodlands located four kilometres apart adjoining 2 to 10 year old Eucalyptus plantations were selected for the study. The western site (site 1) included three fireguards 70 metres wide sustaining



HH Estate staff residences

Figure 1: Map of Mtao Estate showing the study sites S1 with rectangular blocks of eucalyptus plantations bordering miombo woodlands, and S2 to the east.

miombo vegetation which separated the eucalyptus plantation blocks, while the eastern site (site 2) was bordered by a eucalyptus plantation to its western edge only. Site 1 fireguards had beehives placed 40 to 50 metres apart while site 2 was not used for any purpose. Miombo woodlands in both sites were of same age, undisturbed for over 35 years of the estate’s existence, and were found to have attained maximum canopy closure, with capacity to sustain ECM growth.

Natural vegetation within study sites was largely composed of miombo woody species dominated by *Julbernardia globiflora*, *Brachystegia spiciformis* and minor species *Burkea africana*, *Monotessp* and *Pterocarpus angolensis*. The undergrowth was typically sparse perennial herbaceous species of *Lippia javanica*, *Asparagus africanus*, *Commelina africana*, *Lannea edulis*, *Sida* sp., a few annual herbs and a narrow variety of sparse perennial sedges and grasses. The ground was devoid of rock or stone, with light to heavy leaf litter cover. In both sites the fersiallitic sandy soils were more than 40 centimetres deep as determined by direct measurements in auger holes for

both sites. Average land slope (sine), calculated using GPS altitude readings of upper and lower edges of sites was 4% and 5% for sites 1 and 2, respectively.

Both sites experienced minimum human disturbance. There was no tree logging, no wood harvesting, no grass harvesting, no leaf litter harvesting and only minimal stray cattle grazing in both sites. The sites did not experience any fire disturbances. There was prohibition of trespassing in both sites. Site 1 was regularly patrolled by apiary staff with minimal disturbance of vegetation or soil characteristics.

During the current study, both sites received the first summer rainfall spell on 23 December 2017 to 1 January 2018 and the second rainfall spell from 10 February to 22 February 2018 (Table 1).

Research Design and Data Collection

The surveyed plots for mushroom assessment were selected in a randomized complete block design with site location as the blocking factor. Each site was mapped into

Table 1. Rainfall recorded in each site (mm) for the study duration.

	Date											Site totals	
	23Dec2017	31Dec2017	01 Jan2018	29Jan2018	10Feb2018	11Feb2018	12Feb2018	13Feb2018	15Feb2018	18Feb2018	20Feb2018	22Feb2018	
Site 1	87	23	47	4	19	5.5	23	16	18	30.5	29	2	304
Site 2	79	14	31	11	39	0	15	19	20.5	18.5	28	5	280

Forty grids of 50 metre square using a GPSmeter (GarminTrex 30). Fifteen grid squares in each site were randomly selected using Microsoft Excel (2007) random number generator. The centre of each selected grid square was physically located on the ground and a 15 metre radius circular plot marked following the method of Beggs et al. (2005), Soni et al. (2014) and Mbwana et al. (2017). Perimeter tree trunks were scratch-marked at two metres height with a knife. Each plot was randomly subdivided into four equal sub-plots (de Aragón et al., 2007; Iles, 2012) as the observational units so each ECM sporocarp yields could be more closely allocated to both effect of woody species and leaf litter cover.

Identification of woody plant species was done using Flora of Zimbabwe (www.zimbabweflora.co.zw. accessed 21-26 November 2017) guides and the Checklist for Zimbabwean plant names (Kwembeya and Takawira, 2002). Breast-height circumference for determination of breast height diameter (BHD) was measured ($D_{1.30m}$) with a measuring tape for *J. globiflora* and *B. spiciformis* woody species and then used to compute species basal area in square metres for each sub-plot. ECM host tree basal area was chosen as a factor of ECM yield (Martínez-Peña et al., 2012).

Available sporocarps in each sub-plot were harvested from 29 December 2017 to 2 January 2018 during the first sporocarp emergence flush, and 21 to 25 February 2018 (first five days of second flush). In the current study, focus was on four ECM of the most food and commercial value in central Zimbabwe, namely, *Amanita loosii*, *Cantharellus miomboensis*, *Cantharellus heinemannianus* and *Lactarius kabansus* (Mlambo and Maphosa, 2017). Harvested sporocarps (both stipe and pileus) of all sizes were dusted of soil, identified and fresh weight measured using an electronic balance. Mushroom identification was done using Pocket Guides (Sharp, 2011; 2014 and 2016).

Leaf litter assessment was done by marking out a square of 1 metre sides in each sub-plot 7 metres from the plot centre. Leaf litter was scrapped off from the marked squares using a metal plate and packaged in plastic bags labelled with the plot number and sub-plot code. The leaf litter was sun-dried for 48 hours, sieved of soil and weighed. Sub-samples were drawn from each sun-dried

sample, packaged in A4 paper envelopes, weighed and the envelopes sealed. The sub-samples were re-weighed in the laboratory before and after oven-drying for 24 hours at 105°C. The sun-dry weight and oven-dry weight for each sub-sample were used to determine the total oven-dry weight of the original sample. The computed sample oven-dry weight was extrapolated to the sub-plot (176.78m²).

Data Analyses

Data were analysed in GenStat Discovery Edition 4, 2013 (VSN International Ltd. Rothamsted Experimental Station). The dependent variable was mushroom yield in grammes fresh weight for each sub-plot, whole plot and whole site for each flush and for individual ECM species. The independent variables were: basal area of *J. globiflora* and *B. spiciformis* in square metres, taken at breast height (1.30m), and oven-dry leaf litter weight in kilogrammes. A Mann-Whitney U was used to compare mushroom yields between sites ($\alpha < 0.05$). To test mushroom yield differences between the December/January (first) and the February (second) flush in each of the two sites, a Wilcoxon signed rank for paired samples was used, with $\alpha < 0.05$, $n=15$ (the data did not fit a normal distribution). In analysing yield differences between mushroom flushes, sub-plot yields were pooled to enable paired observation analysis.

Spearman's correlation (Tsamba et al., 2015) was used to test associations between basal areas of *J. globiflora* and *B. Spiciformis* with yield of *A. loosii*, *C. heinemannianus*, *C. miomboensis* and *L.kabansus*, and the correlation between individual ECM species yields with leaf litter cover.

RESULTS

Mushrooms yield differences between sites

Yield of *L. Kabansus* was higher ($p= 0.030$) in site 1 than in site 2. Yields for the other three mushroom species were found to be similar between the two sites (Table 2). The lowest mean yield was that of *C. miomboensis* (site 2) and the highest was of *L. Kabansus* (site 1).

Table 2. Mushroom mean yield comparisons between sites in Mtao Estate of Zimbabwe

Site	Mean mushroom yields of each mushroom species (grammes/subplot)			
	<i>A. loosii</i>	<i>C. miomboensis</i>	<i>C. heinemannianus</i>	<i>L. kabansus</i>
1	24.12 ^a	2.67 ^a	15.05 ^a	334.77 ^a
2	13.55 ^a	1.77 ^a	7.90 ^a	97.80 ^b
Overall mean	18.83	2.22	11.47	216.28
N	60	60	60	60
p value	0.887	0.323	0.275	0.030
Z value	-0.143	-0.987	-1.093	-2.170

Means for species with same letter for different sites superscript are not significantly different ($p < 0.05$).

Mushroom yield comparisons between first and second flushes

Higher yields were found for *C. heinemannianus* and *L. Kabansus* in site 1 in second flush than first flush while there were similar yields of the other two ECM species in both flushes (Table 3). In site 2, *L. Kabansus* had a higher yield for the second flush than the first flush while there were similar flush yields for the other species in both site 2 flushes.

Correlation between mushroom yield and dominant miombo woody species basal area

A weak positive correlation was found between yield of *C. Miomboensis* and basal area of *J. Globiflora* ($p = 0.003$) and a weak positive correlation between yield of *A. Loosii* and basal area of *J. Globiflora* ($p = 0.029$) but no correlation between yields of *C. Heinemannianus* and *L. kabansus* with *J. globiflora* basal area (Table 4a).

There was no correlation between yields of any of the four mushroom species and basal area of *B. spiciformis* (Table 4b).

Correlation between mushroom yield and leaf litter quantity

A weak negative correlation was found between yield of *L. Kabansus* and leaf litter quantity ($p < 0.001$), and no correlation between yields of the other mushroom species and leaf litter quantity (Table 5).

DISCUSSION

In the current study, *L. Kabansus* gave higher yields in site 1 than site 2 (Table 2), confirming earlier findings that sites with similar vegetation stand structure may differ in sporocarp productivity (Martínez-Peña et al., 2012). Between-sites yield difference was largely explained by higher

total rainfall received in site 1 (Bonet et al., 2010; Martínez-Peña et al., 2012; Lodge et al., 2014; de-Miguel et al., 2014) during the study period (Table 1). The 'windbreak effect' of eucalyptus plantations in site 1 (Dahl et al., 2008) was likely to reduce soil desiccation, hence maintaining high soil moisture content for mushroom emergence. However, yield similarities found for the other three ECM in the two sites were not consistent with the rainfall difference. This suggests that rainfall amount alone was insufficient to explain yields of *A. loosii*, *C. miomboensis* and *C. heinemannianus*. It is also likely that these three ECM may require a higher rainfall threshold to give higher discernible yields in this study area which normally receives over 500mm rainfall during the same period. (www.mvuma.climatemps.com/precipitation.php accessed 1 July 2018).

Higher yields of *C. heinemannianus* and *L. kabansus* in second flush for site 1 (Table 3) were attributed to both higher residual soil moisture and higher host leaf cover in the season. Site 1 was likely to retain more moisture (the 'windbreak effect') from the December/January rains than site 2. This residual moisture was boosted by late January/February rains (Table 1) to influence better sporocarp emergence. During the second flush of these ECM, most of the woody plant hosts had developed more photosynthetic capacity to export carbon to their symbiont ECM; hence the higher sporocarp yields in the second flushes (Wallander et al., 2010). Failure of *C. miomboensis* to emerge in both early and late sporocarp flushes in site 2 is explained by its probable soil moisture threshold requirement which may not have been met in this site. These findings suggest that a further investigation into soil moisture threshold conditions for *C. Miomboensis* emergence is necessary. *A. loosii* also had similar yields in both flushes probably because its emergence soil moisture threshold requirements were met in both flushes for site 1 but only in the second flush for site 2, further suggesting the influence of rainfall and the 'windbreak effect' in site 1. We therefore propose that the combination of host basal

Table 3. Mean fresh mushroom yields (grammes/plot) for two flushes within the sites.

Flush	<i>A. loosii</i>		<i>C. miomboensis</i>		<i>C. heinemannianus</i>		<i>L. kabansus</i>	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
1	12.7 ^a	0.0 ^a	0.00 ^a	0.00 ^a	1.1 ^b	0.00 ^a	10.8 ^b	0.00 ^b
2	81.4 ^a	54.4 ^a	10.7 ^a	0.00 ^a	60.4 ^a	31.6 ^a	1319.7 ^a	224.4 ^a
Overall mean	47.0	27.2	5.3	0.00	30.7	15.8	665.2	112.2
n	15	15	15	15	15	15	15	15
p value	0.250	0.063	0.500	1.000	0.016	0.125	0.008	0.016

Means with same letter superscript for same species for different flushes are not significantly different ($p < 0.05$).

Table 4a. Correlation for the four mushroom species yields and *J. globiflora* basal area.

Statistic	Mushroom species			
	<i>A. loosii</i>	<i>C. miomboensis</i>	<i>C. heinemannianus</i>	<i>L. kabansus</i>
r value	0.174	0.247	0.114	0.008
n	60	60	60	60
p -value	0.029	0.003	0.108	0.464

Correlation results significant at $p < 0.05$.

Table 4b. Correlation of the four mushroom species yields with *B. spiciformis* basal area.

Statistic	Mushroom species			
	<i>A. loosii</i>	<i>C. miomboensis</i>	<i>C. heinemannianus</i>	<i>L. kabansus</i>
r value	0.055	-0.093	-0.023	0.132
n	60	60	60	60
p -value	0.276	0.157	0.400	0.075

Correlation results significant at $p < 0.05$.

area and a yet unknown amount of effective rainfall are required for *A. Loosii* sporocarp emergence. Studies spanning over longer periods of time are required to get a better insight into interactive effects of these and other factors influencing *A. loosii* yield.

The positive correlation between yields of both *A. loosii* and *C. miomboensis*, and basal area of *J. globiflora* (Table 4a) agree with observations by Sharp (2007). However, the weak correlation that was found, which was also found by Tsamba et al. (2015) may suggest existence of alternative woody hosts for these *A. loosii* and *C. miomboensis*. Hence, the apparent lack of correlation between yield of the four ECM and *B. spiciformis* (Table 4b) may not rule it out as a host because in most mature miombo woodlands

the two woody species tend to co-occur. Molecular methods or similar field surveys on pure stands of the two miombo woody species are required to give conclusive results on mushroom-plant host associations.

No correlation was found between yields of *A. loosii*, *C. miomboensis*, *C. heinemannianus*, and ground litter mass probably because these ECM may depend on the litter for a minor requirement of their carbon. The assumption was that the three ECM species had established their mycorrhizae with their plant host roots for a long time, and hence may not require new spore inoculum. New colonization of host roots by these ECM is therefore largely subterranean. However, a negative correlation found between yield of *L. kabansus* and leaf litter mass

Table 5. Correlation for the four mushroom species yields with leaf litter quantities.

Statistic	Mushroom species			
	<i>A. loosii</i>	<i>C. miomboensis</i>	<i>C. heinemannianus</i>	<i>L. kabansus</i>
<i>r</i> value	0.005	0.137	0.073	-0.338
<i>n</i>	60	60	60	60
<i>p</i> -value	0.473	0.068	0.213	<0.001

suggests this ECM is averse to ground litter, possibly due to acidic conditions arising from decomposing litter. This finding was surprising as leaf litter is supposed to initiate germination of spores of any macrofungus (Lindahl and Tunlid, 2015). This result also suggests that *L. kabansus* carbon needs are either wholly met by the host roots or partially met by below-ground sources such as dead roots or host exudates (Langley and Hungate, 2003; Heinonsalo et al., 2001). It also appears that *L. Kabansus* sporocarp formation responds to light and that thick litter may have inhibitory effect on its sporocarp formation. Further studies are needed to explore these hypotheses.

CONCLUSION

Our investigation into ECM sporocarp yield comparisons between two sites and between two flushes, and also the association between sporocarp yield and woody species basal area and leaf litter cover gave interesting results. Yield for one of the ECM (*L. kabansus*) was higher in site 1 than site 2 but there were similar yields for the other ECM between the two sites. There was an increase in yield for two of the ECM between the first and second flushes. Yields of *A. loosii* and *C. miomboensis* were found to be positively correlated with basal area of *J. globiflora* but no correlation for any ECM between yield and *B. spiciformis* basal area. Only *L. kabansus* yield was correlated with leaf litter but in the negative sense. Hence *J. globiflora* is one of the mycorrhizal partners for both *A. loosii* and *C. miomboensis* while ground leaf litter inhibits emergence of *L. kabansus*. Long term studies of controlled leaf litter removal need to be done to reveal the mode of influence of leaf litter on *L. kabansus* yield. Molecular methods also need to be explored in order to reveal the exact nature of ECM-woody host plant species.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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